Transpiration in various riparian woodland species of the Okavango Delta, Botswana

by

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Contents

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LIST OF TABLES

LIST OF FIGURES

Abstract

In arid and semi-arid areas, evapotranspiration (ET) by phreatophytes is a principal groundwater sink and a significant component of wetland water budgets. Understanding and accurately quantifying ET is necessary for water resources management, especially under an uncertain climatic future. In the Okavango Delta ET consumes about 96% of the total input, mainly from islands which are fringed by riparian woodlands. ET measurements, however, have historically been difficult to make and hence ET tends to have been calculated as the remainder term from the water balance. Using the compensation heat pulse velocity method, sap flow measurements, which are widely used in ecophysiological field studies, were used in this study to estimate tree transpiration in the distal, mid and upper Delta during low, medium and high water levels. These were related to air temperature, relative humidity and soil moisture and groundwater levels. The relationship between sap flow and tree size was also explored. Transpiration for the whole Delta was estimated from sap flow measurements and ET from groundwater fluctuations.

Sap flow varied between and within species in different seasons because of environmental factors and plant characteristics as seasons changed. High temperatures and low relative humidity led to increases in sap flow. Relationships between sap flow and soil moisture were unclear whilst groundwater significantly responded to sap flow, declining with increased sap flow and increasing when sap flow slowed down. ET from the whole Delta (with riparian woodland covering an area of 1.19E+09 m^2) was estimated to be 4.06E+09 L/year from sap flow measurements. This is equivalent to 27% of the total annual input into the Delta. Groundwater fluctuations gave estimates of 8.47E+09 L/year (56%), almost double the sap flow estimates.

Keywords: Sap flow, Compensation heat pulse velocity method, Transpiration

Thesis Outline

Background on wetlands water balance, specifically focusing on evapotranspiration (ET) from riparian phreatophytes is given in Chapter 1. The problem statement, research questions and description of the study area are also given in this chapter. In Chapter 2 sap flow variations in different common riparian species of the Okavango Delta are investigated. Variations were investigated in different seasons and from different parts of the Delta. Relationships between sap flow and air temperature, relative humidity and soil moisture are investigated in Chapter 3. In Chapter 4, sap flow is related to diel fluctuations in groundwater. The findings of the whole study are synthesized in Chapter 5.

1 CHAPTER 1

1.1 GENERAL INTRODUCTION

1.1.1 Wetlands

Wetlands are lands which are permanently wet or filled with water creating a saturated environment, resulting in anaerobic conditions, in which only animals and plants adapted to the saturated conditions survive (Cowardin et al. 1979; Ellery and Ellery 1997). Although wetlands cover only a small proportion of the earth (about 6%) they provide a number of important ecosystem services (Cherry 2012). Among other services, wetlands provide a unique habitat for a variety of flora and fauna, recharge groundwater, support a rich biodiversity, provide food and goods for humans, act as sinks and sources for materials and improve water quality (Mitsch and Gosselink 2000; Butchart 2000; Reddy and DeLaune 2004; Cherry 2012).

1.1.2 Hydrology of wetlands

The hydrology of a wetland is the main component that sets the wetland ecosystem apart from other ecosystems as it creates unique physiochemical conditions (Mitsch and Gosselink 2000). Hydrologic pathways act as transport mechanisms transporting energy and nutrients to and from wetlands. These pathways include precipitation, tides, flooding rivers, groundwater flow and surface runoff (Mitsch and Gosselink 2000). To establish response models between ecological and hydrological factors of wetlands is a relatively new field in wetland research, which can provide a scientific basis for wetland protection, assessment and management (Wang, Wang, and

Sun 2008). This emerging field referred to as ecohydrology tries to identify, investigate, understand and quantify linkages between climate, soil moisture dynamics and vegetation in natural environments (Guswa, Celia, and Rodriguez-Iturbe 2002).

1.1.2.1 Wetland water budget

Wetlands are increasingly seen as important and necessary parts of the landscape, performing functions necessary to maintain a healthy environment. The ability to estimate water use by phreatophytes and hydrophytes is useful in water balance studies of river basins, and in estimation of groundwater recharge, stream flow depletion, and water requirements of wetlands (sometimes called environmental flow requirements) (Allen 1995; Lott and Hunt 2001). Evapotranspiration (hereafter ET) - water lost to the atmosphere through both processes of evaporation and transpiration - information is vital across a number of disciplines including hydrology, ecology, agronomy and meteorology (Wilson et al. 2001). In order to calculate nutrient, energy and chemical budgets one needs to properly identify sources and sinks of water, and the processes involved in the movement of water and associated constituents through the system (Lott and Hunt 2001). Difficulties in accurately calculating ET in wetlands can lead to inaccurate water balances yet this information is vital for many compensatory mitigation projects (Lott and Hunt 2001). This information is also required to help resolve issues of land and water resource management (Loustau et al. 1996).

A thorough appreciation of the wetland water budget is essential in accurately characterizing functions associated with wetland systems (Lott and Hunt 2001). Wetland hydrology (water inputs, outputs and flooding regime) is widely recognized as one of the major controlling forces in wetlands as it dictates the type of vegetation, soils and topography that develop (Owen 1995). This is mediated by the concepts of flood pulse, alternating drying and wetting cycles, and hydroperiod, duration and time of inundation (Marble 1991). Sources, amounts and timing of water entering and leaving a wetland are also crucial for wetland classifications, functional assessments and restoration plans (Hollands 1987). The pattern of water level fluctuations, the duration and timing of flooding are vital components in wetland hydrology. The duration and frequency of flooding varies with sites depending on various characteristics such as rainfall, ET, runoff from adjacent areas, flooding and net seepage of groundwater (National Research Council 1995).

1.1.3 The Okavango Delta

The entire Okavango River system, underlain by Kalahari sands, lies within the Kalahari Basin (McCarthy 1992). The collapse of a segment of the earth's crust caused by rifting has interrupted the course of the Okavango River, which arises in Angola, resulting in a depression (Hutchins, Hutton, and Jones 1976). Sediments from the Okavango River have accumulated in this depression forming a gently sloping, curved alluvial fan known as the Okavango Delta (McCarthy 1992). Apart from the sediments of the Okavango River that dominate the alluvial fan, there are also dormant alluvial fans occurring adjacent to the Okavango fan (Shaw and Thomas 1992). This means that the Okavango Delta is in fact an alluvial fan and not a Delta, as Deltas discharge their waters into standing water bodies such as the sea (McCarthy 1992). However, this alluvial fan has always been referred to as a Delta.

The Okavango Delta, situated in the northern part of Botswana, is a freshwater wetland that gets its water from two sources: local rainfall and Okavango river catchment in Angola (Porter and Muzila 1988). Its principal hydrological feature is the seasonal flood pulse from the catchment and to a lesser extent local rainfall. The seasonality of the floods characterizes the Okavango Delta into hydro-ecological zones (Wolski and Savenije 2006). The Okavango Delta is one of the few parts of the region with a clearly visible surface water surplus and seemingly abundant groundwater supplies (Ringrose 2003). However, as Ringrose (2003) states, being able to quantify water losses is vital especially in all semi-arid areas defined by low rainfall, high temperature, low humidity, high rates of ET and the near-absence of permanent streams. Previous studies (Wilson and Dinçer 1976; Snowy Mountains Engineering Corporation 1987) indicate that most of the water flowing into the Delta is lost to the atmosphere via ET. Mean monthly open water evaporation (E_o) ranges from 80 – 100 mm in June (winter), up to a maximum of 210 – 270 mm, usually in December (summer) whilst potential ET is about 1 400 mm per annum (Snowy Mountains Engineering Corporation 1987). The high evapotranspirational loss leads to low outflow, and more than 96% of water coming into the Delta is lost to the atmosphere (McCarthy 2006). The relative contributions of evaporation and transpiration from the swamps are not known. However, the general absence of saline surface water suggests that transpiration far exceeds evaporation (McCarthy and Ellery 1998). McCarthy (2006) also estimates that between 80 and 90% of the seasonal floodwater infiltrates the ground, recharging the groundwater beneath the floodplains and the many islands on the floodplains. The remainder is lost by evaporation. This groundwater reservoir is transpired into the atmosphere by both aquatic vegetation in the floodplains, and terrestrial vegetation on the islands, and the water table is steadily drawn down following passage of the seasonal flood pulse.

1.1.3.1 Islands of Okavango Delta

Geomorphologically, the Okavango Delta is made of three major components: channels, wetland and islands (Gumbricht, McCarthy, and McCarthy 2004). The Delta contains thousands of islands varying in size and shape (Gumbricht, McCarthy, and McCarthy 2004).

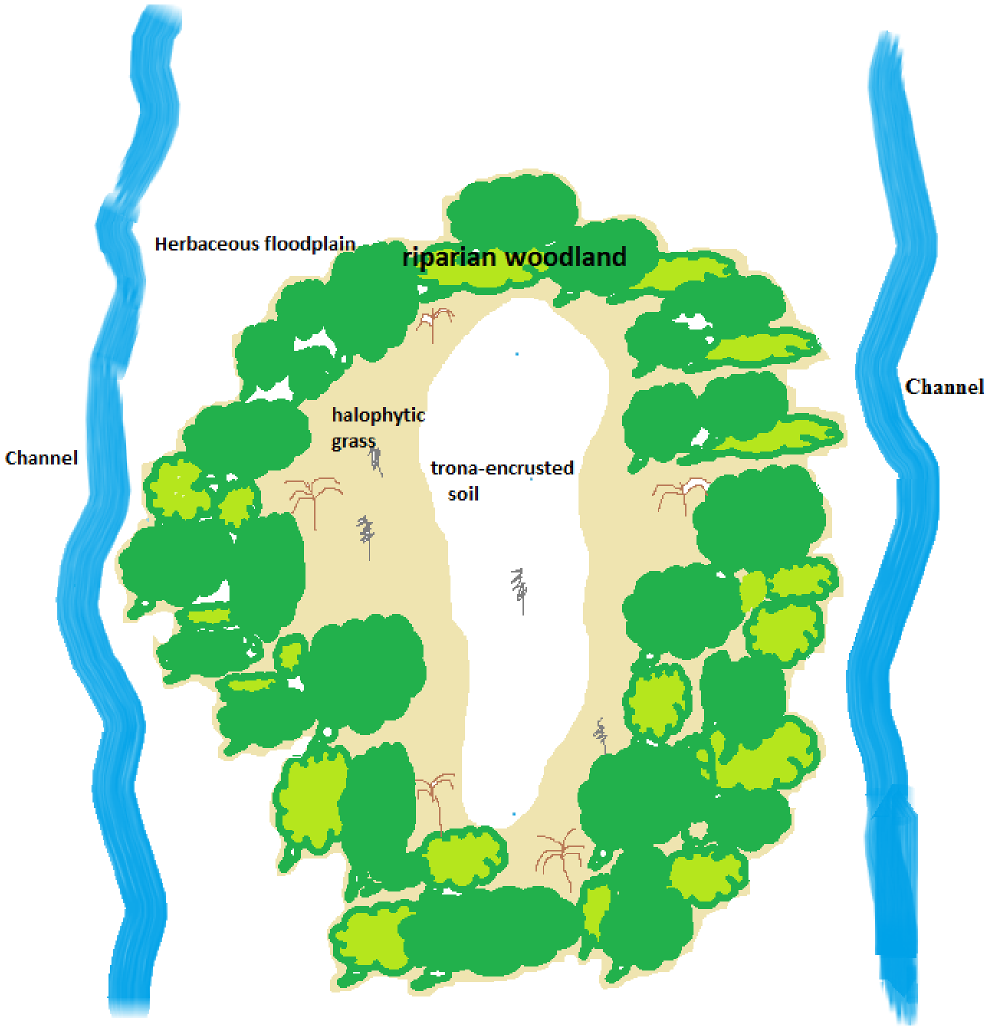


Figure 1-1 Schema of a "typical" island in the Okavango Delta

Islands of the Okavango Delta are defined as those areas that rise above the floodplain and are characterized by non-aquatic vegetation (Gumbricht, McCarthy, and McCarthy 2004). Islands often consist of fine, clayey-like material (Wolski and Savenije 2006; Ramberg and Wolski 2008). Various processes lead to formation of islands. Islands can result from raised and abandoned channel beds (Gumbricht, McCarthy, and McCarthy 2004), point bar deposits formed on the inside of a stream bend or meander bends, sub-surface precipitation of calcite and silica causing the land surface to rise, submergence of former sand dunes which were formed by wind action during arid periods, tectonic uplift – the raising of a geographical area as a result of plate tectonics (McCarthy 1992) whilst other islands start as termite mounds (Gumbricht, McCarthy, and McCarthy 2004). Riparian forest comprising various species of deep-rooted woody plants that get water from permanent ground supplies occupies the edges of islands, where there is no flooding but fresh and shallow groundwater (Wolski and Savenije 2006).

1.1.3.1.1 Evapotranspiration in islands

Water from the Okavango river brings with it an average of 380 000 tonnes of dissolved solutes every year and only 5.5% of these solutes leaves via the outlet (Ramberg and Wolski 2008). If water loss was through evaporation alone, this should mean that the Okavango Delta is a saline aquatic environment but it is not, it is fresh with surface water total dissolved solids generally <150ppm (Ramberg and Wolski 2008). Transpiration by riparian trees on islands maintains the Delta as a fresh water environment (McCarthy and Ellery 1998).

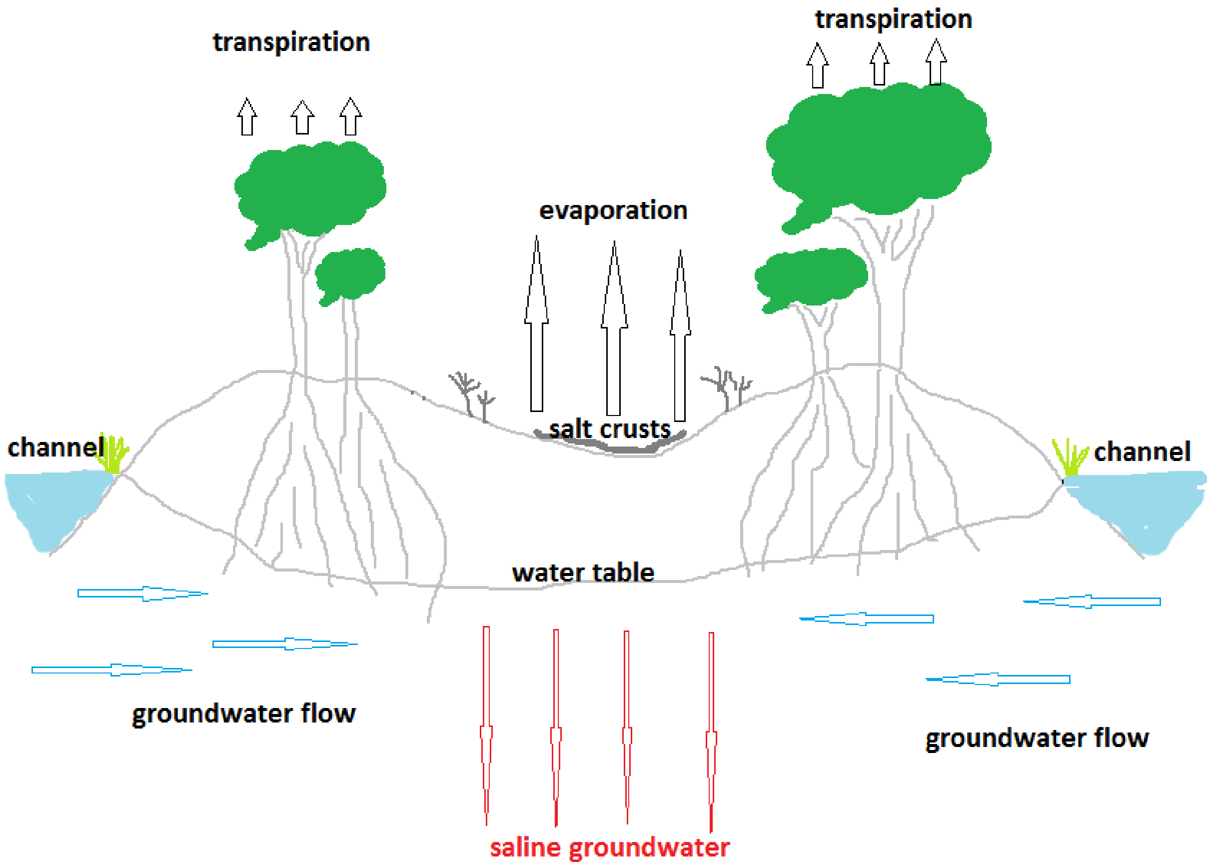


Figure 1-2 Conceptual island model (adapted from Bauer *et al*., 2006)

Deep-rooted trees on edges of islands pump water to the atmosphere leaving solutes behind. These trees continue pumping water even after surface water has disappeared in the surrounding floodplains, lowering the water table in the process. As the water table is lowered, water moves from the surrounding floodplain towards islands to replace water that has been lost hence increasing the concentration of solutes (McCarthy and Ellery 1998). Calcium and magnesium carbonate saturated beneath islands precipitate out of solution as magnesium calcite. The process of precipitation of magnesium calcite is partly responsible for island growth as the volume increase on crystallization causes soil expansion. Sodium remains in solution, accumulating as a concentrated solution of sodium carbonate and sodium chloride; continued evaporation from island center soils produces very saline groundwater and sometimes a trona (hydrated sodium bicarbonate carbonate)-encrusted soil (McCarthy and Ellery 1998). The highly saline island center groundwater, being denser than the surrounding shallow groundwater, periodically sinks to the bottom of the aquifer leaving fresher water on top (Bauer et al. 2002). Groundwater and soil salinity results in species zonation on islands. The island fringes are characterized by evergreen trees, giving way to deciduous species, followed by salt-tolerant grasses and then bare soil where salinity is extremely high for any plant life in island centers (McCarthy and Ellery 1998).

1.1.4 Problem statement

The Okavango Delta, covering an area of about 12 000 km^2, is a large alluvial fan in north-western Botswana (Gumbricht et al. 2004). The Delta gets its water from the Okavango River which flows from the highlands of Angola. It is habitat to a wide diversity of flora and fauna and provides human communities with water for domestic use amongst other services. High temperatures (20-45°C) lead to high evapotranspirative losses (Ringrose 2003). ET, the combined loss of water to the atmosphere through evaporation and transpiration, is an important component of the water budget for many wetland environments (Hill and Neary 2007). However, information on transpiration rates and processes is largely unavailable for Okavango distributaries (Ringrose 2003).

A sound hydrological model of the Delta, that will simulate flows with some known degree of certainty, is needed in order to simulate the impacts of proposed management scenarios and to reconcile the needs of man and nature (Bauer et al. 2004). Availability of such a model will give managers the appropriate confidence in predictive modeling scenarios. A sound model would need reliable estimates of ET rate from different plant communities and land cover types since most of the water is lost to ET (Bauer et al. 2004). Several modeling attempts have been made in the past and those focused on the effect of water abstraction on outflow from the wetland as the outflow supplies communities surrounding the Delta (Gumbricht et al. 2004).

The water balance of the Okavango Delta is presented as inflow + rainfall = groundwater outflow + surface water outflow + ET (Dincer, Child, and Khupe 1987). All the components can be easily estimated except ET and groundwater outflow (Dincer, Child, and Khupe 1987; Ramberg and Wolski 2008). As a result they have historically been calculated as a remainder term from measured inputs and outputs. However, Carter (1996) states that evaporation can be measured fairly easily, but ET measurements, which determine how much water plants use in a day, week, season and/or year are much more of a challenge to make. Of all wetland studies that rely on hydrologic data, very few have actually attempted to measure all components of a wetland's water balance (LaBaugh 1986). The unmeasured components are usually calculated as the remainder term (LaBaugh 1986).

The source and movement of water are crucial for assessing wetland function and predicting how changes in wetlands will affect the associated basin (Carter 1996). In the Okavango Delta, transpiration by trees is the driver for the maintenance of the endorheic drainage basin as fresh, rather than saline (McCarthy, McIver, and Cairncross 1986). The Okavango Research Institute (ORI) has developed a hydrological model specifically for the Okavango Delta (Wolski et al. 2006). Cathey (2011) conducted a global sensitivity and uncertainty analysis (GSA/UA) on the ORI hydrologic model in order to identify the most important model outputs. Results indicated that the most sensitive parameters are volume threshold, floodplain porosity and extinction coefficient, which is used to simulate transpiration from drylands. Extinction coefficient simulates a linear decrease in the rate of ET with depth from the surface (Cathey 2011).

ET from dry components of the Okavango Delta, islands fringed by riparian woodlands, for which information is limited, is thus one of the main areas contributing to uncertainty in current hydrological modeling for the Delta. Ignoring model uncertainty undermines the value of a model for its use in the decision making process (Cathey 2011). The objective of this study was therefore to acquire quantitative estimates of water fluxes through the major woody riparian species in the Okavango Delta, and thus to contribute to the ability to model eco-hydrological change.

1.1.5 Research Questions

Answers to the following general question were sought: How much water is lost by different tree species under different hydrological and phenological conditions in the Okavango Delta, Botswana? Specifically: 1) Is there a difference in water loss rates from common riparian woody species under similar conditions? 2) How does transpiration vary with season in these riparian tree species? 3) What is the relationship between soil moisture (in the vadose zone) and transpiration rate of these species? 4) What is the relationship between temperature & relative humidity and rate of transpiration in these riparian trees? 5) How does canopy cover affect transpiration rate in the riparian species? 6) What is the relationship between groundwater level and rate of transpiration in the riparian areas?

1.1.6 Methodology

1.1.6.1 Study area

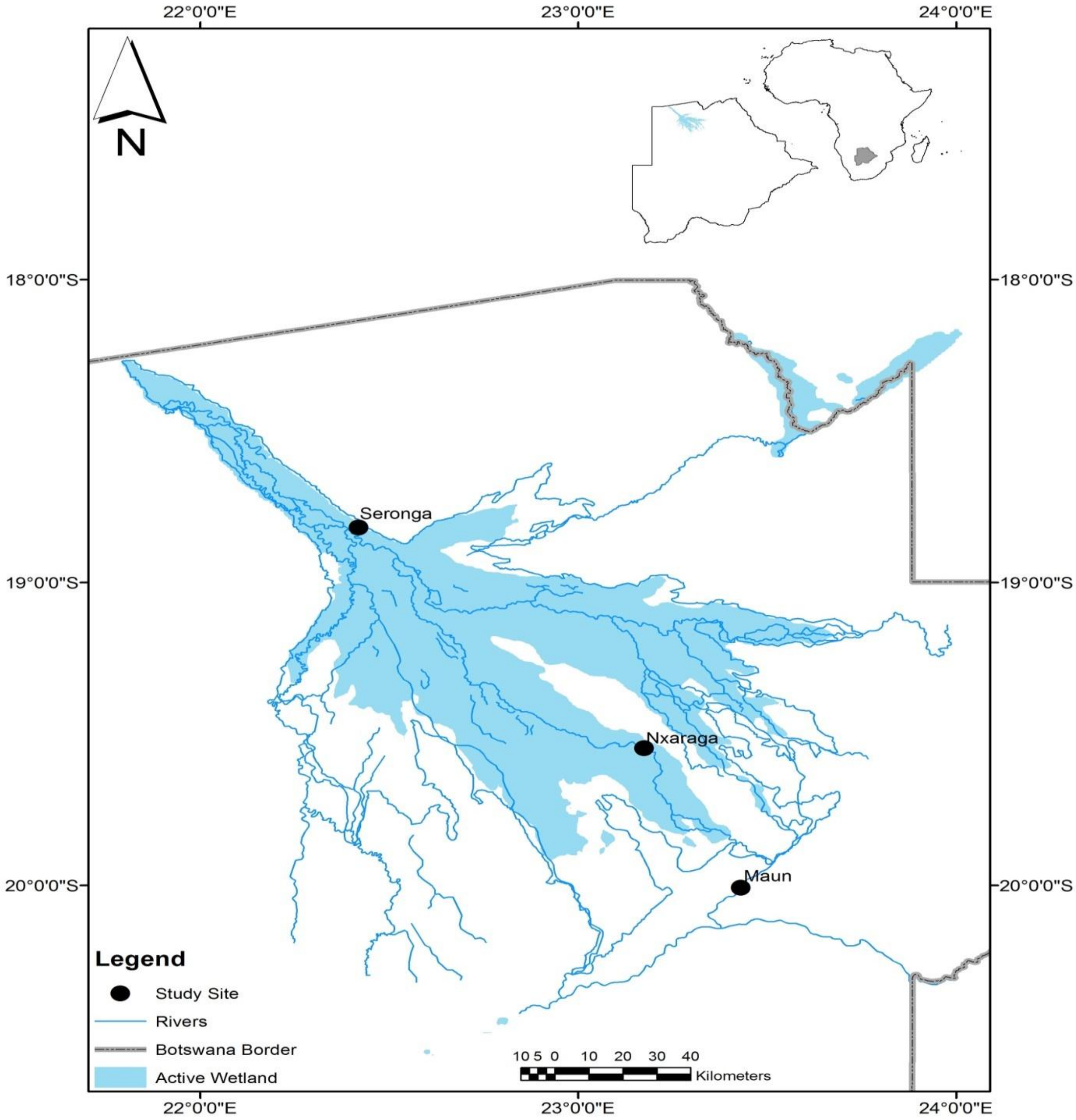


Figure 1-3: The Okavango Delta with the three study sites shown

Located in the northern Botswana Kalahari sands, Okavango Delta is comprised of three major regions: panhandle, permanent swamps and seasonal swamps (Ellery et al. 1993). Discharge from the Okavango River spreads out over the alluvial fan, covering an area of approximately 6000km^2 of permanent swamps and another 6000km^2 of seasonal floodplains (Gumbricht et al. 2004). The climate of the Delta is semi-arid, with one distinct rainy season (Wolski and Savenije 2006) which occurs in the summer months starting in October to March the following year. Local rainfall which averages about 490 mm/year is greatly exceeded by ET which is about 1 400 mm/year (Snowy Mountains Engineering Corporation 1987).

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 components of the Delta. Seronga represented the upper Delta, Nxaraga mid-Delta and Maun lower-Delta.

1.1.7 Approach

Whole-tree transpiration was measured from common species using the compensation heat pulse method (Swanson and Whitfield 1981). Due to constraints in wiring lengths of the sap flow cables, same species could not be investigated across sites as the species were far apart. For comparisons to be made across the different species, transpiration was calculated per unit cross-sectional area, and the data presented in the form of bar charts. Daily sap flow data from each species was tested for statistical differences using one-way ANOVA. Transpiration from the studied trees was related to air temperature and relative humidity which were measured by meteorological stations in and around the study sites. Soil moisture from the vadose zone was also measured and related to the transpiration. Diel groundwater fluctuations were measured to be correlated to transpiration.

Upward hemispherical canopy photos were taken every time transpiration measurements were made. From the photos percentage canopy cover was estimated. The estimated transpiration from individual trees was scaled up to plot level using total woody basal area of the plots studied and also from groundwater measurements.

2 CHAPTER 2

Sap flow variations in various riparian woodland species in the Okavango Delta

2.1 INTRODUCTION

Riparian areas are those zones lining edges of streams, rivers and wetlands. Riparian vegetation, which lies at the interface between terrestrial and aquatic ecosystems, is an essential component of river ecosystems (Cordes, Hughes, and Getty 1997; O'Grady et al. 2002). Water filtration, nutrient cycling, erosion control, maintenance of bank stability, reduction of turbidity in surface water are some of the key ecosystem services provided by riparian vegetation (O'Grady et al. 2002; Cordes, Hughes, and Getty 1997). These services may be impossible or extremely costly to replace. Riparian areas are among the most productive ecosystems, more diverse in terms of species composition than adjacent uplands hence maintaining biodiversity and provide habitats for wildlife (Askey-Doran et al. 1999; Horton, Kolb, and Hart 2001). In the flood-pulsed Okavango Delta, the riparian woodland has been shown to drive critical sequestration of dissolved solids and heavy metals (Bauer et al. 2006; McCarthy, Ellery, and Dangerfield 1998).

Despite the importance of riparian vegetation, limited work has been done globally to examine the water use of riparian vegetation due to high spatial and temporal heterogeneity within the riparian zone (O'Grady et al. 2002; O'Grady et al. 2006). The amount of water used by trees has been the subject of worldwide research for many years (Bosch and Hewlett 1982; McCulloch and Robinson 1993) and studies to determine the water needs of riparian vegetation have since diverged in many directions (Stromberg 2001), one branch being transpiration studies. Riparian

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, Botswana, (hereafter, the Delta) is characterized by high rates of ET especially from trees in islands. Previous studies (McCarthy et al. 1986; McCarthy and Ellery 1994; McCarthy and Ellery 1998; McCarthy 2006; Ringrose 2003) indicate that most of the water flowing into the Delta is lost to the atmosphere via ET. The Okavango river delivers an annual average of about 10 000 MCM of water into the Delta augmented by about 5 000 MCM from local rainfall. These two sources provide around 15 000 MCM of which outflow constitutes approximately 300 MCM, or 2% and regional groundwater outflow a further 200 MCM (1.3%). The remainder, 14 500 MCM, is lost via ET (Dincer, Child, and Khupe 1987). Potential ET is about 1 400 mm per annum, exceeding rainfall by a factor of three (Snowy Mountains Engineering Corporation 1987). Evaporation leads to water loss from open water and from soil surfaces through capillary rise in the barren island centers. The high ET rates result in over 95% of the total input being lost to the atmosphere and only 2% lost to groundwater flow. On small scales, groundwater flows laterally towards islands thereby recharging groundwater beneath islands. At large scales however, surface water – groundwater interactions are mainly through vertical flows (Milzow et al. 2009). From the water balance of the Delta, as shown above, ET exceeds precipitation monthly and annually. This means that recharge in non-flooded areas is quantitatively and temporally limited (Milzow et al. 2009). Water chemistry data has shown that groundwater in areas surrounding the Delta is chemically different from the Delta's surface water (Milzow et al. 2009; Wolski 2007). This means that very little water is lost via groundwater outflow, possibly through the highly fractured basement rocks beneath the Delta as suggested by McCarthy (2006). Wolski (2007) however suggests that water that seeps underground is stored there temporarily and then used by plants.

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 a seasonal contraction and expansion of flooded area, while overall and local topography of the Delta create hydrological gradients with some areas being permanently inundated whilst some are flooded seasonally and others occasionally. This primarily drives the vegetation ecology of the Delta (Murray-Hudson, Wolski, and Ringrose 2006). As in other semi-arid regions, ET in the Delta exceeds rainfall. Information on transpiration rates and processes is largely unavailable for Okavango distributaries (Ringrose 2003) yet this information is needed to help parameterize hydrological modeling. In this chapter the first quantitative estimates of water fluxes through the major woody species in the Delta are presented.

2.2 QUESTIONS

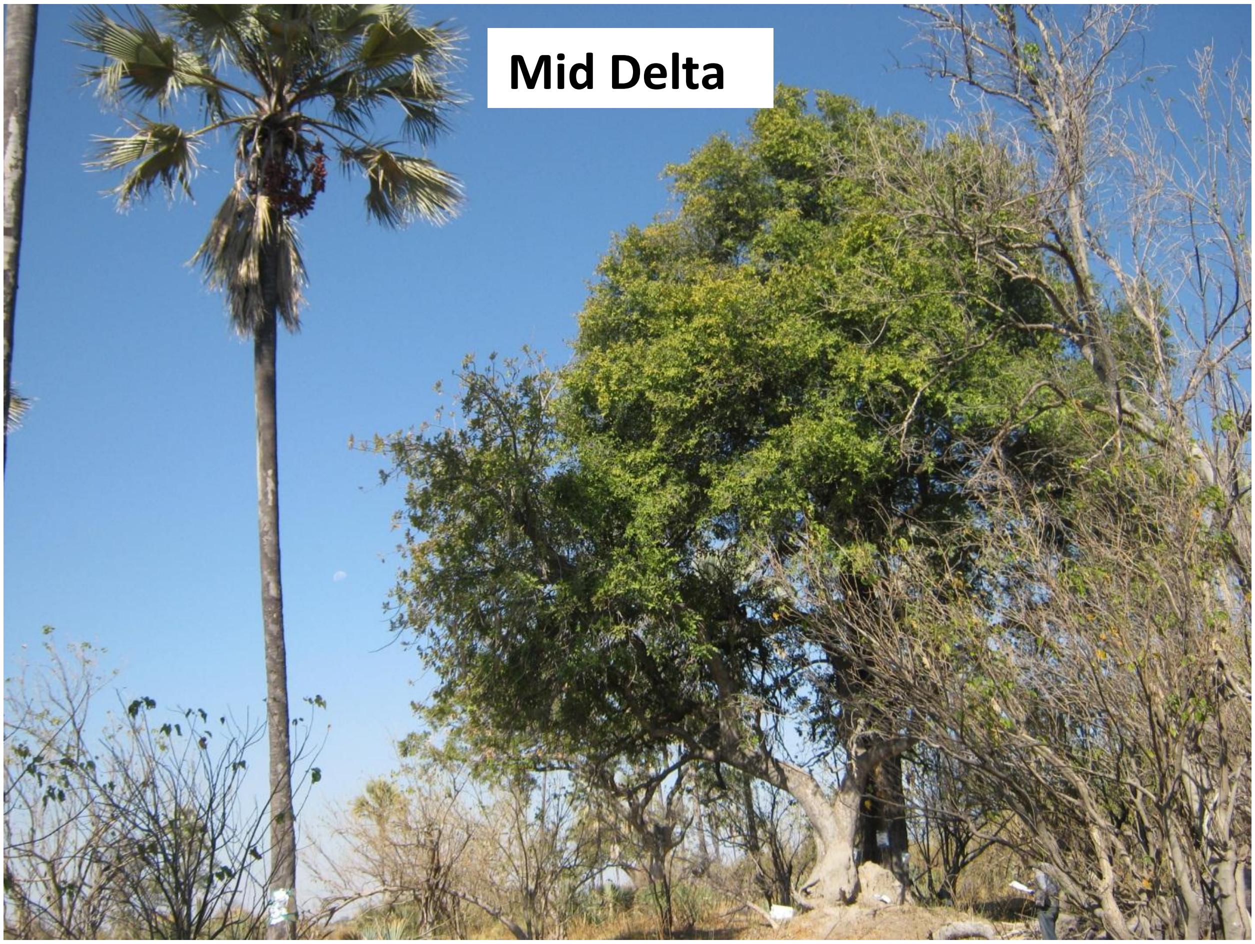
The questions addressed are:

1. How is sap flow related to tree size and species?
2. Does sap flow vary spatially (along a latitude gradient) in different riparian tree species?
3. Does sap flow vary seasonally in different riparian species?
4. How is sap flow related to canopy cover?

2.3 MATERIALS AND METHODS

2.3.1 Study site

Sap flow, the pulling of liquid water from the soil by plants via the stem and branches and ultimately leaves where it is evaporated into the air (Perämäki 2005), of common species was investigated in the upper, mid and distal-Delta sites. These areas lie along a gradient of latitude (latitudes decrease from distal to upper-Delta), rainfall, temperature and other variables like sunlight hours (these variables increase from distal to upper-Delta except temperature which increases downstream). These gradients coincide with the major hydrological gradient of the Delta whereby duration and variation of flooding are greatest in Seronga, intermediate in Seronga and lowest in Maun, such that Seronga is in a perennially flooded area while Nxaraga and Maun are in areas subject to progressively shorter seasonal flooding.



Mid Delta

Figure 2-1 Images of the study sites

2.3.2 Sample trees

Common tree species in terms of abundance, size and canopy cover were investigated in the study. Islands were identified from recent imagery available on Google Earth. Work by Tsheboeng et al. (2013, unpublished) informed the choice of common species. They performed hierarchical cluster analysis of riparian species in Principal component ordination (PC-ORD) to determine vegetation communities. They then used indicator species analysis (ISA) to calculate indicator values for species in groups defined from the cluster analysis. Species diversity and richness were also determined for each vegetation community. From the riparian woodland communities identified, they identified dominant (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 the same species were investigated. The species were distributed across the sites as indicated in Table 2-1.

Table 2-1 Sample trees and their locations

Distal Delta	**Mid Delta**	**Upper Delta**
Diospyros mespiliformis (4 individuals)	*Diospyros mespiliformis*	*Garcinia livingstonei*
	Kigelia africana	*Ekebergia capensis*
	Croton megalobotrys	*Philenoptera violacea*
	Hyphaene petersiana	*Phoenix reclinata*


Kigelia africana


Garcinia livingstonei


Ekebergia capensis


Phoenix reclinata

Diospyros mespiliformis

Croton megalobotrys

Philenoptera violacea

Hyphaene petersiana

Figure 2-2 Images of the studied species

2.3.3 Tree water use

Water use was investigated in July-August 2012, November-December 2012 and February-April 2013 in each study site. The compensation heat pulse velocity method (Green, Clothier, and Jardine 2003) was used to estimate heat pulse velocity which was converted to volumetric sap flow, Q (the total amount of water/sap that moves through a trunk of a specific size). This method uses a set of probes and associated electronics connected to a data logger. Each probe set is comprised of two temperature sensors which are placed one below and the other above a linear heater. These are inserted radially into the stem. The heater introduces a heat pulse of 1-2 seconds into the stem and a data logger then records the time delay for an equal temperature rise at both probes. A heat pulse velocity will then be calculated from the time delay. Theoretically derived corrections are then used to correct the heat-pulse measurements for any probe-induced effects of wounding and to calculate volumetric sap flow (Green, Clothier, and Jardine 2003).

The compensation heat pulse velocity method, which is widely used because of its robustness as time is the primary measurement (Edwards, Becker, and Cermak 1997), uses relatively inexpensive technology to give reliable and accurate measurements of sap flow with minimal disturbance to the tree and the sap stream. It also allows for automatic data collection and storage (Dye, Soko, and Poulter 1996; Green, Clothier, and Jardine 2003). With this method, access to the canopy is unnecessary, as probes can be inserted at the base of the stem, hence the canopy boundary layer conditions are not altered (Dye, Soko, and Poulter 1996). Volumetric sap flow was obtained as the product of sapwood area and wound-corrected sap velocity. Probes were inserted at breast height (1.3 m) but for trees which branched lower than this the probes were inserted below the divergence of the stems.

Two pairs of probes were inserted per tree. 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 minutes and cross-over times, t_z, recorded. t_z is the time delay in seconds for temperatures between the two probes to become equal. From the t_z values raw heat pulse velocity was calculated using the equation: $V_z = (x_d + x_u)/2t_z$, where V_z is the raw heat pulse velocity, x_d and x_u are distances upstream and downstream of the heater. Wound corrections were made using constants as outlined by Swanson & Whitfield (1981). The constants were used to calculate corrected heat pulse velocity using the formula: $V_c = a + bV + cV^2$, where V_c is the corrected heat pulse velocity, a, b and c are constants and V is the raw heat pulse velocity. Sap flow velocity, which is the speed of sap within the lumens, was then derived from the heat pulse velocity. The sap velocity was then expressed on total sap wood area, that is, it was multiplied by the sap wood area to give the total flow within the sap wood, sap flow denoted as ‘Q’.

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 three days. A CR1000 Campbell data logger was used to record data.

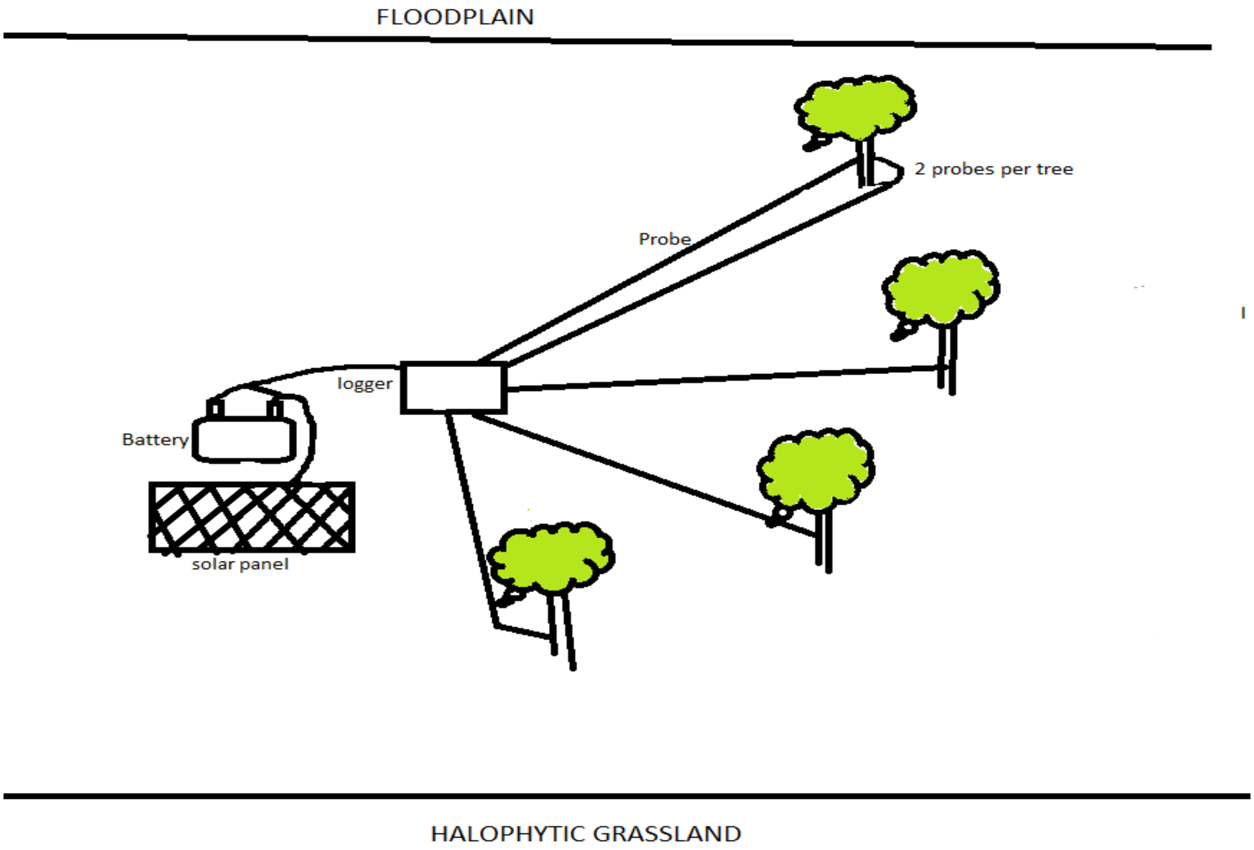


Figure 2-3 Sap flow sampling design illustration

Table 2-2 Study periods and their corresponding seasons*

	Water level		
Site	July-August 2012	November-December 2012	February-April 2013
Maun	High	Low	Medium
Nxaraga	High	Low	Medium
Seronga	Medium	Low	High

*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 four months after onset of the pulse at the apex. Hence water levels vary along the Delta as the flood wave moves downstream. Water levels varied at each study site during the different study periods.

2.3.4 Canopy cover

A Nikon Coolpix 4500 camera fitted with a fish-eye lens (focal length 4.5 mm) was used to take vertical upward canopy photos on days that sap flow measurements were made. The camera was mounted on a tripod stand which was leveled to ensure a vertical upwards image. The photos were taken in the evenings, just before sunset. During cloudy days photos were taken during the day, not necessarily waiting for sunset. When taking hemispherical photos, suitable weather and light conditions must be taken advantage of, usually overcast skies, sunrise or sunset (Rich et al. 1999). Photos were taken every 10 m along transects of the studied trees. Since transects varied in lengths, the number of photos taken per site per day varied, ranging between eight and sixteen.

Can-eye V6.1 software was used to calculate the vegetation cover fraction. Can-eye is an imaging software program that can be used to analyze images to extract different canopy structure characteristics (http://www.paca.inra.fr/can_eye). It processes images in batches, with a minimum of eight and a maximum of 20 images at once (Weiss and Baret 2010). Images acquired from one site under similar conditions were put in one file. These were then loaded onto the software. After loading images they were displayed on a window where undesirable parts, objects other than the trees e. g people, of the images were masked. This is the pre-processing step after which the number of colors in the images is reduced to a number that can be easily manipulated to get good discrimination capacities. The images were then classified. Classification classes were defined and the images were transformed into binarized images. The two colors used for the binarized images were blue (for sky) and green (for vegetation). An output file with a computed canopy cover and sky fraction was generated.

2.3.5 Statistical analyses

To determine if there were significant differences in sap flow between different tree species and between seasons one-way ANOVA was used after testing the data for normality and homogeneity of variance. Tukey test, post hoc test, was used to establish which of the variables were different from each other. Correlation analysis was used to determine the relationships between tree size and sap flow, and evergreen and deciduous species. To get a numerical explanation of the relationships, regression models were produced. One-way ANOVA was also used to determine if there were statistically significant differences between canopy cover and sap flow.

2.3.6 Up-scaling to plot-level transpiration

To estimate transpiration on a per m^2 basis, basal area (BA) of the trees was calculated as:

$$BA\ (m^2) = \pi r^2$$

BA is basal area in m^2, $\pi = 3.14$ and r is trunk radius in cm

The basal area of the trees was then divided by the plot size on which the trees stood to find the basal area per m^2 of woodland. Plot-level transpiration in litres per day per m^2 of woodland ($L/day/m^2$) was then estimated using the formula:

Plot-level transpiration ($L/day/m^2$) = BA (cm^2) per m^2 of woodland x SFD ($L/cm^2/day$)

SFD is the sap flux density which is the sap flow divided by area of the conducting tissue. The units are litres per cm^2 of conducting tissue per day ($L/cm^2/day$).

2.4 RESULTS

2.4.1 Diel variations in sap flow

The rate of sap flow in the studied trees began to increase between 0500 and 0700hrs and reached a maximum just around 1600hrs, after which it decreased to minima which were recorded around 0000hrs (Figure 2-4).

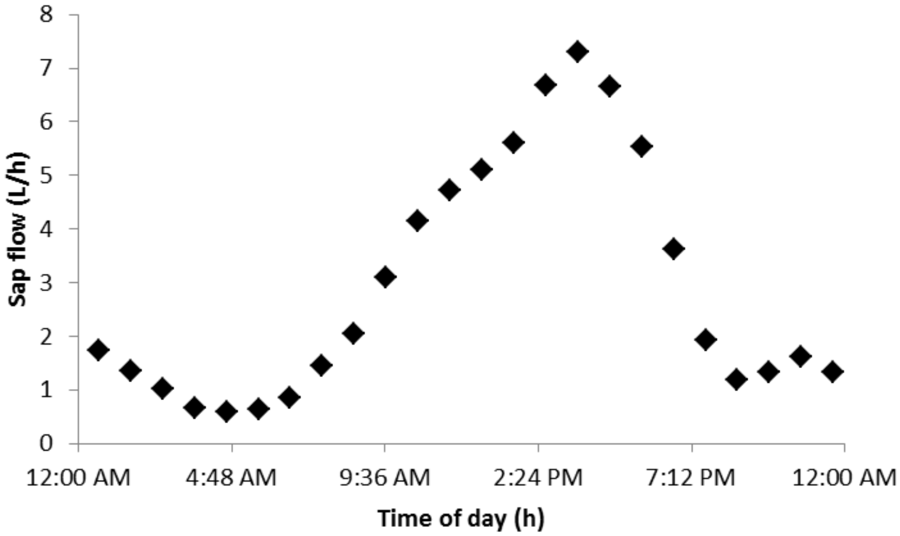


Figure 2-4 Example of a diel sap flow curve from an individual of *Diospyros mespiliformis* showing variations in sap flow with time of day

Sap flow from individual trees was scaled up to plot level to give estimates of plot transpiration measured in litres/m^2/day (L/m^2/day).

2.4.1 Relationship between tree cross-sectional area and sap flow

Table 2-3 Species and their corresponding cross-sectional areas

Site	**Species**	**Cross-sectional area (cm^2)**
Maun	*Diospyros mespiliformis* 1	136.8
	Diospyros mespiliformis 2	47.8
	Diospyros mespiliformis 3	181.4
	Diospyros mespiliformis 4	50.2
Nxaraga	*Croton megalobotrys*	687.8
	Kigelia africana	4899.2
	Diospyros mespiliformis	7912.9
	Hyphaene petersiana	1017.4
Seronga	*Phoenix reclinata*	181.4
	Philenoptera violacea	3378.1
	Garcinia livingstonei	3481.9
	Ekebergia capensis	715.9

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). SFD is sap flow divided by area of conductive tissue. Cross-sectional area for all the species studied ranged from 47.8 – 7912.9 cm^2 (Table 2-3).

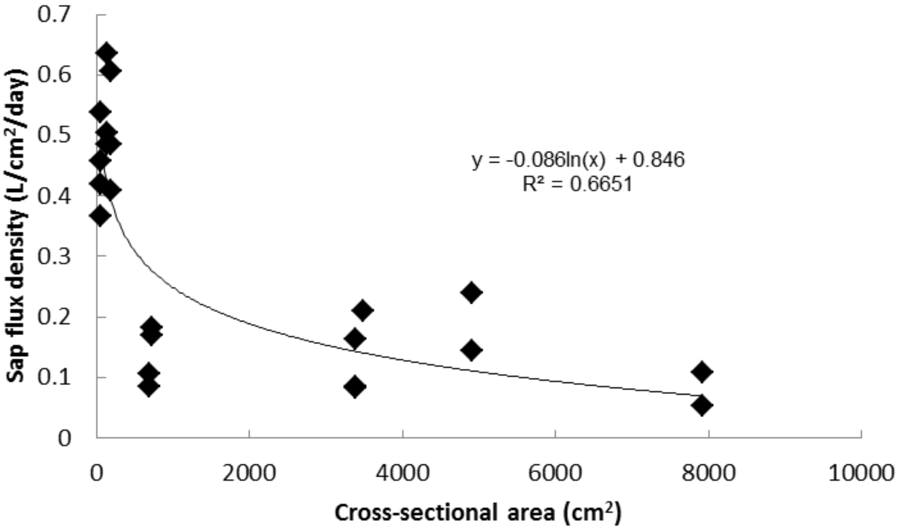


Figure 2-5 Relationship between cross-sectional area and sap flux density

SFD decreased with increasing cross-sectional area. Each data plot represents an individual tree.

SFD varied with tree sizes in all seasons (Figure 2-5). There was a negative correlation between the two variables, SFD and cross-sectional area, $r = -0.66$, $n = 22$, $p < 0.01$. From the regression analysis the relationship between SFD and cross-sectional area is best described by a function of the form $y = -0.086\ln(x) + 0.846$ (Figure 2-5), where y is SFD in L/cm^2/day, x is cross-sectional area in cm^2, 0.086 and 0.846 are constants. About every 3 cm^2 reduction in cross-sectional area lead to about a 0.001 L/d increase in the SFD, that is, as tree trunks get larger proportionally less water is moved through them.

Tree size explained about 67% of the variation in SFD.

2.4.2 Differences in sap flux density between species

One-way ANOVA showed that there were statistical differences between SFD and species (P = 0.00, F = 22.6 in July-August 2012; P = 0.00, F = 13.9 in November-December 2012; P = 0.00, F = 4.9 in February-April 2013) across seasons (Table 2-4). *Croton megalobotrys* exhibited the highest SFD during July-August 2012, *Kigelia africana* the lowest. During November-December 2012 *Ekebergia capensis* showed the highest SFD whilst *Hyphaene petersiana* showed the lowest. During February-April 2013 *Diospyros mespiliformis* in Maun exhibited the highest SFD and *Phoenix reclinata* the lowest (Table 2-4).

Table 2-4 Comparison of sap flux density ± standard deviation measured in different species at different seasons

Species	**Sap flux density ± standard deviation (L/cm^2/day)**		
	July-August 2012	November-December 2012	February-April 2013
Diospyros mespiliformis (Maun)	0.506 ± 0.104^{a}	0.215 ± 0.246^{a}	1.665 ± 1.135^{b}
Diospyros mespiliformis (Nxaraga)	0.787 ± 0.632^{ac}	0.079 ± 0.123^{a}	0.169 ± 0.084^{ab}
Croton megalobotrys	2.752 ± 0.339^{b}	0.090 ± 0.010^{a}	0.108 ± 0.006^{a}
Kigelia africana	0.094 ± 0.013^{a}	0.435 ± 0.252^{a}	0.244 ± 0.009^{ab}
Hyphaene petersiana	0.322 ± 0.291^{a}	0.077 ± 0.010^{a}	0.170 ± 0.050^{ab}
Garcinia livingstonei	1.512 ± 1.000^{c}	0.311 ± 0.161^{a}	1.337 ± 0.002^{ab}
Philenoptera violacea	0.107 ± 0.021^{a}	0.224 ± 0.181^{a}	0.082 ± 0.001^{ab}
Phoenix reclinata	0.098 ± 0.008^{a}	0.601 ± 0.702^{a}	0.072 ± 0.011^{a}
Ekebergia capensis	0.187 ± 0.021^{a}	2.591 ± 1.118^{b}	0.168 ± 0.005^{ab}

*Values with the same letter of the alphabet along a column are not statistically different from each other and those with different letters are significantly different, statistically

Although the different species behaved differently in all the seasons there was an observable contrasting pattern in their SFDs and so they were grouped according to the trends they exhibited. Some species showed a decline in SFD during November-December 2012 compared to July-August 2012, which then increased in February-April 2013. On the other hand, some species had their SFD increase during November-December 2012 as compared to July-August

2012. The SFD then declined in February-April 2013. Species whose SFD declined during the low water level (November-December 2012) were put in one group, Group 1, (Figure 2-6), and those whose SFD increased during that period were put in another, Group 2, (Figure 2-7). After grouping the species, there were still some statistical differences in sap flow.

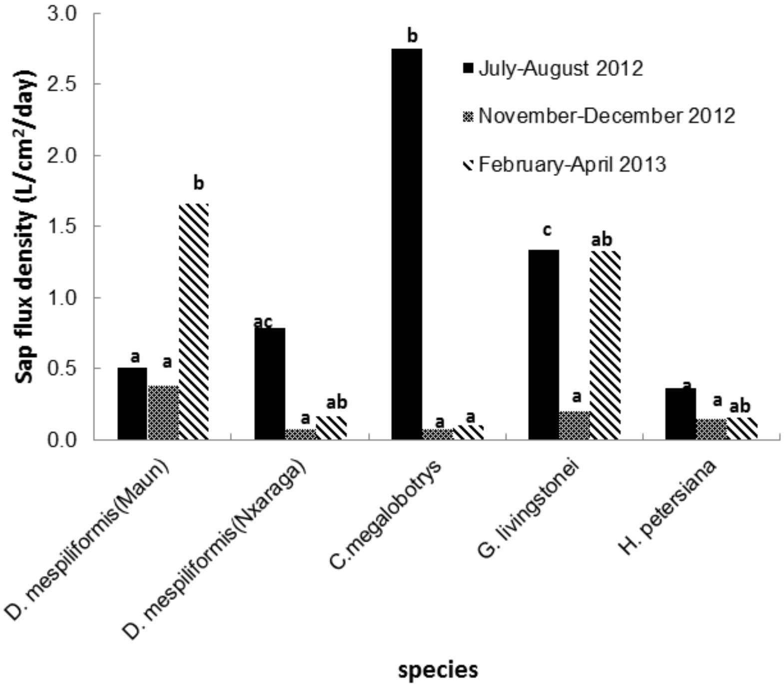


Figure 2-6 Sap flux densities in Group 1 species

Comparison in SFD between species that transpired the least in November-December 2012 compared to the other two seasons. *D. mespiliformis* (Maun) was in the distal Delta site, *D. mespiliformis* (Nxaraga), *C.megalobotrys* and *H. petersiana* from the mid Delta and *G. livingstonei* from the upper Delta. This is data from individual trees except in Maun where the data is an average of four individuals of the same species. Same letters in the bars indicate no statistical differences using ANOVA.

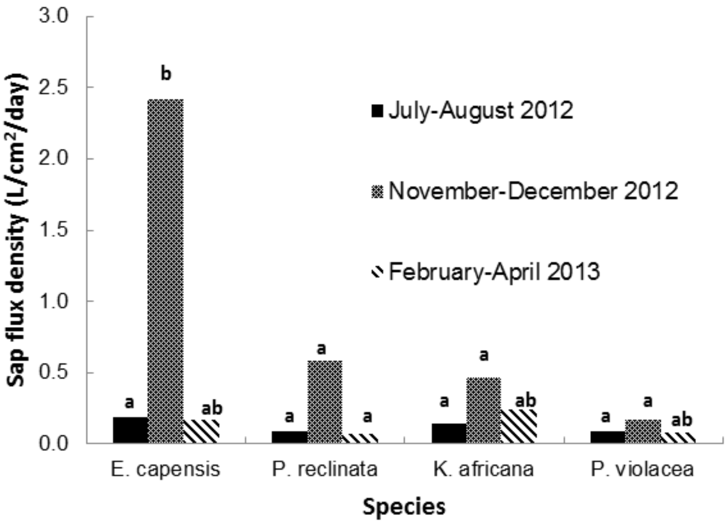


Figure 2-7 Sap flux densities in Group 2 species

Comparison in SFD between individual tree species that transpired the most during low water level (Group 2 species). *E. capensis*, *P. reclinata* and *P. violacea* were from the upper Delta whilst *K. africana* was from the mid Delta. Same letters indicate no statistical differences (ANOVA).

Evergreen trees tended to have higher SFD than deciduous trees in general. There was a positive correlation between *Philenoptera violacea* (deciduous) and *Garcinia livingstonei* (evergreen), r = 0.76, n = 125, $p < 0.01$. On average, a regression model showed that evergreen species transpired 0.7 – 5.7 times as much as deciduous trees at any given point, r^2=0.57 (Figure 2-8).

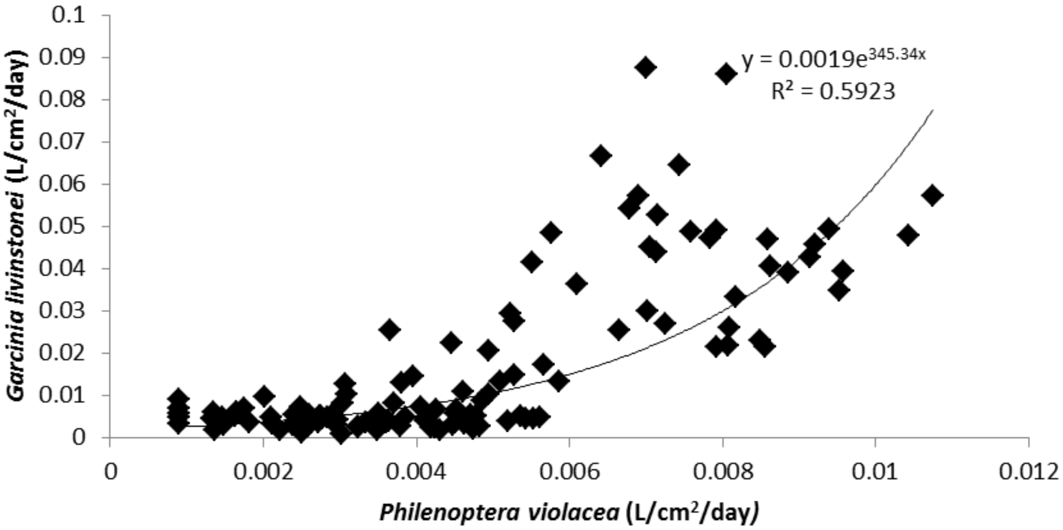


Figure 2-8 Comparison of sap flux density in an evergreen and a deciduous tree measured in three different seasons.

Garcinia livingstonei is an evergreen tree species whilst *Philenoptera violacea* is a deciduous tree.

Note that the axes have different scales.

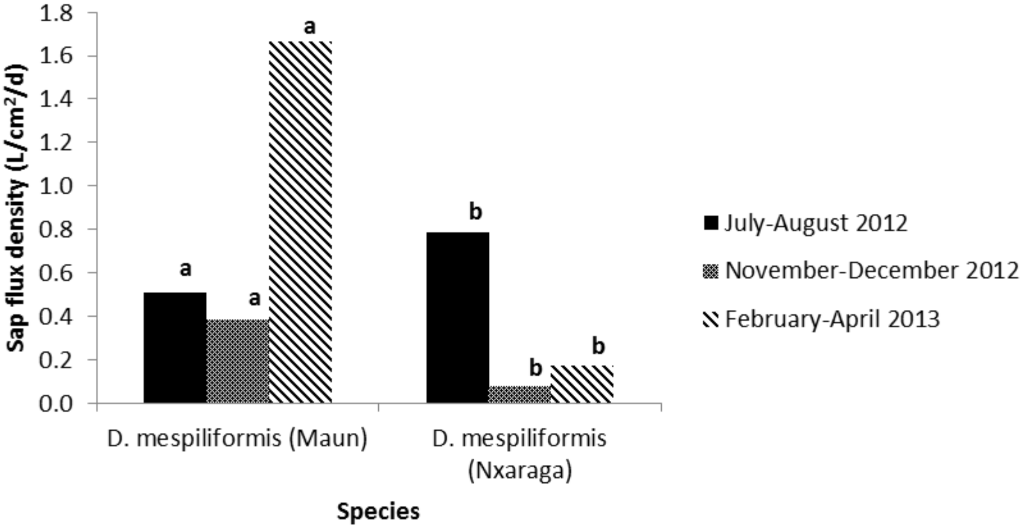


Figure 2-9 Sap flux densities in different individuals of *Diospyros mespiliformis*

Comparison of SFD measured in trees of *Diospyros mespiliformis* occupying different locations. *D. mespiliformis* in Maun exhibited higher SFD than that in Nxaraga in November-December 2012 and February-April 2013. The Maun values are an average of four individuals whereas Nxaraga values are from the one individual of *D. mespiliformis* studied.

2.4.3 Estimating plot-level transpiration

Transpiration from all the trees in the studied plots, that is, plot-level transpiration, varied with seasons in all the sites. In the distal and mid Delta sites, plot transpiration was lowest during November-December 2012 whilst in the upper Delta it was highest during that period (Table 2-5).

Table 2-5 Up-scaled transpiration in Maun, Nxaraga and Seronga during low, medium and high water levels

Site	**Season**	**Plot transpiration (L/m^2/day)**
Maun	July-August 2012	14.1
	November-December 2012	10
	February-April 2013	17.3
Nxaraga	July-August 2012	6.2
	November-December 2012	3.6
	February-April 2013	3.9
Seronga	July-August 2012	7
	November-December 2012	15.1
	February-April 2013	6.8

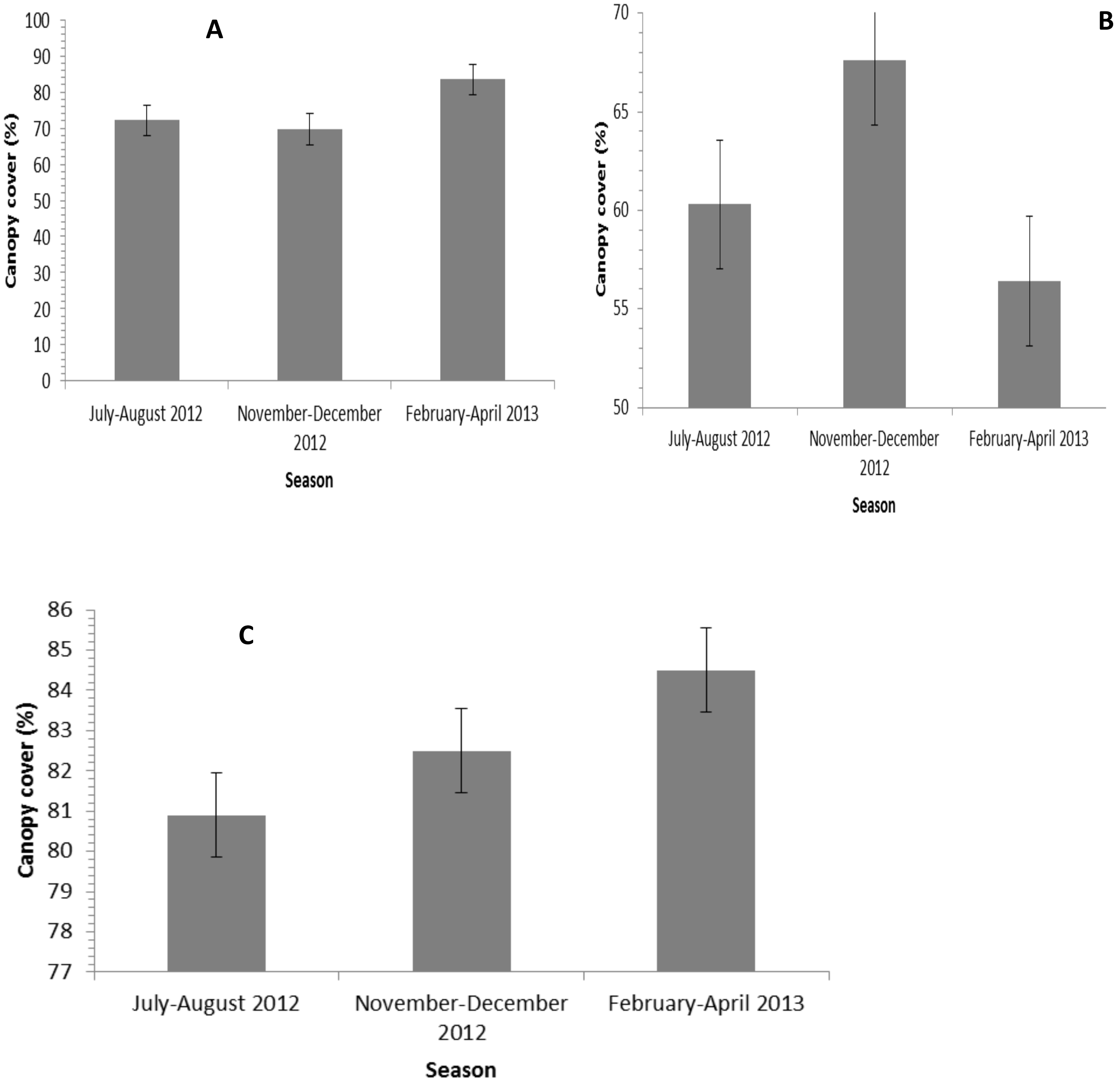


Figure 2-10 Canopy cover measured in different seasons in Maun (A), Nxaraga (B) and Seronga (C)

Canopy cover from the studied plots was lowest in November-December 2012 in Maun. It increased in the following season, February-April 2013 (variance = 0.08), to values higher than in July-August 2012. In Nxaraga, canopy cover was the largest during November-December

2012 (Variance = 2.25) and the lowest during February-April 2013 (variance = 5.06) whereas in Seronga it increased throughout the seasons observed. The variations in canopy cover between sites were significantly different statistically using one-way ANOVA (P = 0.01, F = 11.6).

2.5 DISCUSSION

Sap flow varied with species and time of day. These findings are similar to those found by O'Grady et al. (2006). They examined spatial and temporal patterns of water use, sap flow, in two riparian trees, occupying different locations, 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. They also found that there were no differences in water use between sites and seasons. We however found that there were significant differences between sites and seasons.

2.5.1 Differences in sap flow between tree sizes

To relate transpiration to tree size, we used cross-sectional area which was plotted against sap flow per unit area of stem (SFD). We found that the larger the cross-sectional area the lower the SFD, r^2 = 0.67 (Figure 2-5). These results were corroborated by other studies done elsewhere (Cermak and Nadezhdina 1998; Delzon, Sartore, Granier et al. 2004). These studies found that large trees had deeper sap wood than small ones resulting in declines of sap flow with increased depth into the sap wood. The declines were greater in big trees than their counterparts. The decrease for small trees did not go below 60% of the outermost measurement whilst in the large trees the sap flow declined to as much as 20% of the outermost measurement (Delzon, Sartore, Granier et al. 2004).

In another study Delzon et al. (2004) studied hydraulic responses to height growth in an even stand of maritime pine in south-west France. Their results showed that hydraulic conductivity decreases with increasing tree size. Dye et al. (1991) however proposed an alternative explanation as to why sap flow decreases with increasing depth into the sap wood. They hypothesized that the old xylem that transported sap to the first branches when the tree was still young (which is towards the inside of the stem) no longer participated in the sap transport once the branches have been shaded or died. Dunisch and Morais (2002) determined the relationship of xylem sap flow to water supply in evergreen, semi-deciduous and deciduous high quality timber species from the Amazon. They found that in the deciduous tree species they studied leaves were only formed at the beginning of the wet season of the current year. They said that meant that a direct leaf-level continuum occurred only in the xylem of the current year. In Dunisch and Morris' study, the old xylem does not participate in water transport even though the branches had not died or been shaded. Unlike the situation in deciduous trees, vessels formed in previous years might remain connected to leaves formed during the previous 2-3 years in semi-deciduous and evergreen trees (Dünisch and Morais 2002). These may explain the relationship we found between SFD and tree size. The decrease in SFD with the increase in tree size may have been due to constraints in hydraulic conductivity with increasing tree size or the fact that some older xylem connected to shaded or dead branches no longer took part in transporting water to transpiring organs. To test if this was indeed the case, a 1% methylene dye may be used as a tracer. The dye is introduced under pressure into the xylem of trees. Vessels that take part in water transport will be stained blue (Dünisch and Morais 2002). It should be noted however, that the decline in SFD with increasing tree size does not translate to 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, and Andrade 2001).

In Kruger National Park (KNP), South Africa, Gush and Dye (2006) investigated water use from common woodland tree species. Amongst other species, they studied *Combretum apiculatum* which is a semi-deciduous species. In their paper, Gush and Dye (2006) reported only sap velocities. For comparisons to be made between the KNP study and our study, we calculated area of the *C. apiculatum* from the given stem circumference and proceeded to calculate sap flow and SFD by multiplying the sap velocity by stem area (sap flow) and dividing the sap flow by the area (SFD). The area of the *C. apiculatum* was 240 cm^2, and this was compared to a *Diospyros mespiliformis* from our study whose area was 136 cm^2. Both the *C. apiculatum* and *D. mespiliformis* are semi-deciduous and the tree sizes from both these studies are not far apart hence the comparison. The bigger *C. apiculatum*'s SFD was 0.052 $L/cm^2/h$ compared to 0.054 $L/cm^2/h$ from the smaller *D. mespiliformis*. This shows that indeed the larger the stem cross-sectional area the lower the SFD. The total sap flow from these two species was 306.4 and 177.7 $L/cm^2/day$ (maximum), 17.3 and 12 $L/cm^2/day$ (minimum) for *C. apiculatum* and *D. mespiliformis* respectively. As explained in the preceding paragraph, the increase in sap wood area with increasing tree size ensures that whole-tree water use is more in larger trees compared to their counterparts.

Size-related differences in water use from individual trees influence stand transpiration and in the end the whole ecosystem. We have established that in the Delta an increase of 3 cm^2 in stem cross-sectional area leads to 0.001 L/d less water transpired by trees. This means that as trees get larger proportionally less water is moved through them. As a result, if the Delta were comprised of only large trees (3 378 – 7 912 cm^2), transpiration rates would be significantly reduced leading to low groundwater usage and consequently reduced inflow to island groundwater. On the other hand, if only trees with cross-sectional areas ranging from 47-687 cm^2 (these were the size classes ranges that exhibited the highest sap flow) made up the Delta, assuming constant basal area, transpiration rates would be high, creating large hydraulic heads beneath islands. As a result water would be moved at a faster rate from the surrounding swamps towards islands thereby recharging the groundwater beneath 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 might mean that during unfavorable conditions, for example during the hot summer months, tree water use of the small trees might be greatly reduced due to the sensitivity of the stomata. Mixed stands of large and small trees may have a greater overall impact on the hydrological balance because trees in mixed stands draw on both soil water and groundwater resulting in increased total water discharge (Dawson 1996).

Forest succession leads to differences in tree spacing and crown diameters at the stand scale. This can either increase or decrease transpiration (Moore et al. 2004) depending on the structure of the resulting forest after succession. Basal area largely influences transpiration. If trees in the Delta were exposed to elephant damage such that only large trees survived, stem density would be reduced, the overall basal area would be large but sapwood basal area would be smaller than in small trees which might translate to less transpiration. Thinning experiments have however demonstrated that trees compensate for reduced stem density by expanding crowns and increasing leaf area: sapwood area ratio (Moore et al. 2004). Large crowns and increased leaf area: sapwood area ratio would result in high transpiration rates.

2.5.2 Differences in sap flow between species

Ecosystems with pronounced wet/dry seasonality and well-drained soils may be characterized by the presence of both evergreen and deciduous trees with evergreens growing as isolated individuals and deciduous trees growing close together (Sarmiento, Goldstein, and Meinzer 1985). Evergreen trees have leaves year all round, and shed them more or less regularly through all seasons whereas deciduous trees shed their leaves during the unfavorable season of the year (Lincoln, Boxshall, and Clark 1998). In the distal and upper Delta sites, even though there were rarely trees growing in isolation, deciduous trees tended to be found on the lower ground (pers. obs.). Isolated trees tend to use more water than those growing close together due to larger canopies and greater exposure (due to reduced potential for the development of a canopy microclimate) (Nisbet and Britain 2005). Though sometimes growing in isolation *Hyphaene petersiana* has a small canopy with very water-conserving leaf structure, which might account for the low SFD compared to those trees growing close together.

In group one, comparisons in SFD were made between *Croton megalobotrys*, *Diospyros mespiliformis*, *Hyphaene petersiana* and *Garcinia livingstonei*. *C. megalobotrys* showed the highest SFD during July-August 2012 losing 2.75 L/cm^2/day. *C. megalobotrys* is a deciduous tree that sheds its leaves during the dry season (June - August) (Heath and Heath 2009). The shedding of leaves however varies with individuals; some lose their leaves later than June. The study was done in July-August 2012, and at that point *C. megalobotrys* individuals still had leaves and were in preparation for flowering, which occurs sometime between September and November. Compared to the other trees, *C. megalobotrys* has the largest leaf size range, usually 8x5 cm (Ellery, Ellery, and McCarthy 1993). It however does not spread its roots to great depths in search of water whenever it becomes scarce, but instead relies on water from shallower depths which might explain why its SFD dropped from a high of 2.75 L/cm^2/day during high water level to 0.08 and 0.11 L/cm^2/day during low and medium water levels, respectively. *G. livingstonei* and *D. mespiliformis* showed the highest SFD in November-December 2012 and February-April 2013. *G. livingstonei* is an evergreen tree with a deep root system and a dense crown (Orwa et al. 2009). These characteristics are possibly what made *G. livingstonei* to exhibit high SFD. Evergreens tend to have large roots enabling them to access water during the dry seasons from deeper sources of water (Goldstein et al. 1989; Hasselquist, Allen, and Santiago 2010). Even when water levels were low *G. livingstonei* still showed high sap flux densities. Goldstein et al. (1989) studied water relations of evergreen and deciduous tropical savanna trees in the Llanos of Venezuela and found that generally evergreen species exhibited higher rates of water loss than deciduous. We also have established that evergreens use more water than deciduous by transpiring at least 1 to7 times the deciduous (Figure 2-8). During periods of low flows during the day (which could have been due to cloudy, cool and humid conditions) the relationship between evergreen and deciduous was almost 1:1 but during high flows evergreens transpired about eight times more than the deciduous. Evergreen trees have more efficient water transport systems than deciduous. In addition to deep roots, they have hard leaves covered with a waxy cuticle. The cuticle helps minimize water loss hence these trees can afford to have their stomata open whilst the deciduous trees would have to close their stomata as a means of minimizing water loss as they lack the waxy cuticle (Kaile 2011). Deciduous leaves also undergo senescence when conditions are unfavourable, they shed their leaves and by so doing reduce water loss. Evergreen leaves have an increased life span, the trees have leaves all year-round ensuring that trees transpire throughout hence the higher transpiration rates compared to the semi-deciduous. *D. mespiliformis*, though a deciduous tree, does not completely lose its leaves; instead leaf fall occurs immediately prior to the eruption of new leaves (making it semi-deciduous) (pers. obs.) and it has a dense crown for most of the year. This might explain why it exhibited the highest SFD during November-December 2012 and February-April 2013.

Diospyros mespiliformis occurred in two of our study sites; Nxaraga and Maun. Statistically there were differences in SFD between *D. mespiliformis* situated in Maun and that found in Nxaraga throughout the seasons (Figure 2-9). In Nxaraga, *D. mespiliformis* co-occurred with *K. africana* which had a much bigger canopy that rose above that of the *D. mespiliformis*. In Maun the *D. mespiliformis* did not occur in isolation either but there were gaps in the canopies that allowed light through. This might account for the higher SFD in Maun than Nxaraga during November-December 2012 and February-April 2013. Trees in Maun were smaller in trunk size than those in Nxaraga and as we have already established SFD is highest in trees with small stem cross-sectional area. The differences may be age-related as well as changes in stem and branch hydraulics with age may decrease the rate at which old trees can transport water (Moore et al. 2004).

Kigelia africana, *Philenoptera violacea*, *Ekebergia capensis* and *Phoenix reclinata* were in group two. *E. capensis* exhibited the highest SFD during the periods July-August 2012 and November-December 2012. This species thrives where water is in abundance and has a heavy, flattish crown (Orwa et al. 2009). It produces succulent fruits in December, exactly the time when measurements for November-December 2012 were taken, which might explain the high SFD recorded during that as some fruit trees need a lot of water for them to produce juicy, succulent fruits (Woods et al. 2005). It also had healthy looking, green leaves. During July-August 2012 it had yellowish, purplish leaves, apparently senescing. In this group, *K. africana* was the largest individual tree. As findings of this study indicate that larger trees transport less sap per unit area than small trees, it would be expected that it showed the least SFD. But that was not the case during the first two campaigns of data collection. This species can spread its roots to great depths and lengths in search of water (Ronne and Joker 2005), and a round, dense, wide-spreading crown. It flowers around August and fruits around December producing very big fruits which can weigh up to 12 kg (Jackson and Beckett 2012). During flowering, *K. africana* literally looks red; it has more flowers than leaves yet its SFD was second highest after *E. capensis*. The amount of water in the soil is vital in controlling water loss from trees (Nisbet and Britain 2005). The *K. africana* was found growing next to a *D. mespiliformis*, on a termite mound, which was always wet at the bottom. A symbiotic relationship has been found to exist between termites and *D. mespiliformis*; the termites feed on the roots of the tree and in turn aerate the soil (SANBI 2007) but this does not mean that a *D. mespiliformis* will always be found next to a termite mound. *K. africana* may have benefited from co-existing with *D. mespiliformis* on the mound by utilizing the moisture from the mound.

2.5.3 Changes in sap flow with season

In November-December 2012, sap flow was generally lower than in July-August 2012 in the distal and mid Delta. November-December corresponds to a period of low water level and July-August to high water level in both these areas. Annual flow into the Okavango Delta from the catchment in Angola recharges the groundwater table during the onset of the floods (Ringrose 2003; Wolski and Savenije 2006). Riparian trees remove a large proportion of groundwater by transpiration (Ringrose 2003). Our results show higher sap flow during high water levels (July/August 2012) than during low water levels (November/December 2012). This might possibly mean that since shallow groundwater is more available during high water levels trees need not to expend a lot of energy in pumping the water hence high sap flow. However, Ringrose (2003) inferred that relatively little water is lost during winter despite the high water levels, based on the low reflectance values she obtained despite the vegetation being green, suggesting little available plant moisture. Ringrose (2003) studied trees in the distal parts of the Delta. The observed low reflectance values might be from the fact that the flood had not reached those parts at the time of the study. That would mean that the water tables were depressed. Depressed water tables, coupled with relatively little available energy to drive ET would mean low sap flow as inferred by Ringrose (2003).

July-August is mid-winter in Botswana and November-December is early-summer (Botswana Meteorological Services). Normally it is expected that sap flow would be higher in summer when temperatures are high than in winter when temperatures are cool. David et al. (2004) characterized seasonal patterns of an evergreen oak tree in Southern Portugal. Their transpiration rates were high in summer and declined in winter, contrary to what we found. The climate in Southern Portugal is Mediterranean with hot and dry summers and cool wet winters (David et al. 2004) whereas in Botswana the climate is sub-tropical with rainfall occurring in summer. This therefore means that rainfall might have been a significant factor influencing declines in sap flow, by creating conditions that do not favor transpiration, in both David et al. (2004)'s study and our study. Rain in the Okavango Delta is relatively low, 490 mm on average annually, but nevertheless it makes a significant contribution in the Delta's water balance by adding about $6x10^9$ m^3 of water to the total water balance (McCarthy 2006). Rainfall generally lowers air temperatures and increases relative humidity resulting in trees transpiring less water than when temperatures are high and the air dry.

High transpiration rates recorded in winter, July-August 2012, in this study may have been due to a number of factors. Winter months in Botswana are dry with peak of the winds in August (Botswana Meteorological Services). Transpiration is strongly affected by temperature, humidity of the air and wind speed (Nisbet and Britain 2005). It is possible that these factors contributed to the high sap flow observed in the July-August 2012 campaign.

Sap flow increased in February-April 2013 from a low in November-December 2012 in the distal and mid Delta. It was still summer in February-April 2013 but there were no rains unlike in November-December 2012. This means that temperatures were warmer than they were in November-December 2012 and relative humidity lower hence the increase in sap flow.

In the upper Delta July-August 2012 was medium water level, November-December 2012 low water level and February-April 2013 high water level. From our results the higher the water level the lower the sap flow in this part of the Delta. During the periods November-December 2012 and February-April 2013 there was abundant surface water 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 limit to sap flow. Our study trees in the upper Delta are just on the edge of the main channel. Large bodies of water alter micro climatic conditions by reducing air temperature within the river channel resulting in lower evaporative demand (O'Grady et al. 2006). During high and medium water levels water was not only confined to the channel, it spilled onto the islands. This means that the micro climatic conditions in the islands may also have been altered by the presence of surface water and the fact that the trees were growing close together forming a closed canopy with little light reaching the understorey.

Diel sap flow curves showed that sap flow starts to increase very early in the morning, around 6am in most cases, reaching a maximum in the late afternoon, mostly around 1600hrs (Figure 2-4). O’Grady et al. (2006) in their study found that water use increased in the morning reaching a peak in the late morning and declining in the afternoon. Both these studies indicate that sap flow starts increasing in the morning and reaches a maximum in the afternoon. The only difference is in the peaks which can be attributed to temperature differences and other variables. Our trees showed sap flow even during the night contrary to the commonly held assumption that sap flow is zero at night as stomata are closed in the dark. The assumption is consistent with the nearly universal observation that stomatal conductance is at its highest during day light hours over a diel cycle (Ritchie 1974). Dawson et al. (2007) found that most species they studied transpired at night contributing a significant fraction of total daily water use for some species. This was corroborated by (Caird, Richards, and Donovan 2007).

2.5.4 Estimating plot-level transpiration

Overall, canopy cover was lower in Seronga than Nxaraga and greater in Maun (Figure 2-10). Changes in canopy cover, in percentage, and tree height are detectable along a hydrologic gradient in the downstream reaches of the Delta, decreasing along the gradient (Ringrose et al. 2007). Ringrose et al. (2007) did their study in the distal reaches of the Delta aiming at mapping riparian woody species distribution in the context of reduced flow levels in the Delta. Their results may help to explain the changes in canopy cover in our study as water levels decrease downstream. However, our results show a higher canopy cover percentage in Maun than Nxaraga. Our plot in Maun is situated in an enclosed, fenced area which has not been open to large herbivores since the late 1980s. This might explain the results which contrast those of Ringrose et al. (2007).

Canopy structure plays a significant role in seasonal fluctuations of transpiration (Gazal et al. 2006) predominantly via the amount of foliage and the stomatal conductance of the leaves (Wallace and McJannet 2010). Sap flow and plot transpiration changed with changes in canopy cover, increased with increasing canopy cover in Maun and Nxaraga (except in November-December 2012) (Figure 2-6A, 2-6B). A larger canopy would mean more leaves exposed to capture energy required for transpiration hence higher transpiration rates in such trees than those with small canopies. On the other hand, a lot of leaves per canopy may lead to some leaves shading others, depriving them energy to transpire leading to little water lost. The degree of foliation is the dominant factor controlling seasonal canopy conductance in temperate deciduous forests (Oren and Pataki 2001). Li et al. (2003) investigated the effectiveness of summer pruning of mature apples on canopy control and the impact on canopy gas exchange. Four pruning treatments at four levels of intensity (unpruned, light, moderate and severe) were carried out. Canopy transpiration reduced in proportion to pruning intensity. They attributed that to less light interception by a small canopy. In Seronga canopy cover increased progressively (Figure 2-10C) and seemed to have no bearing on sap flow and plot transpiration, these fluctuated in response to water levels. As explained in the preceding paragraphs describing sap flow in different seasons, in Seronga the more the water level the less the sap flow.

Plot transpiration can be estimated by scaling up water use by individual stems even in woodlands with trees of varying sizes and spacing (Hatton, Moore, and Reece 1995). Plot transpiration was highest in Maun and the least in Nxaraga (Table 2-5). The differences could be attributed to the basal area differences, 2.73, 1.55 and 1.65 m^2/ha in Maun, Nxaraga and Seronga respectively. Granier (1987) investigated transpiration in a Douglas-fir stand from a plantation in the forest of Amance. Measurements were made in a thinned and an un-thinned plot. Results showed lower transpiration in the thinned plot than the un-thinned as a result of the lower basal area. Our up-scaled estimates followed the same trend: the individual sap flow measurements exhibited were attributable to availability of water, weather variables (temperature and relative humidity) and species characteristics, and to a certain degree canopy cover.

2.6 Summary and Conclusions

Sap flow in the distal, mid and upper Delta varied along a latitude gradient, with tree size, species, season and canopy cover. The distal and mid Delta sites behaved similarly in the seasonal variation of sap flow, the trends were similar but the rate of transpiration different. During July-August 2012 these two sites exhibited the highest sap flow despite the fact that it was during winter. This might have been because during summer sap flow measurements coincided with rainy days. In the upper Delta, sap flow seemed to increase with decreasing water levels. There were inter and intra species differences in sap flow in different seasons and sites.

3 CHAPTER 3

Environmental controls on transpiration in northern Botswana

3.1 INTRODUCTION

Transpiration is a major component of the water balance of watersheds (Strelcova, Mindas, and Skvarenina 2006) and it is important to know how this component might change in response to climate and/or land use change (Wallace and McJannet 2010). Its quantification needs accurate measurements of water use patterns and interactions with climate and soil water availability (Burt et al. 2002). For trees to transpire there has to be a supply of water to the plant and energy to evaporate the supplied water. The ease with which water vapor can escape from the leaves is another important factor that determines transpiration rate (Forbes and Watson 1992). Transpiration involves moving water from the soil (source), through the plant and out into the atmosphere. Therefore soil is yet another important factor influencing transpiration as it influences the amount of water that is available to maintain transpiration. Movement of water through the soil is due to water potential gradients, that is, water moves from areas of large potentials to regions of small potentials (Burt et al. 2002). In addition to influencing transpiration, soil moisture also influences root uptake and the extent and timing of water table fluctuations (Gold and Kellogg 1996). Most tree species however are insensitive to soil drying until plant available water is depleted, due to tree roots reaching and accessing water at a depth and their stomata being more sensitive to atmospheric humidity than dry soil (Nisbet and Britain 2005).

Water obtained from the soil has to be evaporated off the surface of the plant's leaves and that process requires energy. The primary source of this energy is the sun, solar radiation (Forbes and Watson 1992; Hayashi and van der Kamp 2007). Air temperature is correlated with net radiation as the wavelength of radiation depends on the temperature of the source (Hayashi and van der Kamp 2007). Solar radiation raises leaf temperature. A rise in leaf temperature leads to a rise in the energy of movement of water molecules in the leaf hence the rate of evaporation of water from the leaf surface increases (Forbes and Watson 1992). Humidity, amount of water vapor in the air, is yet another driver of transpiration. It depends on the amount of moisture available and on the temperature. When leaf temperature is just about the same as air temperature then humidity drives transpiration (Forbes and Watson 1992).

In Amazon and Australia forests, transpiration varies within and between days, largely due to changing weather conditions, primarily atmospheric humidity and radiation (Shuttleworth 1988). The influence of these two variables on transpiration is strongly modified by the structure and response of the plant (Forbes and Watson 1992). In the Okavango Delta, ET is the dominant sink of water input, especially by riparian trees on islands, due to the semi-arid nature of the Delta. High temperatures and dry (less humid) conditions primarily drive ET.

In this chapter sap flow will be related to air temperature, relative humidity and soil moisture.

3.2 QUESTIONS

The questions addressed in this chapter are:

1. What is the relationship between transpiration and air temperature?

2. How is relative humidity related to transpiration?
3. What is the relationship between transpiration and soil moisture content?

3.3 MATERIALS AND METHODS

3.3.2 Weather variables

In this study, air temperature was measured and not radiation. In Maun air temperature and relative humidity were measured by a meteorological station that was located about 50 m away from the study site for the first and second phase of data collection. A meteorological station about 100 m away was used in Nxaraga for the first two campaigns. In Seronga weather variables data was obtained from the meteorological office for Shakawe which is about 108 km away in the first and second data collection phases. In the third phase of data collection, a mini meteorological station (Delta-T WS-GP1 Compact weather station) was erected in the study sites.

3.3.2 Soil moisture

A Delta-T theta probe soil moisture sensor Type ML2x was used to measure soil moisture. A pit 50 cm deep was dug around the edges of the canopies of the study trees and soil moisture taken on the surface and at 10 cm increments. The measurements were made on the same days sap flow measurements were made and these were taken once just before sunset. The same pits were used for the same campaign, a fresh slice of soil 10 cm wide was cut each day to make new measurements. The pits were covered after taking measurements to prevent rainwater from collecting in them during the rainy season. At the end of a campaign the pits were filled up with soil. In some seasons, due to equipment failure, measurements were not made. Here we present only the data we managed to collect.

3.4 RESULTS

3.4.1 Weather variables

3.4.1.1 Temperature

SFD was highly correlated with air temperature. It increased with increasing temperatures and declined with decreasing temperatures (Figure 3-1).

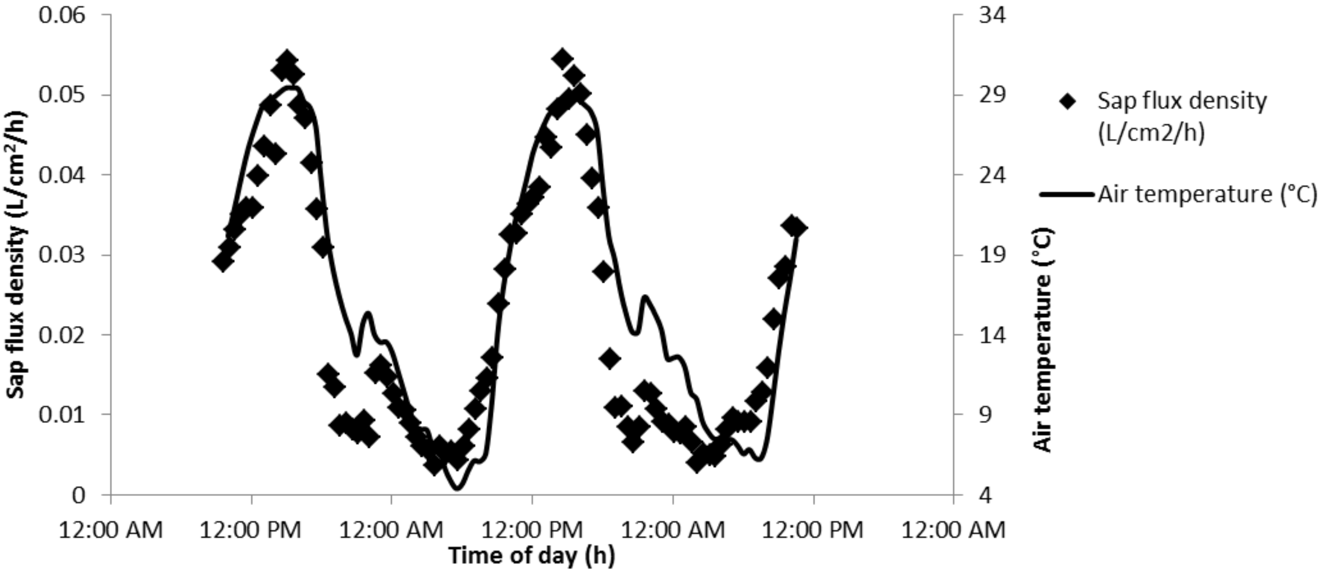
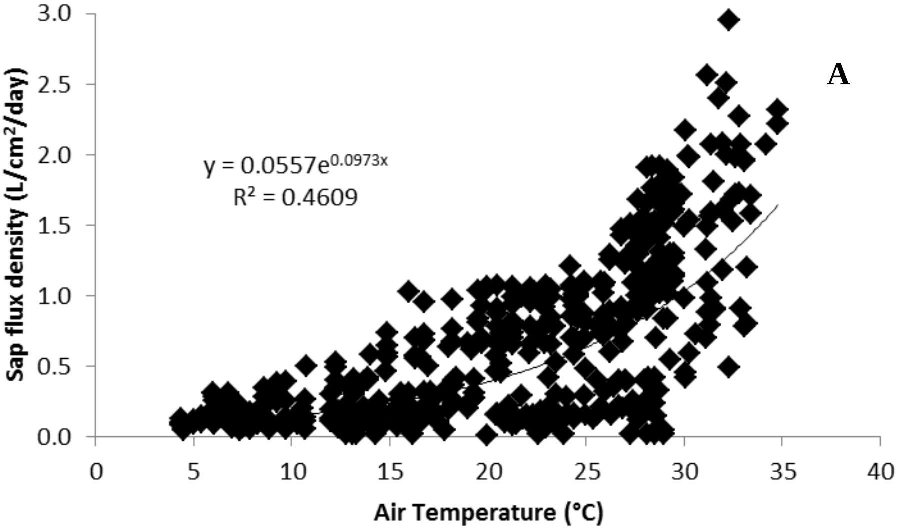


Figure 3-1 Relationship between SFD and air temperature

Both SFD and air temperature reached a maximum around three o’clock in the afternoon and a minimum around three o’clock in the morning.

Regression models showed correlations between SFD and air temperature in all the sites during the three seasons (Figure 3-2). The relationship was weakest in Seronga (Figure 3-2C).



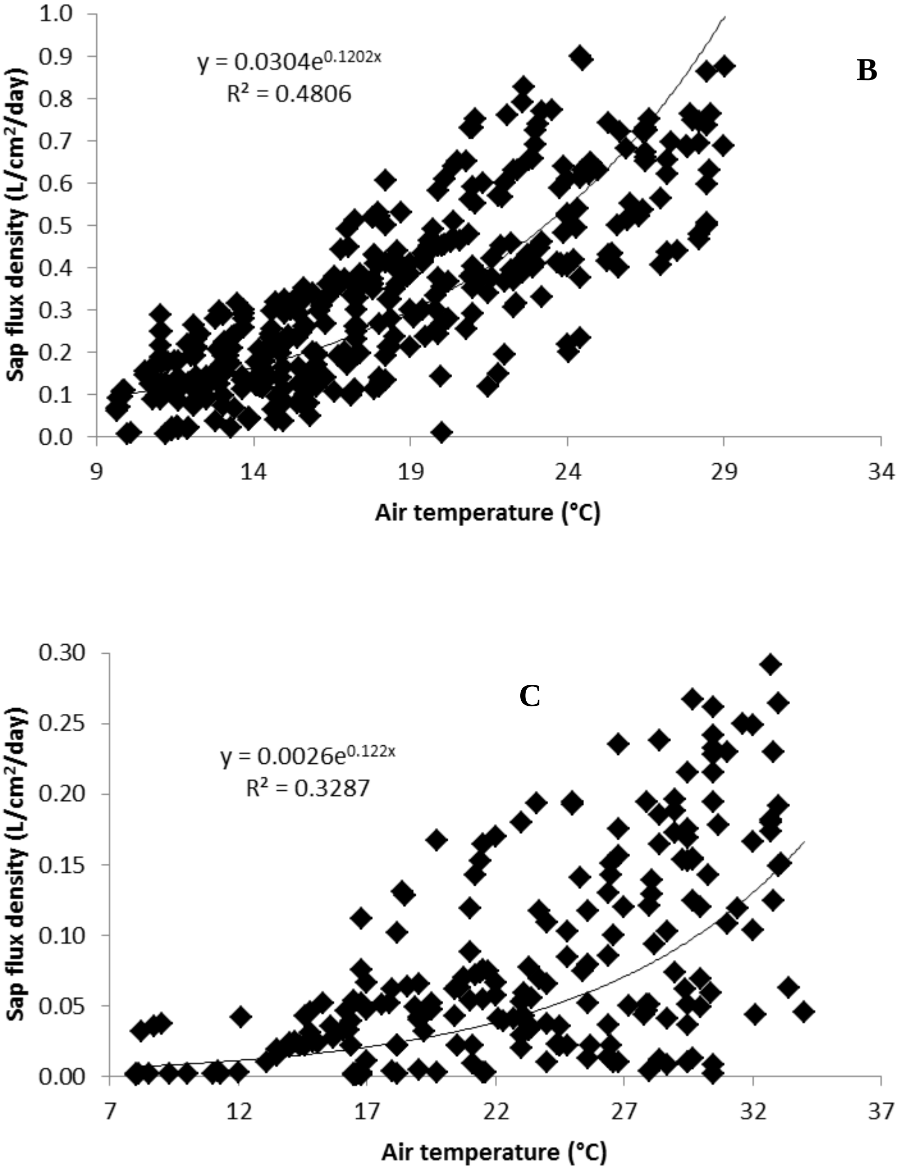


Figure 3-2 Correlations between air temperature and SFD in Maun (A), Nxaraga (B) and Seronga (C) during the three seasons

Air temperature explained less than 50% of the variation in SFD in all the sites.

3.4.1.2 Relative Humidity

SFD decreased with increasing RH levels (Figure 3-3), the higher the moisture content in the atmosphere the lower the SFD.

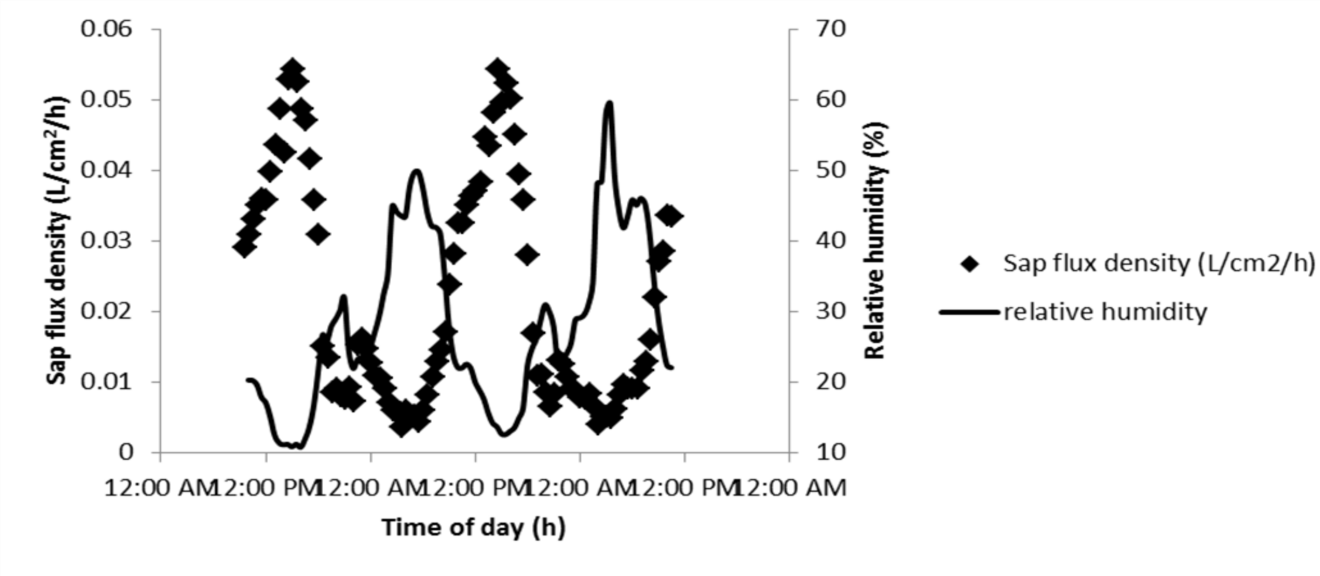
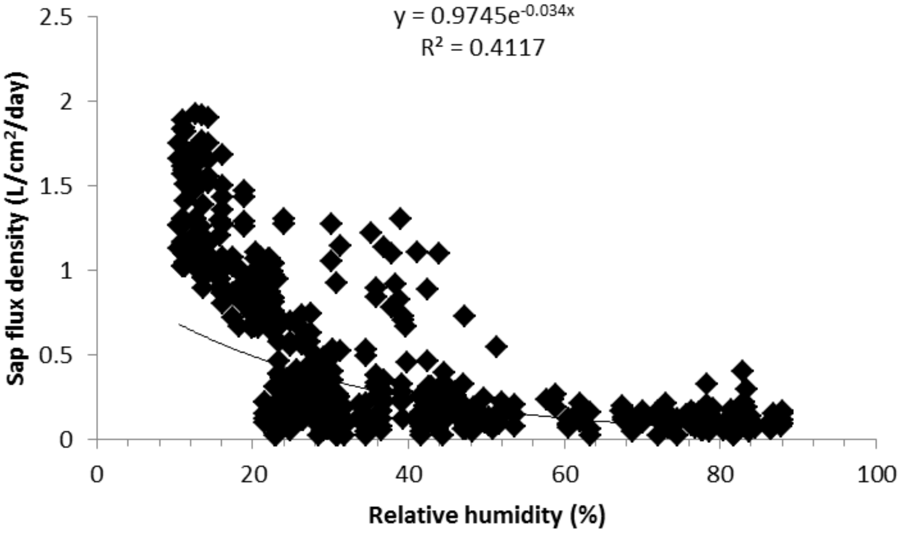
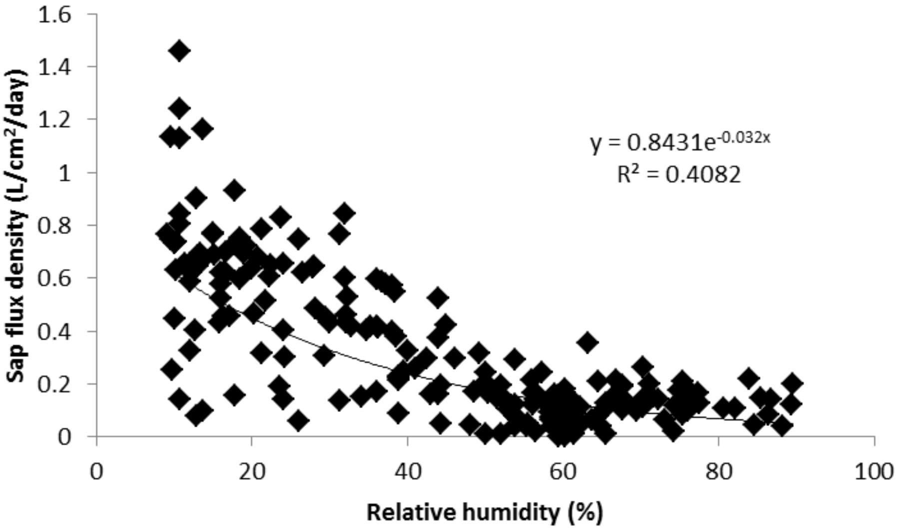


Figure 3-3 Relationship between SFD from an individual of *Diospyros mespiliformis* and relative humidity in Maun during July-August 2012

Relative humidity (RH) was lowest just around 1500hrs when SFD was highest.

RH explained about 42 (Maun), 41 (Nxaraga) and 41% (Seronga) variation in SFD when data from all the seasons, all the species was brought together (Figure 3-4).





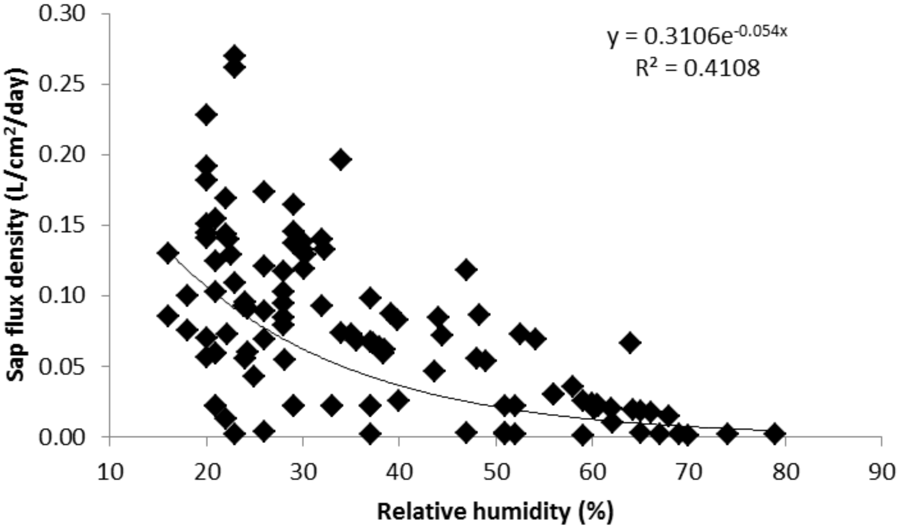


Figure 3-4 Correlations between SFD and relative humidity in Maun, Nxaraga and Seronga during the three seasons

Relationship between SFD and RH was weakest in Nxaraga.

3.4.2 Soil moisture

Table 3-1 Mean soil moisture content (± standard deviation) in three sites in the Okavango Delta in different seasons

Site	Depth (cm)	Soil moisture content (%)		
		July-August 2012	November-December 2012	February-April 2013
Maun	Surface			28.1 ± 9.5
	0-10			26.4 ± 5.2
	10-20			29.1 ± 12.2
	20-30			26.1 ± 16.1
	30-40			27.6 ± 14.4
	40-50			40.3 ± 9.1
AVERAGE				**29.6 ± 11.1**
Nxaraga	Surface		14.8 ± 3.5	23.6 ± 3.4
	0-10		19 ± 7.6	33.7 ± 13
	10-20		21.4 ± 6.5	40 ± 15.4
	20-30		23.8 ± 3	37.7 ± 13.2
	30-40		25.1 ± 6.1	38.6 ± 14.2
	40-50		22.8 ± 3.3	41.5 ± 14.7
AVERAGE			**21.1 ± 5**	**35.8 ± 12.3**
Seronga	Surface		33 ± 1.5	48.1 ± 32.9
	0-10		31.6 ± 3.8	60.5 ± 31.3
	10-20		30.6 ± 2.7	65.9 ± 11
	20-30		29.3 ± 2.6	79.9 ± 5.9
	30-40		28.8 ± 1.8	84 ± 0.8
	40-50		27.4 ± 1.1	86 ± 0.7
AVERAGE			**30.1 ± 2.2**	**70.7 ± 13.8**

Soil moisture was higher in February-April 2013 than November-December 2012 in Nxaraga and Seronga. The measurements were taken once a day from six points per pit; there were two pits in every campaign, for three days. When soil moisture was related to SFD by means of regression a weak relationship was established (r^2 = 0.044).

3.5 DISCUSSION

3.5.1 Weather variables

3.5.1.1 Temperature

Temperature is a significant driver of transpiration. Increases in temperature lead to increases in transpiration rate (Figure 3-1). Temperature stimulates opening of stomata, it raises leaf temperature and lowers atmospheric humidity (Forbes and Watson 1992). The size of the stomatal pore in some species increases with increasing temperatures up to about 30°C (Forbes and Watson 1992). Stomatal responses in various species are variable (Burt et al. 2002). All these effects of temperature lead to increased transpiration rate. When stomata are open, water vapor easily leaves the plant leaves via the open pores. A rise in leaf temperature also gives water molecules in the leaf energy and as they are heated the molecules become less dense and evaporate. Dry air outside the leaf leads to movement of water molecules from the more humid environment within the leaf to the outside less humid air.

In this study SFD, sap flow per unit stem cross-sectional area, increased with increasing temperature. These results are in agreement with results from other studies. Baig and Tranquillini (1980) studied effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and found that the rate of transpiration significantly increased at increased temperatures. They measured cuticular transpiration at 15, 20 and 25°C and temperatures in this current study ranged between 5 and 29°C during July/August 2012. Increases in transpiration at higher temperatures may have been from an increased vapor pressure gradient between the leaves and ambient air or temperature-mediated stomatal opening (Baig and Tranquillini 1980). Transpiration is influenced indirectly by environmental factors that stimulate stomatal opening (Ku, Edwards, and Tanner 1977). Various experiments that were carried out under constant evaporative conditions but varying temperatures showed that stomata opened with an increase in leaf temperature provided there was no water stress (Schulze et al. 1974). Our study trees have access to groundwater throughout hence stomatal opening might be the cause of transpiration increases experienced.

SFD of different species in our study followed a similar pattern, transpiration increased with increasing temperature, but varied in magnitude. Some trees exhibited higher sap flux densities than others. Different plant species employ different mechanisms to manage their water balance throughout the day in response to increasing temperatures. Some use a combination of stomatal closure and a sustained water supply from an extensive and effective root system whilst others use water reserves within plant organs (Forbes and Watson 1992). Comparisons of sap flux densities in our studied trees and the possible explanations of the variations have already been given in Chapter 2.

Transpiration rates vary considerably as a function of species and geographic region (Burt et al. 2002). Moderate (not weak, not too strong) correlations existed between SFD and temperature. In Maun and Nxaraga regression coefficients (r^2) were 46 and 48% respectively whilst in Seronga the regression coefficient was 33% when all species were grouped together throughout the seasons. On average temperatures were highest in Seronga yet temperature accounted for only 33% of the transpiration. As explained in Chapter 2, our study trees in Seronga were along the main channel and large bodies of water alter micro climatic conditions by reducing air temperature within the river channel resulting in lower evaporative demand (O'Grady et al.

2006). The weak correlation cannot have been from the fact that these variables were measured from a meteorological station which is over a 100 km away because temperature and RH are consistent; the only thing that might differ is rainfall. Between Maun and Nxaraga, temperatures were higher in Nxaraga than Maun, on average 18.1 and 17.5°C respectively during July-August 2012, which might have led to the higher correlations in Maun than Nxaraga. Transpiration in different species is made complex by structural factors such as root, leaf and sapwood area (Chen, Zhang, and Ewers 2012). In semi-arid regions where water is limiting, plant leaves must have a relatively high diffusion resistance to water vapor as leaves with low internal diffusion resistance will have a high rate of transpiration (Gates 1968). Leaf size also plays an important role in plant water use. Small leaf size, characteristic of semi-arid plants, maintains the leaf temperature near to air temperature (Gates 1968) leading to reduced transpiration as there is not much of a gradient to move water from the leaves to the atmosphere.

3.5.1.2 Relative humidity

Relative humidity (RH) is the ratio of the absolute humidity, the quantity of water vapor present in the air, and the potential of water saturation the air can hold. RH depends on temperature of the air. A lowering of air temperature results in a rise in RH. Unlike temperature, high RH leads to low transpiration rates and low RH results in high transpiration. In concurrence with results from other studies our results showed an increase in SFD with a decrease in RH and a decline in SFD with an increase in relative humidity. Transpiration increases with declining RH until a point after which there is either no further change or the rate even declines as the stomata gradually close (Forbes and Watson 1992). Regression analysis in a study by Rawson et al.

(1977) adequately described the relationship between the rate of transpiration and the difference in absolute humidity in all species they studied (r^2=0.96-0.99). Their RH fluctuated between 35 and 55%. RH, which we measured, is the measure of absolute humidity relative to temperature. In our study, the strongest correlation was in Maun (r^2=0.4117). Rawson et al. (1977) studied individual leaves under a controlled environment. We on the other hand studied whole plant tree water use using sap flow measurements in a natural environment. This might explain why their relationships were stronger than ours.

Correlations between SFD and RH in all the sites were below 50% just like the correlations between air temperature and SFD. As already stated, relative humidity relies on temperature so weak correlations between temperature and SFD might lead to weak correlations between RH and SFD. Stomata respond to changes in the evaporative conditions in the atmosphere. Stomata were found to be open at a high humidity and closed at a low humidity in some studies. High humidity means the air outside the leaf is more saturated with water vapor than the air within the leaf hence no or little water will be lost from the leaf, hence plants can afford to have their stomata open in such conditions. When the air outside the leaf dries out some plants close their stomata to minimize water loss. This mechanism of stomatal closure is known to regulate plant water status under decreasing humidity (Sperry 2000).

With the compensation heat pulse velocity method (CHPM), used in this study, as mentioned in the method section, the velocity of the heat pulse is determined by recording the time it takes for the pulse to travel by convection to the midpoint between temperature sensors, at which time the sensors record the same temperature. However, during low sap flow rates the heat pulse might dissipate by conduction before it reaches the measurement point. Consequently, the sensors will record the same temperature as temperatures would have returned to initial values meaning low, zero and reverse flows would be overestimated (Burgess et al. 2001). This, coupled with the fact that lower limits to measurement depend on the sensitivity of temperature sensors and rates of thermal diffusivity in xylem (Burgess et al. 2001), might account for the correlations below 50%. However, methods that use heat pulse are often favored and of the heat pulse techniques, the CHPM has been the most widely used despite the limitations.

3.5.2 Soil moisture

Climate and soil moisture control vegetation dynamics and in turn vegetation exerts important controls on the entire water balance and is responsible for many feedbacks to the atmosphere (Porporato and Rodriguez-Iturbe 2002). Soil moisture is one of the sources for transpired water. Table 3-1 depicts soil moisture content values measured in our study. From table 3-1, soil moisture content was lower in November-December 2012 (low water level) than in February-April 2013 in Nxaraga and Seronga. Upward extension of the capillary fringe in areas with shallow water tables ensures that even above the water table, the soil remains somewhat close to saturation (Gillham 1984). During the low water levels water tables are at their deepest therefore water movement by capillary action is through longer distances compared to when water tables are raised, which might explain the low soil moisture content during November-December 2012.

Regression analysis in our study showed a rather weak or unclear relationship between soil moisture content and SFD ($r^2 = 0.044$). The influence of soil moisture on transpiration has not been consistent among studies. Our results however are in agreement with those from Chen et al. (2012). They found no significant correlation between evaporation and soil moisture content. Studies in the tropical rainforests have also found little or no correlation between soil moisture and transpiration (Wallace and McJannet 2010). Wallace and McJannet (2010) in their study on processes controlling transpiration in the rainforests of north Queensland, Australia found that there is no obvious relationship between soil moisture and transpiration. In the Amazonian rainforest, Roberts et al. (1996) found very little evidence that declining soil moisture influenced stomatal conductance at any of their forests. High soil water availability and/or substantial rooting depths (allowing trees to still tap into the water supply during the dry season) of the Amazonian forests may explain the little or no relationship between soil moisture and transpiration, or the water tables that are close enough to the surface to allow trees roots to access water from the phreatic zone (Wallace and McJannet 2010).

The weak correlation in our study might mean that the studied trees depend mainly on groundwater more so that the Okavango Delta is characterized by shallow water tables. Water flow from the soil to the plant is via a number of parallel pathways. As a result the root system compensates for spatial variations in soil moisture by extracting water from wet regions at a high rate when some of the roots are water-stressed (Guswa 2005). The study trees may possibly be rooted in different patches of the soil profile hence no significant relationship between soil moisture content and SFD. Soil moisture content is an important driver for tree transpiration for longer time scales rather than sub-daily or daily scales (Chen, Zhang, and Ewers 2012). This might also explain the weak correlations. Soil type and texture may also have an influence on transpiration. In thick soils, roots may be restricted to growing in the soil in which case soil water content would greatly influence transpiration (Huang et al. 2011). The Okavango Delta soils are sandy and trees growing in sandy areas are expected to root deeper than those in thicker soils because water easily infiltrates sandy soils. With the water table in the Delta shallow, rooting deeper would mean gaining access to the water table and using water directly from the saturated zone. Consequently, soil moisture would play a very limited role in transpiration. *Croton megalobotrys* is a shallow-rooted species. It was plotted against soil moisture to determine if there would be any correlations. The relationship was also weak, $r^2 = 0.012$. This might mean that though the *C. megalobotrys* is classified as a shallow-rooted species, its roots go deep enough to penetrate the shallow water table characterizing the Delta.

In Nxaraga, rain fell on day 2 of our campaign in December 2012 and soil moisture increased in the first 20 cm only. In Meerveld and McDonnel's (2006) study, frequent storms replenished soil moisture. The storms rewetted the shallow surface layers but not the deeper layers. The increased soil moisture in the upper 20 cm showed a greater decline than the layers beyond 20 cm. The moisture could have been utilized by the grasses that were growing under the canopies of the studied trees. Soil water dynamics investigated in the cerrado savannas of central Brazil showed that of the 82% water used by the trees during the dry season, 67% was from depths below 1 m (Oliveira et al. 2005). This deep soil water use was significant not only during the dry season but during periods of low rainfall and during the growing season as well. Our trees might as well have used water from soil compartments deeper than the 50 cm we investigated.

3.6 Summary and conclusions

SFD increased with increasing temperature and decreasing relative humidity. With temperatures expected to rise with global warming it might be expected that ET will also increase. This means that Delta trees will transpire more until water is limiting. SFD was weakly correlated with soil moisture content, the relationship was unclear. This might mean that the investigated trees rely on groundwater as their source of moisture. Dry areas are expected to become drier because of climate change. This would mean that local rainfall would go below the mean annual 450 mm.

Local rainfall contributes a significant amount to the water balance of the Delta, a reduction in precipitation would mean a reduction in total input into the Delta hence less water available for transpiration. Climate change is also likely to affect precipitation patterns in the catchment, Angola. If rainfall amount reduced as well in the catchment, the total surface inflow into the Delta via the Okavango River would be reduced. The inflow makes 66.7% of the total input. Flooding indicates groundwater recharge. Reduced inflows would result in water table lowering which will compromise the health of the trees as a lot of energy is expended in drawing water at depths.

4 CHAPTER 4

Relationship between sap flow and diel groundwater fluctuations

4.1 INTRODUCTION

Groundwater hydrographs can provide information regarding ecohydrological processes occurring in riparian ecosystems (Martinet et al. 2009). The dynamics of groundwater level position, both spatial and temporal, have been shown to control vegetation composition and nutrient processing in riparian areas (Burt et al. 2002; Hefting et al. 2004; Leyer 2005). Groundwater levels are never stable. They are constantly changing due to many reasons. These can be natural or human-influenced or both (Inkenbrandt, Doss, and Pickett 2005). Human influences include pumping of wells and natural factors include transpiration by trees and gravitational effect such as the orbit of the moon.

The groundwater-vegetation relationship is a bi-directional one. Transpiration can play a major role in controlling groundwater movement and solute concentrations within wetlands (Humphries et al. 2011). The water table may fluctuate daily in response to daily water plant uptake as the roots tap into the groundwater (Schilling 2009). Hence diurnal water table fluctuations have been used to estimate evapotranspiration (ET) (Schilling 2009; Bauer et al. 2004). This method, pioneered by White (1932) and later refined by Butler et al. (2007) and Loheide and Steven (2008), estimates ET as the amount of water stored and de-stored (lost or used up) in the soil per diurnal cycle. It assumes that ET is the sole process that lowers the water level and that recovery of the water table is driven by lateral flow from the source of supply (Bauer et al. 2004; Martinet et al. 2009). Little is known on groundwater dynamics in sub-humid and semi-arid wetlands as most studies were done in temperate and tropical environments (Lamontagne et al. 2005). Temperate and tropical environments are characterized by high rainfall and humidity, warm summers and cold winters, occasionally subzero. Trees in these regions form dense canopies (Lincoln, Boxshall, and Clark 1998). On the other hand sub-humid and semi-arid environments are drier, experience lesser rainfall than their counterparts and there are no forests in these regions, trees do not form closed canopies like in the rainforests. Therefore it would be expected that the groundwater dynamics would be different in these different environments. ET from the groundwater table is an important component in hydrological modeling. This component is difficult to determine in the field owing to the fact that transpiring plants obtain their water from different depths and the extent of direct evaporation is unknown (Bauer et al. 2004).

Groundwater plays an important role in the hydrology of the Delta as groundwater recharge influences the extent of inundation and outflow (McCarthy, Bloem, and Larkin 1998). A considerable amount of floodwater infiltrates the soil to recharge groundwater (Gumbricht et al. 2004). Soils in the Delta have their grain size ranging from 0.20 – 0.25 mm and dry bulk density ranging from 2 305 – 2 470 kg/m^3. Total porosity ranges between 0.33 – 0.46% (Bauer et al. 2004). Riparian woodland found growing on dry land next to water in the Delta is almost entirely dependent on groundwater from the adjacent floodplain or channel (Murray-Hudson, Wolski, and Ringrose 2006). This vegetation has been found to play a vital role in regulating groundwater levels beneath islands (Ellery et al. 1993). Groundwater tables are shallow on islands and as a result evaporation and transpiration rates are high (Bauer-Gottwein et al. 2007). The free-standing water table exhibits a steep gradient from surface water in the floodplains to the island fringes. These island fringes are dominated by woody trees which suggests that transpiration is the main factor lowering the water table; in addition these trees provide dense shading, ensuring that evaporation from the soil surface in the wooded parameter is minimal (Ellery et al. 1993).

The water table in the Delta is generally shallow with the result that significant amounts of water may be drawn from the phreatic zone by vegetation. Bauer et al. (2004) employed a technique to estimate ET rate from diurnal fluctuations of groundwater. They did their study on Thata Island, located in the perennially inundated areas of the Delta. No work has been done in the seasonally inundated parts. Here we estimated ET from diel fluctuations of groundwater from islands subjected to seasonal flooding as well as those in the perennially inundated areas. We simultaneously measured sap flow in riparian trees in the same plots to allow comparison of the estimates of ET from the two methods. Transpiration was scaled up from whole tree water use (sap flow) and groundwater levels to plot-level transpiration.

In this chapter, relationships, if any, between sap flow and groundwater fluctuations will be determined.

4.2 QUESTIONS

The questions addressed in this chapter are:

1. How is sap flow related to groundwater fluctuations?
2. How do plot-level estimates of ET from sap flow measurements and from groundwater fluctuations compare?

4.3 MATERIALS AND METHODS

4.3.1 Diel groundwater fluctuations

Groundwater level fluctuations were determined over a period of three days, running parallel with the sap flow measurements. Holes for piezometers were drilled using a 50 mm hand auger, penetrating the saturated zone as far as possible without inducing well collapse. Polyvinyl chloride (PVC) pipes were used to construct the wells. The pipes were perforated along the bottom one meter, capped at the bottom end, and the perforated part covered with a screen of nylon fabric. The wells were covered at the soil surface to prevent rainfall and overland flow from entering. After installation, total well depth and static water levels were measured relative to the top of the piezometer pipe.

In Maun, a square grid of nine piezometers, 10 m apart, was made around the study trees whereas in Nxaraga and Seronga line transects of piezometers were made based on the arrangement of the trees studied. Barometric pressure transducers (BPTs) (Down-hole TD-divers, Eijkelkamp, Giesbeek, The Netherlands) were lowered into the piezometers, into the water, and set to measure groundwater levels every 10 minutes. One BPT was placed just above the water level to measure atmospheric pressure. The measured data were corrected for atmospheric pressure by subtracting the barometric values from the BPTs that were in the water. The correction removes effects of atmospheric air pressure. Measurements were made for five consecutive days initially, running parallel with the sap flow measurements, and reduced to three days after establishing that there were no major variations between days. During some seasons groundwater level measurements were not made due to equipment failure.

4.3.2 Scaling up ET to plot-level

Diameter at breast height, DBH, (1.3 m) of all trees found in an investigated plot was measured and basal area (BA) for each tree calculated from the formula:

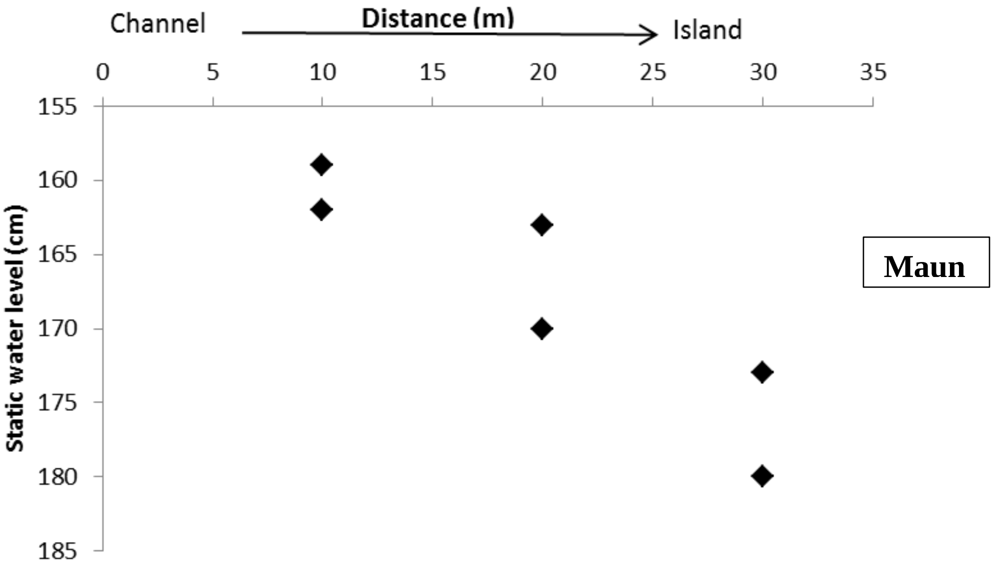
$$BA\ (m^2) = \pi(DBH/2)^2$$

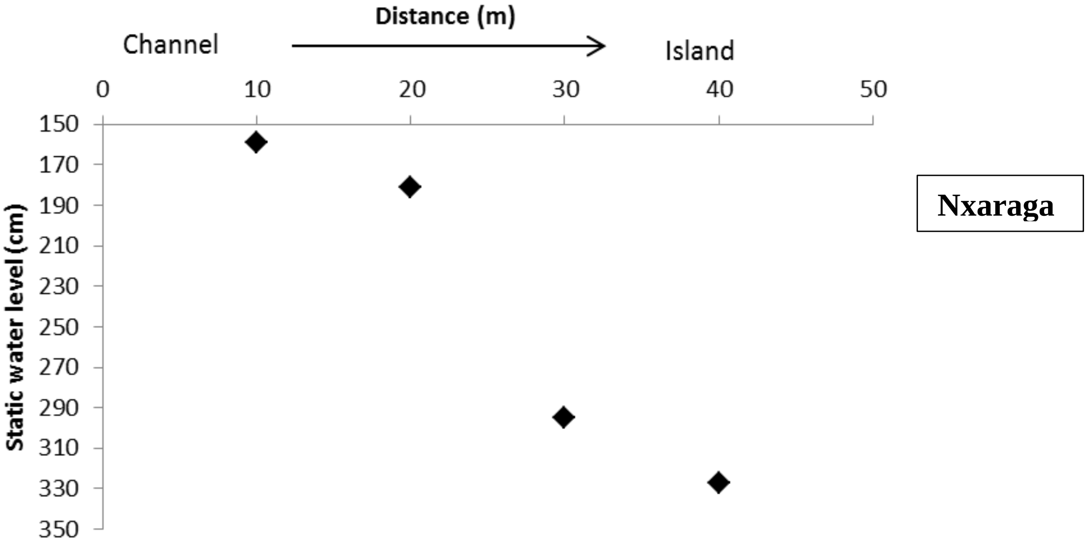
BAs for all the trees were added to give total plot basal area. Sap flow was added for all the trees studied and multiplied by plot basal area to give plot transpiration. For groundwater calculations, to give volume of water consumed by the trees, the drawdown was multiplied by the porosity of the soil. 0.33 was used as the porosity value. This was obtained by Obakeng and Gieske (1997).

4.4 RESULTS

4.4.1 Water table depths

Water table deepens from the channel towards the island (Figure 4-1).


Channel
Distance (m)
Island
0
5
10
15
20
25
30
35
155
160
165
170
175
180
185
Static water level (cm)
Maun


Distance (m)
Channel
Island
0
10
20
30
40
50
150
170
190
210
230
250
270
290
310
330
350
Static water level (cm)
Nxaraga

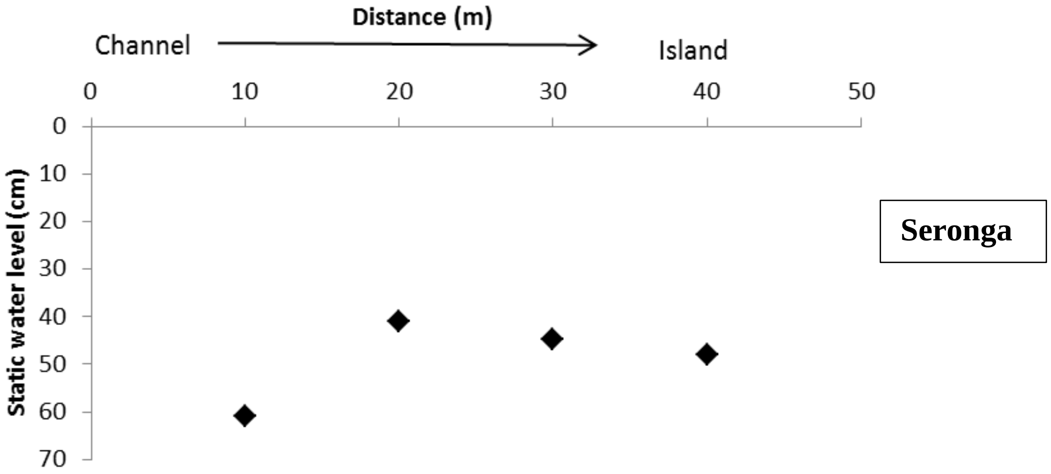
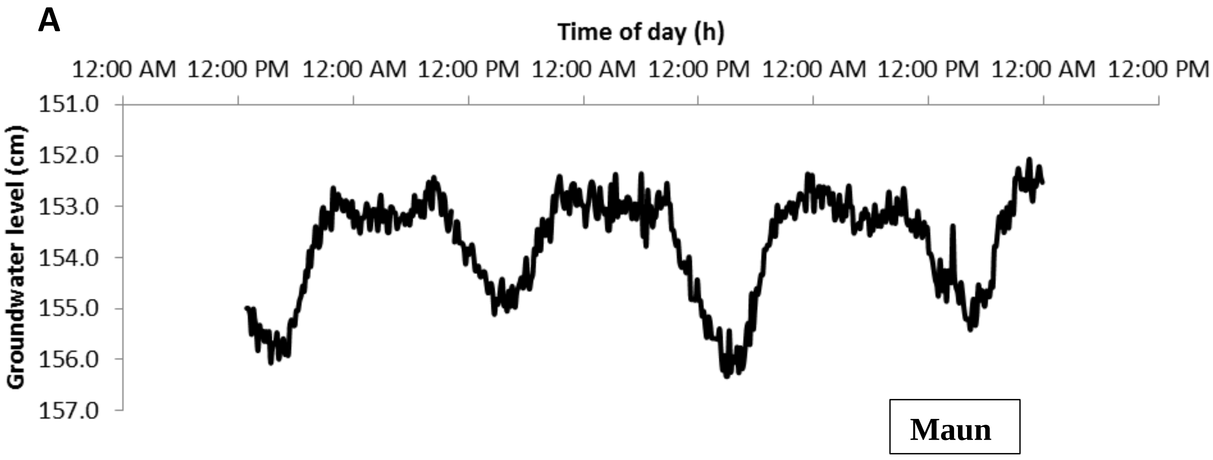


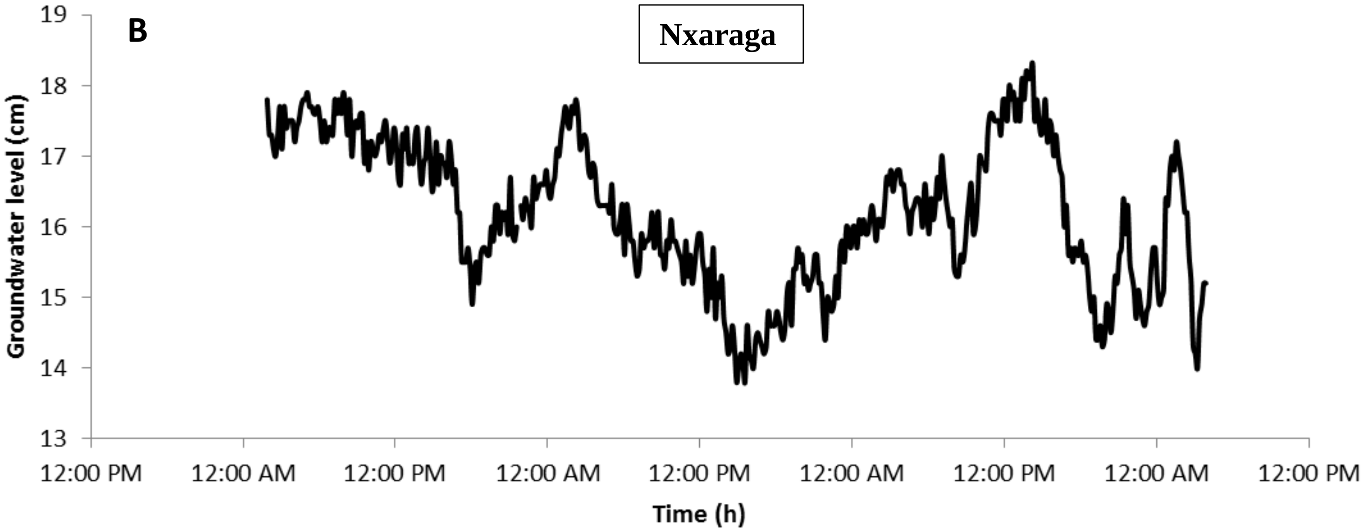
Figure 4-1 Static water levels in Maun, Nxaraga and Seronga during February-April 2013

In Seronga, unlike in Maun and Nxaraga, the piezometer closest to the channel is the deepest. The water table gradient is steepest on the fringe and flattens towards the island center. The y-axis shows depths of the piezometers relative to the ground surface.

4.4.2 Diel groundwater fluctuations

Groundwater levels showed a consistent pattern, rising in the late afternoon from minima to maxima attained in the early morning, just after midnight (Figure 4-2).


A
Time of day (h)
12:00 AM
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
Groundwater level (cm)
151.0
152.0
153.0
154.0
155.0
156.0
157.0
Maun


B
Nxaraga
Groundwater level (cm)
19
18
17
16
15
14
13
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
12:00 AM
12:00 PM
Time (h)

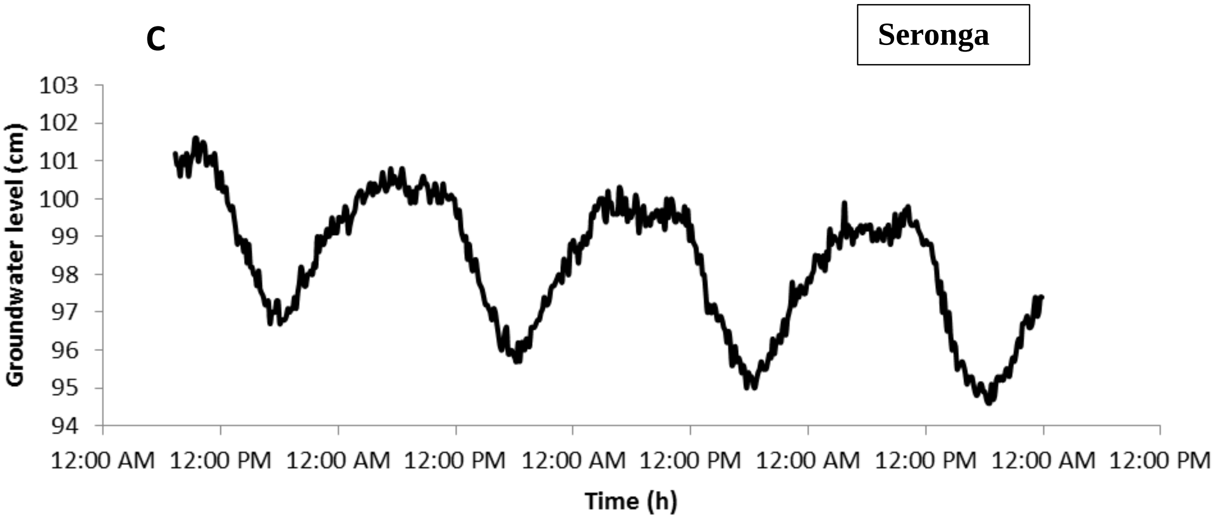


Figure 4-2 Examples of diel groundwater level fluctuations in Maun (A), Seronga (C) during July-August 2012 and Nxaraga (B) during November-December 2012

Groundwater levels were drawn down to their lowest around 1500hrs and recovered steadily thereafter reaching a maximum between midnight and 0400hrs. The levels started to decline after 0400hrs. In Seronga however, maximum sap flow decreased with days, the highs were lower than that of the previous days'.

When sap flow was plotted against groundwater level, the sap flow plot mirrored that of groundwater. Sap flow attained its maximum at the lowest groundwater level (Figure 4-3).

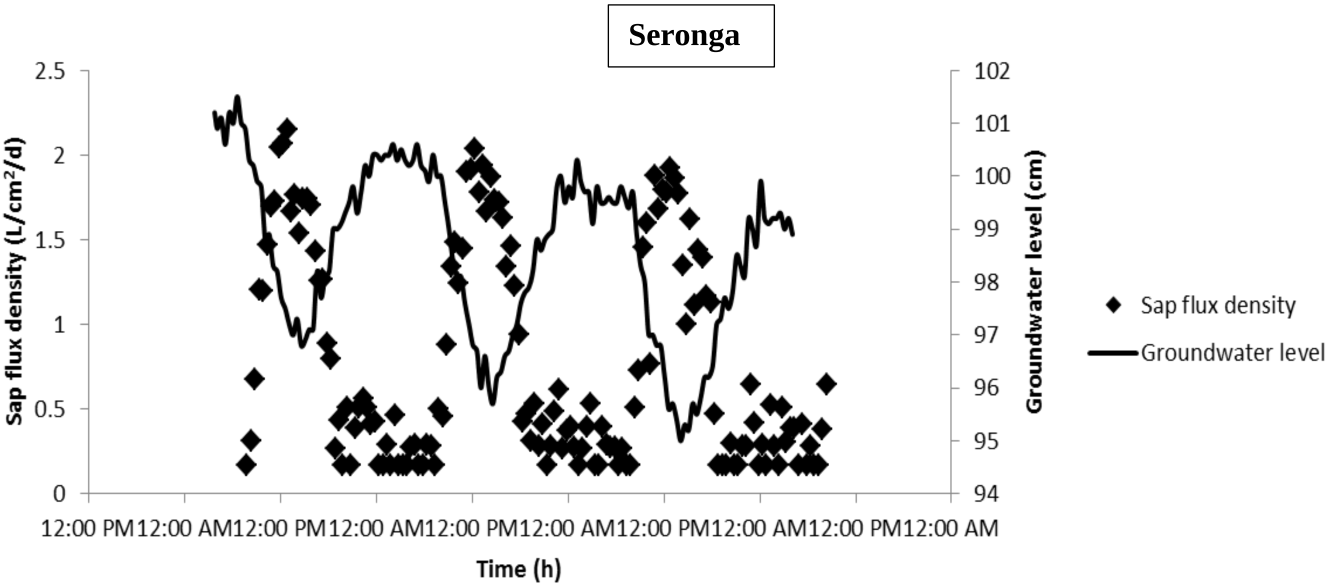


Figure 4-3 Comparisons between sap flow and groundwater level at different times of the day

Sap flow decreases with decreasing groundwater level, a drop in groundwater level leads to a decrease in sap flow.

Groundwater levels fluctuated by different magnitudes throughout the day depending on the rate of sap flow (Table 4-1).

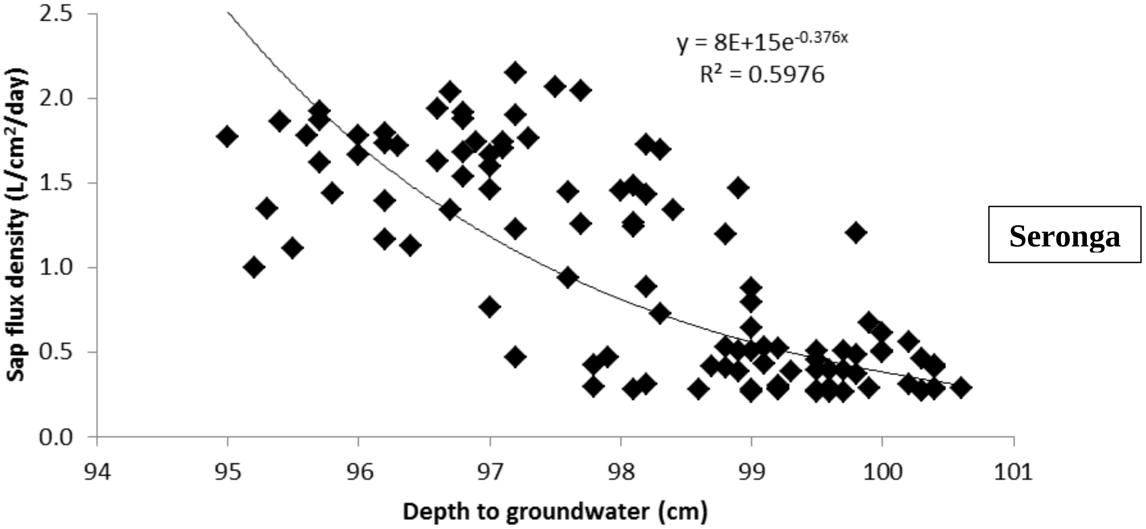
Table 4-1 Diurnal groundwater fluctuations (cm)

Water level variations measured in Maun, Nxaraga and Seronga during low, medium and high water levels.

Site	**Season**		
	Low water level	Medium water level	High water level
Maun	4.4	5.1	4.9
Nxaraga		5.5	
Seronga	7.0	8.7	

4.4.3 Comparisons between groundwater level and SFD

Strong correlations existed between SFD and groundwater level throughout the seasons in all the sites. Figure 4-4 shows results for just one season.



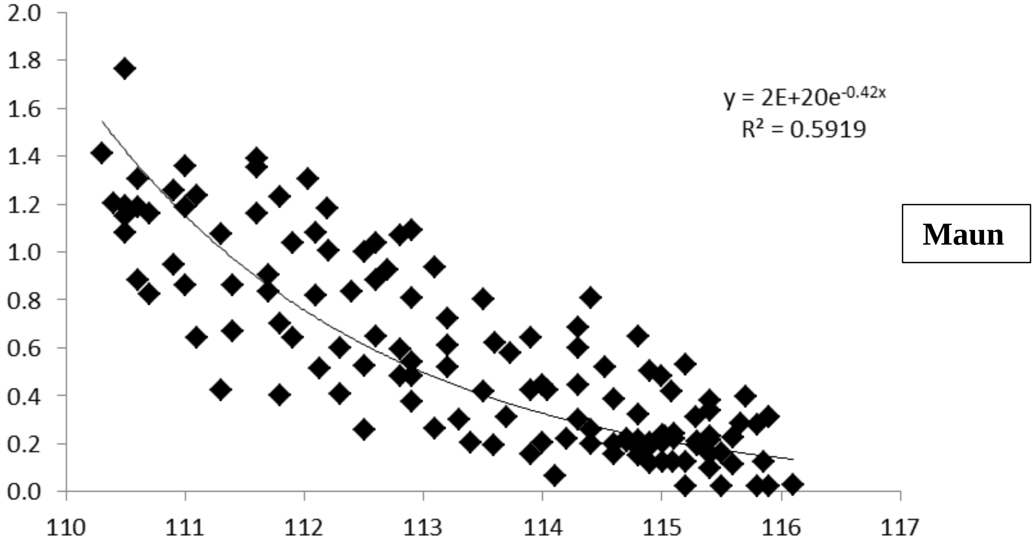


Figure 4-4 Relationship between groundwater level and SFD in Seronga and Maun

4.4.4 Plot transpiration

Table 4-2 Seasonal plot transpiration estimated from Maun, Nxaraga and Seronga

Plot transpiration was estimated from sap flow of studied trees and groundwater fluctuations

Site	Season	Plot transpiration estimated from sap flow (L/m^2/day)	Plot transpiration estimated from diurnal groundwater fluctuations (L/m^2/day)
Maun	July-August 2012	14.1^a	35.3^b
	November-December 2012	10^a	28.8^b
	February-April 2013	17.3^a	36.1^b
Nxaraga	July-August 2012	6.2	
	November-December 2012	3.6^a	28.2^b
	February-April 2013		
Seronga	July-August 2012	7^a	47.4^b
	November-December 2012	15.1^a	37.9^b
	February-April 2013		

*Values with different letter superscripts across rows are significantly different statistically.

4.5 DISCUSSION

4.5.1 Water table depths

Water table depths increased from the channel towards the island center (Figure 4-1). They were deepest during November-December 2012 (low water levels) except in Nxaraga where the water table was deepest during February-April 2013. During November-December 2012 rain events were experienced yet water tables were at their deepest during that time. This could mean that the rainfall was not sufficient to raise the water table as fairly substantial rainfall is necessary to cause a noticeable effect on the water table (McCarthy 2006). The relationship between groundwater depth and SFD was stronger in Seronga during medium water level than during low water level. This implies that when water levels are low transpiration rate also decreases as trees have to invest a lot of energy pulling water from greater depths. This is evident in figure 4-3 whereby groundwater levels were declining on a daily basis and sap flow also declined.

Average depth to groundwater was greatest in Maun and Nxaraga, the seasonally-inundated areas. This result is in agreement with that of Gazal et al. (2006). As explained earlier, they related transpiration to groundwater depth amongst other variables and found that depth to groundwater was greatest at the intermittent stream site than at the perennial stream site.

4.5.2 Diel groundwater fluctuations

An oscillation pattern of high water levels during the early morning and low levels during the late afternoon is characteristic of groundwater fluctuations induced by vegetation (Martinet et al. 2009). Our groundwater fluctuations results showed this pattern (Figure 4-2). During the daylight hours, plants transpire water resulting in water table declines provided significant amounts of groundwater are used. During the night when transpiration slows down or stops, the water table rises as water lost during the day is restored from net inflow (Loheide II, Butler Jr, and Gorelick 2005).

Groundwater fluctuations graphs were somewhat the inverse of the sap flow graphs (Figure 4-3). When sap flow was at its maximum, the groundwater level was at its lowest and when sap flow was minimal groundwater levels were highest. This pattern was repeated throughout the seasons. Butler et al. (2007) investigated phreatophyte-induced fluctuations in the water table along the Arkansas River, Kansas, and found a tight coupling between plant water use and water table response. Groundwater levels increase during night time to the next daily maximum, which is often lower than that of the previous day’s (Mould et al. 2010). This was observed in some of our data (Figure 4-3) and Mould et al. (2010) interpreted that to mean that daily total ET was higher than groundwater recharge. Significant nighttime ET may account for the low recharge as plants continue to pump water from the vadose zone at the same time recharge is taking place.

McDonald (2010) studied hydrologic impacts of saltcedar control along a regulated dry land river, the Pecos River in Texas, and found that transpiration peaked around 1600hrs while the minimum occurred midnight and 0400hrs. Martinet et al. (2009) in their study on groundwater fluctuations along the Rio Grande riparian corridor in central New Mexico found that minimum depth to groundwater occurred before the sun rose, corresponding to a period of the day during which little groundwater consumption occurs. In their study the maximum depth to the water table occurred in the late afternoon. These results are in agreement with results of this study.

Diel groundwater variations, in cm, were highest in Seronga, followed by Nxaraga and lastly Maun. The variations ranged between 4.4 and 8.7 cm. These values are close to those found by Bauer et al. (2004) in their study on estimation of ET rate from diurnal groundwater fluctuations in the perennially flooded eco-region of the Okavango Delta. They found mean fluctuation depths ranging from 3.4-7.5 cm. Our maximum value, 8.7 cm, was calculated in Seronga during high floods. This is comparable to Bauer et al. (2004)'s 7.5 cm. Both these high values were from localities in which total variation in groundwater level on an annual basis is <1 m (McCarthy et al. 2000).

4.5.3 Comparisons between groundwater levels and sap flux density

Regression analysis showed strong exponential relationships between groundwater levels and SFD (r^2 = 0.60 and 0.59) (Figure 4-4), the rate of change of the groundwater level depended on the groundwater depth. McDonald (2010) related groundwater fluctuations to transpiration in the Pecos River, Texas. Contrary to our results, they found that diel fluctuations in groundwater levels were not strongly correlated with transpiration. They attributed that to tree maturity and low tree density. Water use by riparian vegetation is dependent on several factors such as stand density, tree size, width of stand, depth to water table and environmental factors that drive transpiration. The climate in the Pecos River is semiarid and subtropical with an annual precipitation of 330 mm (McDonald 2010). Riparian ET is a minor component of the water budget along the river. The riparian corridor is narrow and dominated by saltcedar (*Tamarix* spp.). Saltcedar in the Pecos River exhibited low transpiration rates because of relatively low tree density, low sapwood area and small aerial extent of the trees as a function of the narrow riparian corridor (McDonald 2010). On the other hand, riparian ET in the Delta constitutes most of the water losses incurred. The Delta receives more rainfall annually than the Pecos River, the riparian area is larger and it is dominated by various riparian trees whose sap flow differs significantly. These might explain the differences in the findings of our study and that of McDonald (2010).

The relationship between SFD and groundwater level was strongest in Maun. This result concurs with that of Gazal et al. (2006). They studied seasonal patterns of cottonwood transpiration from trees located in the perennial site along the San Pedro River and those from a reach with intermittent stream flow. They found that a stronger relationship existed between transpiration and water table depth at the intermittent site, lower rates of transpiration corresponded with greater depth to groundwater.

4.5.4 Plot transpiration

Transpiration from whole trees can be used to estimate transpiration of an entire stand. This can be made possible by taking into consideration the contribution of each tree class in that particular stand (Granier 1987). Transpiration is regulated by an interaction between climatic conditions such as temperature and the physiological and phenological status of plants (Vose et al. 2003). Plot transpiration changed with seasons (Table 4-2), in some areas corresponding to the water table depth. In Seronga however, transpiration was low when water tables were raised which might be a physiological or phenological effect. The soil can become saturated during flooding, creating anoxic conditions. Most plant species respond to anoxic conditions by closing their stomata (Akeroyd et al. 1998). Stomatal closure will result in decreased transpiration rates.

The changes in plot transpiration with season and site from groundwater fluctuations were not statistically different ($P = 0.05$) (Table 4-2) whilst estimates from sap flow were statistically different with season and site as discussed in Chapter 2. When the two methods were compared, there were statistical differences, groundwater fluctuations estimates were almost double those from sap flow (Table 4-2). McDonald (2010) compared their transpiration estimates from sap flow to those from another study that estimated ET using the White method, which was used in this study. They found that the ET estimates were ten times higher than the transpiration estimates during the same time period. They attributed the differences to high rates of soil evaporation and direct evaporation from the stream, which was 40 m away from the riparian zone they studied, as the White method is said to be accurate. In our study, most of the soil from the plots was shaded by the studied trees canopies, eliminating possibilities of high rates of evaporation from the soil. Direct evaporation from the stream would not have also contributed to our high groundwater estimates as our wells were restricted to wooded areas. These might explain why our ET estimates were only twice that of sap flow. The difference may have been made by the understorey grasses as the White method does not only measure water use by trees as is the case with sap flow but measures water loss incurred through both evaporation (be it from soil, open water, grasses or plant parts) and transpiration.

The White method over-estimates stand transpiration even though applied conservatively (McDonald 2010). This was one of the possible reasons brought forward by McDonald (2010) for the ten times difference in their stand transpiration estimates. However, investigations by Bauer et al. (2004) in the Delta showed that the groundwater fluctuations method can be applied to give reasonable estimates of ET provided there are reliable estimates of porosity. The porosity estimate used in this study was from a study by Obakeng and Gieske (1997). The same value was obtained by Bauer et al. (2004). We may therefore conclude that our ET estimates are reasonable.

4.6 Summary and conclusions

Sap flow responded to groundwater levels, decreasing with decreased water levels. When sap flow slowed down during times of low evaporative demand, groundwater recovered. However, there were no significant statistical differences in groundwater plot estimates with season and site. Statistically significant differences were found between estimates from sap flow and groundwater fluctuations. The groundwater approach yielded higher estimates than sap flow probably due to the fact that the former measures both evaporation and transpiration whilst the latter measures only transpiration.

5 CHAPTER 5

Water use by riparian trees in the Okavango Delta

5.1 INTRODUCTION

This study sought to provide quantitative estimates of water fluxes through the major woody riparian species in the Okavango Delta which will in the end allow cross-calibration of ecohydrological models of both the catchment and Delta processes. That is, this study will allow for precise measurements of the water balance of the Delta and the catchment as a whole to be made by amending existing models. Riparian evapotranspiration (ET) is a major component of the water balance for many semi-arid watersheds where ET exceeds precipitation. Accurate estimates of ET are therefore vital to characterize wetland functions and to manage water as a resource in such areas (Scott et al. 2008). The information is also critical in the ecological assessment of impacts of water abstraction on the wetland. However, there is a paucity of information on water use by riparian trees due to high spatial and temporal heterogeneity within the riparian zone (O'Grady et al. 2002; O'Grady et al. 2006).

In the tropical Okavango Delta, transpiration by trees is an important process partly responsible for maintaining the swamp as a fresh water environment rather than saline. All components of the water balance have historically been estimated fairly easily except ET and groundwater outflow whose measurements are difficult. Estimating ET from terrestrial landforms of the Delta, which are fringed by riparian woodlands, is one of the main areas contributing to uncertainty in current hydrologic modeling in the Delta (Cathey 2011). This study set out to find out if there is a difference in water loss rates from different riparian woody species and if transpiration from trees varies with season. The study has also sought to characterize the relationships between soil moisture, air temperature, relative humidity, and groundwater level and transpiration rate. In this chapter, key results will be discussed and conclusions drawn.

5.2 SYNTHESIS

5.2.1 Quantification of water fluxes through the common riparian trees

Mass-balance water budget estimates for the Delta indicate that ET from a variety of plant communities (historically calculated from the remainder term) must constitute a significant fraction of the loss term (Dincer, Child, and Khupe 1987; Ramberg and Wolski 2008). This study provided the first estimates of transpiration from riparian trees in the upper, mid and distal parts of the Delta (Figure 5-1).

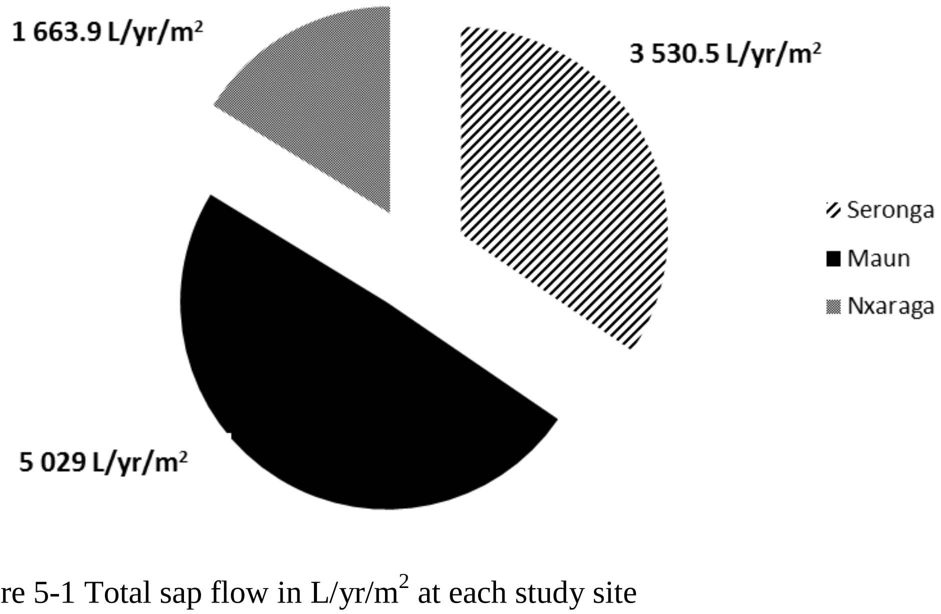


Figure 5-1 Total sap flow in L/yr/m^2 at each study site

Sap flows in L/d/m^2 from three seasons in every site were added to calculate total sap flow. These were multiplied by 365 to give yearly estimates. The total sap flow was highest in the distal Delta and lowest in the upper Delta.

SFD (sap flow/ cross-sectional area) was used to estimate the total sap flow in L/d from each site. Most water effluxes, from the three seasons, were incurred in Maun. Nxaraga exhibited the least sap flow. Basal area was used in the estimates. It was the highest in Maun and lowest in Nxaraga. Riparian tree density tends to decrease downstream of the Delta (Tsheboeng et al., 2014, unpublished). This might mean that basal area would decrease downstream as well, as high plant density has been shown to translate to high basal area. Thinning experiments done by Granier (1987) in a douglas-fir stand in Amance, France, whose climate is temperate showed that thinned plots had lower basal area than un-thinned plots, resulting in higher sap flow rates in un-thinned plots. In this study however, basal area decreased from upper to mid Delta and increased in the distal Delta. Our plot in the distal Delta was denser than the other two. It was situated in an enclosed area which had not been exposed to large herbivores for over two decades. The high basal area in the distal Delta site is from the high tree density unlike in the mid and upper Delta sites where trees compensated for decreased stem density by increasing diameters. Our sap flow results, corroborating those of Granier (1987), showed that sap flow increased with basal area.

5.2.2 Sap flow variations in various riparian trees

Transpiration varied as a function of species, season and site (Table 5-1). Trees that showed the highest sap flow rates in this study tended to have large canopies, deep root systems, large diameters at breast height and large leaves.

Table 5-1 Seasonal variation in SFD from different species

Species	**SFD in different seasons (L/cm^2/day)**		
	July-August 2012	November-December 2012	February-April 2013
Distal Delta			
Diospyros mespiliformis 1	0.488	0.088	0.635
Diospyros mespiliformis 2	0.439	0.417	2.521
Diospyros mespiliformis 3	0.486	0.406	0.607
Diospyros mespiliformis 4	0.611	0.623	2.897
Average	**0.506**	**0.383**	**1.665**
Standard deviation	**0.064**	**0.191**	**1.052**
Mid Delta			
Diospyros mespiliformis	0.787	0.079	0.169
Croton megalobotrys	2.752	0.090	0.108
Kigelia africana	0.094	0.435	0.244
Hyphaene petersiana	0.322	0.077	0.170
Average	**0.989**	**0.170**	**0.173**
Standard deviation	**1.048**	**0.153**	**0.048**
Upper Delta			
Garcinia livingstonei	1.512	0.311	1.337
Philenoptera violacea	0.107	0.224	0.082
Phoenix reclinata	0.098	0.601	0.072
Ekebergia capensis	0.187	2.591	0.168
Average	**0.476**	**0.932**	**0.415**
Standard deviation	**0.599**	**0.968**	**0.534**

Diameter at breast height is directly related to sap wood area (Macfarlane et al. 2010), and as a result, the bigger the diameter the larger the sapwood area resulting in a lot of water transported via the xylem to the atmosphere. This relationship was evident from the study as sap flow was positively correlated with tree size (diameter at breast height) corroborating results from other studies (Vertessy et al. 1995; O'Grady et al. 2006; Teskey and Sheriff 1996). According to the pipe model theory (Shinozaki et al. 1964) the greater the living biomass a tree has the more sapwood area it has and this relationship is species-specific.

Evergreen trees in general showed higher sap flow rates than deciduous except during high water level when *C. megalobotrys* showed the highest sap flow rate taking advantage of the available water. *C. megalobotrys* may be opportunistic in its water uptake by using the water source that requires the least amount of energy expenditure hence the high sap flow exhibited during high water. Evergreens have evolved mechanisms that enable them to cope with differing water levels over the seasons that other species largely avoid (Warren and Adams 2004). They have relatively large root systems ensuring they have access to deep water sources during drought conditions which might explain why they transpired more than the deciduous species. By accessing deep water sources, evergreens are able to avoid competition with more shallow-rooted vegetation occurring with them (Dawson and Ehleringer 1991).

To establish the relationship between sap flow and tree size, cross-sectional area was used as a proxy for tree size. In agreement with results from other studies (Cermak and Nadezhdina 1998; Delzon, Sartore, Granier et al. 2004; Delzon, Sartore, Burlett et al. 2004; Dye, Olbrich, and Poulter 1991), trees with large cross-sectional areas exhibited low sap flux densities. These studies found that sap flow decreased with increasing depth into the sapwood with the declines greater in large trees than 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. However, as mentioned in the preceding paragraph, trees with large diameters conducted more sap than those with small diameters. The increase in sap wood area with increasing tree size compensated for the decrease in SFD.

Contrary to results from David et al. (2004)'s study, results from this study showed higher sap flow rates during winter than summer in Maun and Nxaraga (Table 5-1). Rainfall might have contributed to the observed trend by depressing sap flow due to high relative humidity during the rainfall events as sampling periods, which were short (3 days), coincided with rainy and cloudy days. Groundwater data showed that the water table depressions (drawdown in cm) were smaller during November-December 2012 (the period when it rained) than February-April 2013 (the period when it did not rain). Sap flow was found to be high during high water levels despite assertions by Ringrose (2003) that relatively little water is lost despite the prevalent flood during that time. Ringrose (2003) made this assertion after obtaining low reflectance values from trees in the distal Delta, indicating low available plant moisture. This suggested that sap flow was independent of flood level. Since sap flow seemed to be independent of flood level, 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 (cloud cover) environment. On the other hand, the inference by Ringrose (2003) was made after studying trees in the distal Delta. The flood may have not reached those parts when the study was conducted. 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 as inferred by Ringrose (2003).

Another possible explanation might be the fact that high water levels coincide with winter and though winters are dry and windy temperatures are cooler than in summer hence low evaporative demand. On the other hand summer coincides with low water levels. Though temperatures are higher and day length longer in summer than winter, trees have to draw water from greater depths as groundwater levels are low hence the little drawdowns in groundwater as shown by the groundwater data. Shallow groundwater in the Delta floats on more saline deeper groundwater (McCarthy 2006) and groundwater salinity tends to increase with depth. Scott et al. (2000) studied water use of two dominant vegetation communities in the semi-arid San Pedro River, southeastern Arizona, USA which has a mean maximum temperature of 24.8°C, minimum 9.9°C and mean annual rainfall of 343 mm. They found that water use increased after the recession of flooding and they attributed that to salt leaching. As the water table fell, leaching the salts, water use increased as the plants could use the then available water, saline-free water. This might explain our Seronga results. The trees exhibited high sap flow rates after flooding. On the other hand, Maun and Nxaraga trees showed the least sap flow rates after the flood had passed, that is during the low water level. This might also be explained by salinity. If Delta trees roots reached the saline water during low water levels, that would mean less water available for trees to use hence the low sap flow recorded during low water levels.

Trees also have mechanisms in place to minimize water loss during unfavorable conditions thus low sap flow rates were recorded in the hot summer. When demand exceeds supply plants must regulate their water use either by finding additional water sources or finding other means for conserving water so that their requirements for metabolism or growth are not compromised (Dawson 1993). In a study on mesquite trees, Scott et al. (2000) found that water use by their trees depended more on the energy available than rainfall. 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 and Poole 2004). Therefore, plants need to employ mechanisms to maintain their water balance throughout the seasons especially in arid regions where ET exceeds rainfall. These mechanisms can either be physiological or structural. Physiological control occurs when changes in stomatal conductance (measure of the rate of passage of carbon dioxide or water vapor through the stomata of a leaf) result in changes in water vapor flux from the surface of vegetation (Smith and Jarvis 1998). Temperature is one of the environmental factors that stimulate stomatal opening with an increase in temperature resulting in an increase in the stomatal aperture (Forbes and Watson 1992). There is however a temperature threshold beyond which stomatal aperture cannot increase anymore, and at that point the stomata close to regulate fluxes in the leaf. 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) might indicate that the trees' stomatal conductance decreased, the trees actually closed their stomata as possibly demand exceeded supply to prevent desiccation. When demand for water exceeds uptake from the soil, trees can adjust their stomatal conductances downwards to a point where uptake by the roots will be able to satisfy demand (Smith and Jarvis 1998). 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. Gazal et al. (2006) studied controls on transpiration in a semi-arid riparian cottonwood forest in the San Pedro River, in a perennial and intermittent stream, and found that stomata closed during the dry period in response to high VPD in the intermittent stream. However, in the perennial stream stomatal closure was less apparent. This might explain our results whereby trees in Seronga exhibited high sap flow during the dry (low water level) season.

Structural mechanisms that help regulate water losses in trees include thick, hard leaves, often with few stomata. The stomata in such leaves are normally on the lower side of the leaf. All of our studied trees had leathery, glossy leaves except *Croton megalobotrys*. *C. 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. In arid and semi-arid regions, some trees have their stomata in pits on the leaf surface with water vapor within the depressions high so as to reduce water loss from the plant. Some plants have small leaf sizes whilst others have a waxy, impervious cuticle on their leaves to minimize water loss. In regions where water is limiting, plant leaves must have a relatively high diffusion resistance to water vapor as leaves with low internal diffusion resistance will have a high rate of transpiration (Gates 1968).

5.2.3 Environmental controls on transpiration

Transpiration is not only regulated by the physiological and phenological status of plants but by abiotic factors as well. Hence sap flow was related to air temperature, relative humidity and soil moisture.

Weak correlations existed between sap flow and soil moisture content. These results were in support of results from other studies. Weak relationships between soil moisture and sap flow might be from the fact that the studied trees use water straight from the saturated zone as tracer studies have shown that riparian trees may selectively use deeper groundwater even when shallower groundwater is available (Hayashi and van der Kamp 2007). Dawson and Ehleringer (1991) in their study in Utah showed that trees growing in the riparian zone used little or none of the surface stream water. Using the hydrogen isotopes ratio analyses of water they showed that the most active roots of mature trees were those in deeper soil layers, though their roots were distributed throughout the soil profile. The trees were only dependent on water from the upper soil layers during establishment after which they shifted to the deeper and more constant water source (Dawson and Ehleringer 1991).

Diurnal fluctuations of temperature showed an increase in sap flow with an increase in temperature and a decline in sap flow with a decline in temperature. Increasing temperatures lead to increases in vapor pressure deficit (VPD) which promotes water loss. Kume et al. (2012) in their study on spatial variation in sap flow velocity in semiarid region trees found that daytime VPD was very high on sunny days leading to high water losses. However, overall sap flow was low during summer when temperatures were highest. As discussed earlier, high temperatures coincided with periods of low water levels leading to low sap flow rates. This might mean 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. On the other hand, sap flow increased with decreased relative humidity. An increase in humidity led to a decrease in sap flow which might explain the decreased sap flow that was observed during the rainy season. Meiresonne et al. (1999) studied transpiration from a poplar stand in Flanders, Belgium and found that sap flow rates decreased during rainy events, and remained low for some time after the rainy period. Whole-tree studies of sap flow were conducted in an upland oak forest in Tennessee by Wullschleger et al. (2000). They found that there was a considerable day-to-day variation in transpiration which, they explained, was bounded on one extreme by rainy days and cloudy skies and on the other by sunny days, clear skies and moderate atmospheric humidity deficits. Their estimates of whole-tree transpiration were lower on rainy days than those measured during dry weather conditions. This backs our results where transpiration was higher during winter, which is dry, than rainy summer days.

5.2.4 Relationship between groundwater fluctuations and sap flow

Relationship between sap flow and diel groundwater fluctuations was also explored in this study. Results concurring with those from other studies (Butler et al. 2007; Loheide II, Butler Jr, and

Gorelick 2005; Martinet et al. 2009) showed positive correlations between the two variables. Diel fluctuations in sap flow were correlated with diel fluctuations in static water level. The correlations however, as shown by exponential regressions, were strongest in the distal Delta with an r^2 value of 0.66 during high water level. Due to equipment failure, groundwater measurements could not be made in the mid and upper Delta during medium (mid Delta) and high (upper Delta) water levels. The stronger relationship between transpiration and depth to groundwater found in the distal, drier part of the Delta than the mid and upper Delta was also evident in Gazal et al. (2006)'s study. They related cottonwood transpiration in the San Pedro River to groundwater depth and found that the relationship was stronger in the intermittent stream, which in our case may be represented by Maun (distal site), than the perennial stream.

Lower rates of transpiration corresponded with greater depths to groundwater in both our study and Gazal et al. (2006)'s in the distal and intermittent stream sites. In Seronga, transpiration was highest during low water level when the water table depth was deeper than the high water level. This might have been from the fact that the period of high evaporative demand (summer) coincided with low water tables and the water tables were not too low to limit transpiration. Mean groundwater fluctuations in all the seasons from all the sites were 4.4 – 8.7 cm. These were in the range of those found by Bauer et al. (2004) who estimated ET from diurnal groundwater fluctuations in the Okavango Delta. Their mean fluctuations were 3.4 – 7.5 cm. They did their study on an island which is only an island during high floods (Thata Island). During the time of their study, the surrounding floodplains were mainly dry and the permanent water bodies several kilometers away from the island. If we take this period to correspond to our low water level then the groundwater variations from our study range from 4.4 – 7 cm, with our maximum value closer to the 7.5 cm found by Bauer et al. (2004).

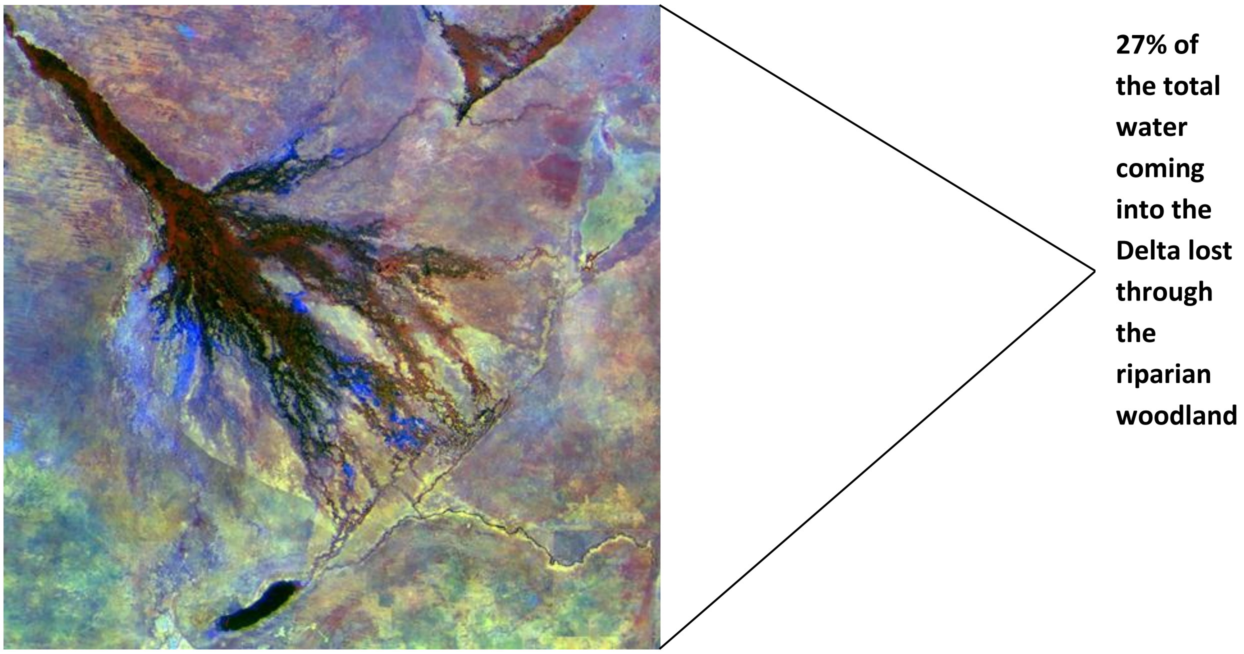
Sap flow and groundwater fluctuations data was used to estimate plot-level transpiration.

Whole-tree transpiration was scaled up to plot transpiration. Plot transpiration responded to the changes in canopy cover, increasing or decreasing with the cover in different seasons. This was however, only evident in Maun and Nxaraga. In Seronga transpiration seemed to have no bearing on canopy cover whatsoever. Plot basal area was used in the up-scaling process. We found that the larger the basal area the more the transpiration rate. Basal area therefore better explained the differences in transpiration in Seronga than canopy cover.

Estimates of plot transpiration from groundwater fluctuations were generally higher than those from sap flow measurements in all the sites throughout the seasons. The differences were statistically different. However, groundwater estimates were not statistically different between sites and seasons. Diurnal groundwater fluctuations estimate both evaporation from the soil and plant surfaces and transpiration from different types of vegetation cover (e.g. grasses and shrubs). They are an integrated response to a group of highly heterogeneous and difficult-to-characterize water stresses at the scale of a number of phreatophytes (Butler et al. 2007). This might explain why the figures were higher than those from sap flow measurements as those only account for water lost from trees via the stomata. Even though the groundwater values were higher than the sap flow, the two data sets showed the same trends with seasons, decreasing and increasing at the same time except in Seronga during low water level. During this period, transpiration from sap flow estimates was higher than in the previous season whilst estimates from groundwater were lower. As water tables are at their lowest during low water levels, the seedlings and grasses which might have contributed to the high estimates during medium floods might have not had access to the groundwater, limited by their rooting depths, hence transpiration rates were lower.

5.2.5 Estimating system-level transpiration

From Landsat imagery, only 7.5% of the active Delta is covered by riparian woodland (Wolski, unpublished data), or 1.19E+09 m^2. This figure is in agreement with that calculated in a field investigation into the mokoro industry in the Okavango Delta (Ecosurv 1988). As discussed in the introduction, about 96% of the hydrological input into the Delta is lost via ET, especially from islands fringed by riparian woodlands. From our plot transpiration estimates, we estimated system-level transpiration, that is, transpiration losses incurred in the whole Delta from the riparian woodland annually.



27% of the total water coming into the Delta lost through the riparian woodland

Figure 5-2 Annual estimated percentage of water losses incurred in the Okavango Delta

To scale up sap flow to system level the following equation was used:

$Q_{system} = SFD_{avearge} \text{ x } BA \text{ x } 365 \text{ x } 1.19E+09$

where Q_{system} is total annual water loss in litres per year (L/yr), $SFD_{average}$ is the average sap flux density in all seasons across sites (L/m^2/day) , BA is the basal area (m^2), 365 is number of days in a year, 1.19E+09 m^2 is total area covered by riparian woodland (m^2).

The L/yr estimates were converted to MCM and the result expressed as a fraction of the total input into the Delta.

The above equation was modified to up-scale groundwater estimates to system-level. $SFD_{average}$ was removed and instead average drawdown and porosity (0.33) were introduced in the equation.

On average, 27% of the total water coming into the Delta is lost via transpiration through the riparian woodland (Fig 5-2). Estimates made in the past estimated the loss from the riparian woodland to be 24% (Wolski 2007). This figure is not far off from what we have found. The discrepancy may be from the fact that transpiration measurements were not made to come up with the 24%, transpiration was just calculated as the remainder term as explained in the introduction. Groundwater estimates indicated that about 57% of the total input is consumed by ET, almost double the sap flow as already discussed.

In trying to understand and accurately predict ET, it is not known how global climate change will affect ET. With temperatures expected to continuously rise with time, global warming, it is unknown if the increases in temperature will significantly increase ET or the carbon dioxide enriched atmosphere would lead to more efficient water use by plants and cause ET to decline (Miller et al. 2010). However, climate change predictions of warmer, drier summers will put pressure on water supplies (Nisbet and Britain 2005). Our results show that sap flow increased with increased temperature, decreased relative humidity (RH) and raised water tables (in the mid and distal Delta). This means that ET will increase with increasing temperatures (as a result of increased VPD and decreased RH) until water is limiting.

Climate change might affect the pattern and temporal distribution of precipitation and thus groundwater recharge (Naumburg et al. 2005). Apart from rainfall-derived recharge, groundwater can be recharged by floods. Flood frequency is taken as being indicative of groundwater recharge hence the absence of flooding infers groundwater table lowering. 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, and Auble 1999). Lowered groundwater levels may lead to a decline in pioneer species (Stromberg, Tiller, and Richter 1996), as riparian vegetation is sensitive to changes in the hydrological regime (Horton, Kolb, and Hart 2001), which might mean 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 and Mahoney 1990). Smith et al. (1991) studied riparian trees along reaches of streams in Sierra Nevada which were subjected to stream diversions. They found that those trees had reduced leaf area, leaf thickness and significantly lower stomatal conductance and midday lead water potentials than similar species along un-diverted reaches.

Changes in the timing of floods may be enough to cause significant environmental change (Nilsson and Berggren 2000). Since climate change might affect the temporal distribution of precipitation, the flooding regime in the Delta might change. Changes in depth to groundwater occur naturally but anthropogenic alterations may exacerbate the fluctuations and consequently affect vegetation reliant on groundwater (Naumburg et al. 2005). 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 can result in water stress as the accessibility of a permanent water source is decreased (Naumburg et al. 2005). On the other hand, deeper water tables increase the soil volume available for storage of precipitation and hydraulically lifted water which can significantly promote plant water use and growth. This might result in a shift from trees that rely primarily on groundwater (obligate phreatophytes) to a community of shallow-rooted trees or those that use both water from the saturated and unsaturated zone (facultative phreatophytes). Obligate phreatophytes may be lost if the water table declines become detrimental giving way to a new community. This would ensure that biodiversity is maintained.

5.2 RECOMMENDATIONS FOR FUTURE RESEARCH

Another study expanding on this one should be done whereby sap flow is monitored for more than three days, maybe a month, because even small changes in the environmental variables seemed to largely influence sap flow. Some variables like soil moisture are significant at longer time scales rather than daily scales. We did not find clear relationships between soil moisture and sap flow, maybe because of the issue of scale or the fact that the trees studied used primarily groundwater. Measuring soil moisture for weeks or even months would rule out the scale issue.

In this study we assume the trees use groundwater because of the general belief that riparian trees utilize groundwater. From the fact that soil moisture was poorly correlated with sap flow we can conclude that it is so, riparian vegetation use groundwater. But it would be interesting to know the exact source of the transpired water, whether it is indeed groundwater, stream water or unsaturated soil moisture and if these sources change with seasons.

5.3 CONCLUSIONS

This study has provided the first quantification of water fluxes through the common riparian woody species of the Okavango whose water does not go to sea but instead the bulk of it is lost to the atmosphere via ET, especially from riparian woodlands. It has therefore provided critical information needed for reducing uncertainty in hydrological modeling of the Delta and given unique insights for evapotranspirative losses in other sub-tropical wetlands. From our results riparian woodlands transpire 27% of the total input in a year. A reduction in total input into the Delta might mean a decrease in transpiration rates which might lead to salinization of water which people, flora and fauna are dependent on. Understanding the hydrological cycle of the Delta will enable the society and policy makers to make sound decisions on maintaining the integrity of the Okavango Delta. Results from this study will be presented to the Department of water affairs to inform them on the total losses from the riparian woodland and their variations with seasons so as to help parameterize hydrological models. The same results will also be presented to the Seronga (one of the study sites) community. Awareness of the role of transpiration by riparian trees on their lives and the integrity of the Delta might make the people of Seronga appreciate the trees more and conserve them.

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