STEM HYDRAULIC ARCHITECTURE AND XYLEM VULNERABILITY TO CAVITATION FOR MIOMBO WOODLANDS CANOPY TREE SPECIES

Royd Vinya

Wolfson College

&

School of Geography and the Environment

Thesis submitted to the University of Oxford in fulfilment of the requirements for the degree of Doctor of Philosophy

Oxford Michaelmas 2010

STEM HYDRAULIC ARCHITECTURE AND XYLEM VULNERABILITY TO CAVITATION FOR MIOMBO WOODLANDS CANOPY TREE SPECIES

Royd Vinya

Michaelmas 2010

ABSTRACT

Africa's miombo woodlands constitute one of the most important dry tropical forests on earth, yet the hydraulic function of these woodlands remains poorly researched. Given the current predictions of increased aridity by the end of this century in the miombo ecoregion, understanding the likely response of miombo woodlands tree species to water stress is crucial in planning adaptation strategies. Predicting the response of miombo woodlands to future climate trends is hampered by a lack of knowledge on the physiology of the common miombo woodlands tree species. In particular, plant-water relations for this woodlands type are not well understood.

An understanding of plant-water relations for this woodlands type will provide insights into how water limits tree species distribution in this ecosystem. This will also improve our prediction model on the likely response of this ecosystem to predicted climate change. For this reason, the overall objective of this research was to evaluate the hydraulic architecture and xylem vulnerability to cavitation for nine principal miombo woodlands tree species differing in drought tolerance ability and habitat preference. This was achieved by; examining the hydraulic properties and evaluating the extent to which each hydraulic design was vulnerable to water stress-induced xylem cavitation; investigating how seasonal changes in plant-water relations influences seasonal patterns of leaf display and; analyzing the relationship between stem hydraulic supply and leaf functional traits related to drought tolerance ability.

This research has found that drought-intolerant tree species with mesic specialization have more efficient stem hydraulic systems than co-occurring habitat broad ranging species. Broad ranging tree species attain wider habitat distribution by adjusting their hydraulic supply in response to changing ecosystem water availability. The finding that hydraulic properties differ significantly between tree species with contrasting habitat preference suggests that tree hydraulic design may have some adaptive ecological role in influencing species habitat preferences in miombo woodlands.

The evaluation of xylem vulnerability to cavitation revealed that mesic specialized tree species were more vulnerable to water stress-induced cavitation than habitat broad ranging tree species. Vulnerability to cavitation in individuals from the same broad-ranging species growing in contrasting habitats showed only marginal and statistically insignificant ($P > 0.05$) differences between wet and dry sites.

In the investigation of the influence of seasonal changes in stem water relations on seasonal leaf display, seasonal rhythms in stem water status were found to exert significant controls on leaf phenology. Mesic specialists had strong stem water controls throughout the year in comparison to broad ranging tree species.

An analysis of the relationship between stem hydraulic supply and leaf functional traits suggests that stem hydraulic supply constrains leaf biomass allocation patterns among miombo tree species. Mesic specialists tend to invest more in leaf longevity than broad ranging tree species.

This thesis has uncovered some interesting relationships between plant-water-relations and the distribution of miombo woodlands tree species. These results lead to the conclusion that in an event of increased ecosystem drying under future climate trends, tree species with mesic

specialisation are at a greater risk of experiencing cavitation related species mortality than broad ranging ones.

ACKNOWLEDGEMENTS

I am very grateful to the following institutions who financially supported this research; Association of Commonwealth Universities, Copperbelt University, Wolfson College, Duff memorial fund, and Environmental Change Institute. I would like to acknowledge the efforts of many people who individually and severally rendered valuable support throughout the duration of this research. Talks with Paul Smith and Jonathan Timberlake from the Royal Botanic Gardens at Kew inspired me to rethink my original hypothesis and refocus on plant-water relations in the miombo woodlands. I held many helpful academic discussions with experienced researchers in Zambia. In this regard, I would like to thank:

Mr Lishomwa Mulongwe, Division of Forest Research, Forestry Department of Zambia

Mr Felix Chileshe, Division of Forest Research, Forestry Department of Zambia

Mr Sichamba Mpande, Division of Forest Research, Forestry Department of Zambia

Dr Jacob Pacific Mwitwa, School of Natural Resources, Copperbelt University

Professor Emmanuel Chidumayo, School of Natural Sciences, University of Zambia

Mr Godwin Muhalu, Zambia Forestry College

My research assistants in Zambia, Milimo Miyoba, Metson Kasowe, Japhet Kabonso, and Kennedy Kayuma played such a pivotal role in ensuring that experiments were done within the set duration. My two supervisors here in the UK, Professor Yadvinder Malhi and Dr Nick Brown were kind enough to mentor me into an independent researcher. Their valuable criticisms and academic inputs greatly helped shape up this thesis. Had it not been for professional contributions from one of the leading plant physiologists, Timothy Brodribb, this study could have turned out to be a mammoth task. Valuable comments from Dr Peter Savill and Dr Katie Parr during the upgrade stage greatly helped to remove some of the potential bottlenecks from the final fieldwork

design. Fellow researchers in the Ecosystem lab provided support and encouragement throughout the duration of this research. In particular I am indebted to Nicholas Babbier, Joshua Fisher, Luis Aragoa, Liana Anderson, and Przemyslaw Zelazowski, who had a direct input into this thesis. Throughout this DPhil, my family provided the much needed social and spiritual support. My lovely wife Judith and our children Emmanuel, David, Enia, Muchafara, and Kundiso were such a great company. My brother Cleopas who was very supportive during some of the most difficult times greatly helped to stabilize my thoughts. Great lord who spared me from going to the grave following a fatal snake bite during field work has always been merciful to my family and me. Indeed he is an awesome God.

Dedicated to my beloved late parents, Mr Emmanuel Vinya and Mrs Enia Vinya

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACRONYMS AND NOTATION

ANOVA	Analysis of variance
A_L	Leaf area (cm^2)
A_S	Sapwood cross-section area (cm^2)
BCI	Barro Colorado Island
D	Mean vessel diameter (µm)
D_H	Hydraulic mean vessel diameter (µm)
D_{95}	Mean vessel diameter accounting for 95% flow (µm)
DMC	Dry matter content ($g\ g^{-1}$)
g:	Gramme
GLM	General linear model
g_s	Stomatal conductance
HV:	Huber value
K_H	Hydraulic conductivity ($kg\ m\ s^{-1}\ MPa^{-1}$)
kg	Kilogram
K_L	Leaf specific conductivity ($kg\ s^{-1}\ MPa^{-1}\ m^{-1}$)
kPa	Kilo Pascal
K_S	Hydraulic specific conductivity ($kg\ s^{-1}MPa^{-1}m^{-1}$)
m	Metre
MPa	Mega Pascal
PLC	Percent loss in conductivity (%)
s	Second
SLA	Specific leaf area ($cm^2\ g^{-1}$)

SPAC	Soil-Plant-Atmosphere continuum
V_D	Vessel density
V_L	Vessel length (m)
Ψ	Water potential (MPa)
Ψ_{50}	Water potential causing 50% loss in hydraulic conductivity (MPa)
Ψpd	Predawn water potential (MPa)

CHAPTER 1

1

GENERAL INTRODUCTION

1.1 MIOMBO ECOSYSTEM

Miombo woodlands are the most widely distributed tropical forest in Africa covering an estimated land surface area of about 270 million ha south of the equator (Chidumayo 1997; Frost 1996). This biome is located within White's (1983) Zambezian phytoregion which is considered to be the largest phytochorion in Africa (Fig. 1.1).

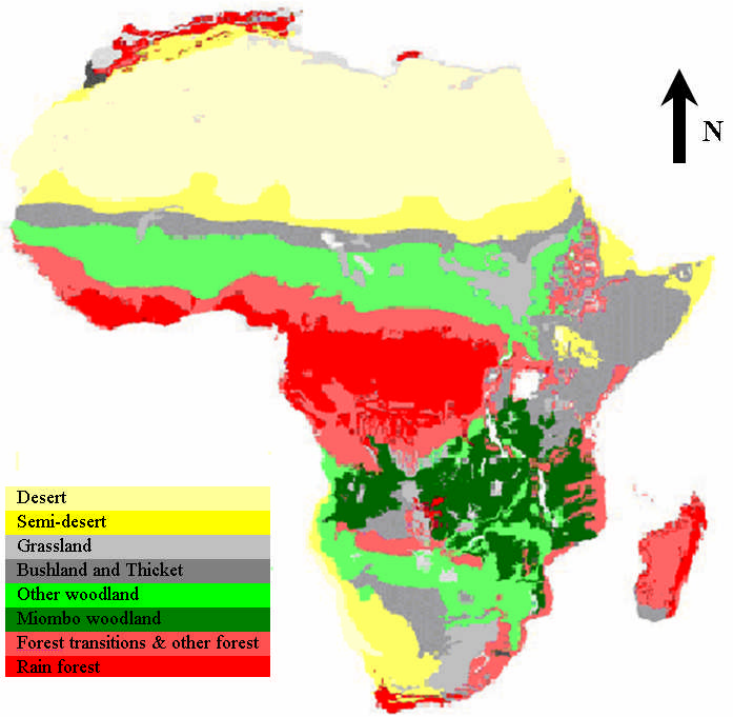


Figure 1.1: White's (1983) original distribution of African ecosystems. Courtesy of http://www.geos.ed.ac.uk/homes/cryan/miombo/

Miombo woodlands form a transitional zone between the semi-arid open savannas and closed rain forests (Lawton 1978). In wet northern regions near the equator, the woodland

develops into exceptionally dry evergreen forests, and southwards towards the Kalahari Desert transforms into dry deciduous forests (Storrs 1979).

1.1.1 Soils

Soils in miombo woodland are shallow, acidic and underlined with a laterite base (Chidumayo, 1997). Most of the soils appear to be primarily derived from the solid geology underlined by metasediments of the Katanga system. There are occurrences of feldspathic sandstones and conglomerates in most of the areas. In wet miombo, the predominant soil types are the Oxisols and Ultisols (Malaisse, 1978). Soils in the wet miombo are characteristically deep, acidic (pH 4-5), and substantially leached. By comparison, the dry miombo forest soils are relatively shallow, with high clay mineral content (2:1) and rich in bases (Kanschik & Becker, 2001). The organic matter concentration for most of miombo woodland soils is exceptionally low (1 and 2 percent for the wet and dry miombo woodlands respectively) (Walker & Desanker, 2004).

1.1.2 Climate

The climate of miombo eco-region is characteristically tropical with a distinct wet and dry season. Summer rains fall between November and April (Boaler 1966; Frost 1996; Jeffers & Boaler 1966). This is followed by an extensive seasonal drought lasting for more than five months (Fig 1.2).

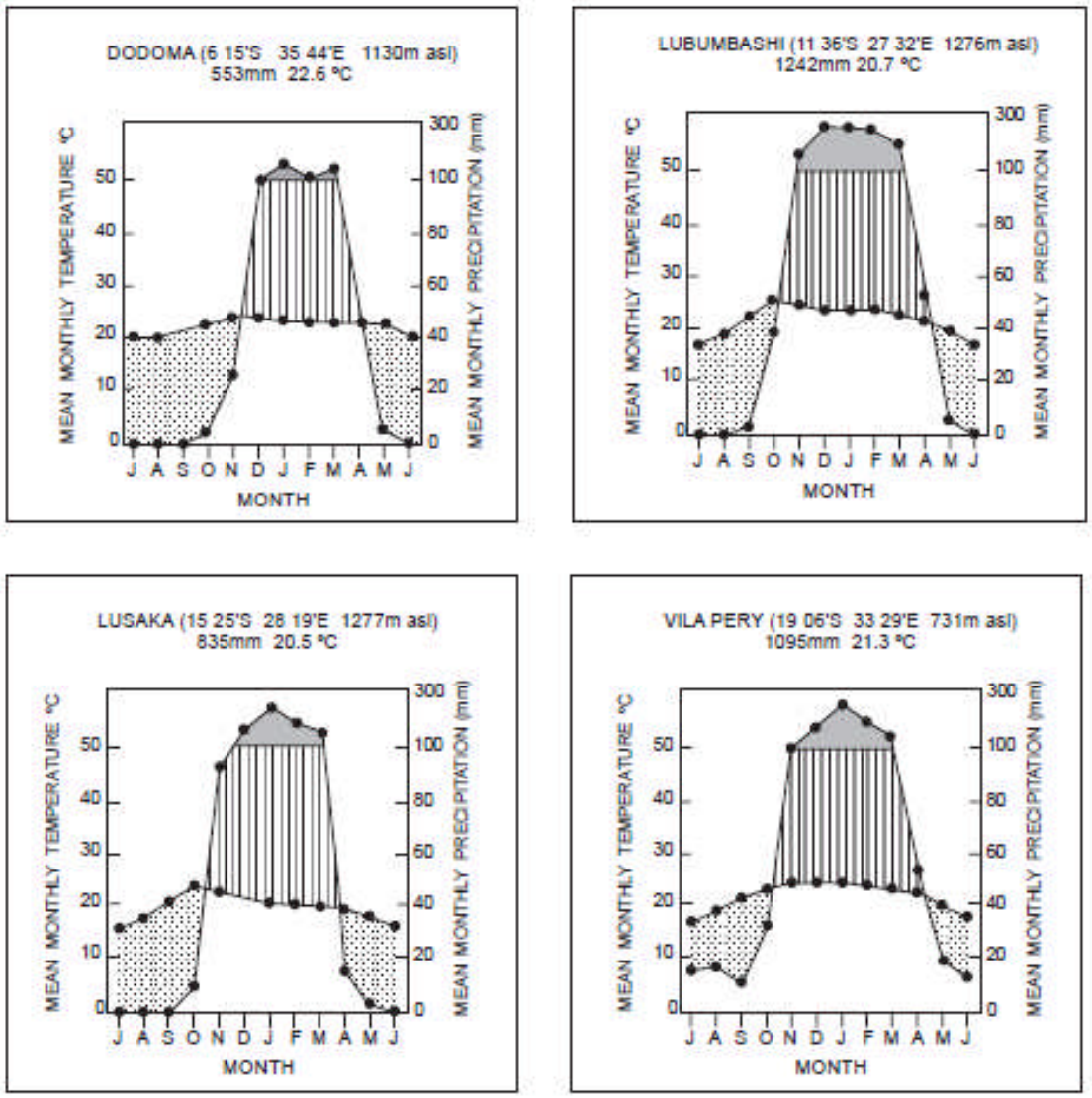


Figure 1.2: Climate diagrams for four localities in miombo ecoregion (Dodoma – Tanzania; Lubumbashi – Democratic Republic of Congo; Lusaka – Zambia; Vilapery – Mozambique). The dotted regions represent dry season; vertical lines are the moist months and the rainy season is indicated by solid shading (after Frost 1996).

Mean annual precipitation varies from 1,200 mm near the equator to less than 600 mm near the tropic of Capricorn (Chidumayo 1997; Frost 1996; Malaisse 1978). The climate of the miombo ecoregion belongs to Köppen's Cw type (Peel, *et al.* 2007).

1.1.3 Vegetation,

The vegetation of miombo woodlands consists of two main layers – an upper tree layer and a lower shrub or herbal layer (Plate 1.1). The canopy is light, above a sparse grass stratum; occasional herbs and suffruticose herbs and shrubs and rarely creepers (Jeffers & Boaler, 1966). Associated with the better developed areas of miombo woodland, there is often patchy thicket, which when dense, transforms the woodland into dry deciduous forest or very exceptionally dry evergreen forest (Lawton, 1978; Malaisse, 1978). Average dominant tree heights range from 8 m in dry miombo, to 24 m on some better quality sites in wet miombo. The height of the understorey shrub layer rarely exceeds half the height of the canopy layer. Miombo woodland is subdivided into wet (occurs in areas that receive above 1000 mm) and dry (found in areas with annual precipitation below 1000 mm) miombo woodlands (Chidumayo, 1987; White, 1983).

Plate 1.1 Typical miombo woodlands a) wet miombo woodlands in Kitwe, northern Zambia b) dry miombo woodlands in Choma, southern Zambia (Photos: R. Vinya)

1.1.4 Tree canopy composition, structure and stand dynamics

The key feature of miombo woodland is the low diversity of the canopy tree species (Frost, 1996). The dominant trees forming much of the canopy in this open two-storied biome are *Brachystegia*, *Julbernardia* and *Isoberlinia* species. In dry miombo woodlands, the dominant canopy tree species are *Brachystegia boehmii*, *Brachystegia spiciformis,* and *Julbernardia globiflora*. The dominant and widely distributed canopy tree species in wet miombo woodlands are *Brachystegia floribunda*, *Brachystegia longifolia*, *Brachystegia wangermeeana*, *Julbernardia paniculata*, *Isoberlinia angolensis*, and *Marquesia macroura* (Chidumayo 1987; Fanshawe, 1971). Wet miombo woodland is distinctly species rich (nearly all the principal miombo woodlands species are present), whereas dry miombo is species impoverished.

Tree density in miombo woodlands varies between 300 and 1400 stems per hectare in undisturbed forests (Backéus, *et al*. 2006; Frost, 1996). At regional level, stand basal area increases proportionally with increasing mean annual precipitation. Average stand basal area ranges from 7 m^2 ha^{-1} in dry miombo to 22 m^2 ha^{-1} in wet miombo woodlands (Frost, 1996). As expected, biomass has also been observed to increase with increasing mean annual precipitation (Grundy, 1995; Malimbwi, *et al*. 1994; Stromgaard, 1985). Reported mean biomass values range from 55 mg ha^{-1} in dry miombo woodlands stands to 155 mg ha^{-1} in wet miombo woodlands (Frost, 1996; Williams, *et al*. 2008). Lawton (1978) describes miombo woodland as climax vegetation, which is constantly maintained by fire and human disturbances (Malaisse, 1978; White, 1983). The dynamics are externally driven by frequent unpredictable rainfalls which continuously upset the dynamics and prevent them from reaching any ecological equilibrium (Frost, 1996).

Much of the functioning of the miombo woodland has been linked to precipitation (White, 1983) although nutrient availability has also been proposed. The capacity of miombo forest to recover from disturbance has been a subject of intense debate in the recent past (Trapnell, 1959; Campbell, *et al*., 1996; Stromgaard, 1986; Frost, 1996; Chidumayo, 1997). However, there is ample evidence suggesting that vegetation succession in this biome is significantly affected by the initial floristic composition (Chidumayo, 1997; Frost, 1996). Unless the original woody plant species have been thoroughly uprooted during the initial disturbance, most of the subsequent development of woodlands derives from re-growth of coppice from surviving stems and rootstocks (Boaler, 1966).

1.1.5 Disturbances

While it is widely acknowledged that climate plays a crucial role in the dynamics of any ecosystem, in recent years human activities have substantially contributed to the altering of miombo woodlands landscape (Campbell, et al. 1996). Livelihood factors such as agricultural production and use of fire have constantly altered miombo woodlands (Chidumayo, 1997). The main direct causes of miombo woodlands modifications include clearing land for agriculture expansion, charcoal production, extraction of construction materials, and fuelwood harvesting all being driven by human population increases (Chidumayo, 2002; Chipika & Kowero, 2000). It is these human and natural driven disturbances that have tended to alter the composition and structure of miombo woodlands.

1.2 WHY STUDY HYDRAULIC ARCHITECTURE AND CAVITATION RESISTANCE FOR MIOMBO WOODLANDS?

A central issue in seasonally dry tropical forests is to understand how water stress structures these ecosystems (Gentry 1998; Murphy & Lugo 1986). Evidence from many water-limited ecosystems suggests that plant response to water stress will depend on hydraulic architecture (Brodribb & Hill 1999; Maseda & Fernãndez 2006; Pockman & Sperry 2000). Given that tree hydraulic architecture imposes considerable restrictions on tree species distribution in water-limited ecosystems (Pockman & Sperry 2000), understanding mechanisms that promote drought tolerance in plants is crucial to explaining mechanisms that control tree species distribution in these ecosystems (Olivares & Medina 1992). Climate change prediction for miombo ecoregion indicates a reduction in annual precipitation by more than 20% by the end of this century (IPCC 2007; Sithole & Murewi 2009). However, this will not be the first time that the Zambezian phytoregion will be experiencing considerable climatic shifts (Scott 1982). Pollen-based vegetation studies have shown that during the last 4,200 years considerable drying resulted in habitat shrinkage for miombo woodlands (Vincens *et al.* 2003). This suggests that miombo woodlands are sensitive to major droughts and drought has serious implications on plant survival under future climate change predictions. There have been attempts in the past to predict the potential impacts of drought-based climate change on miombo tree species using climate envelope models (Desankar & Prentice 1995). While this study, pin pointed which miombo species would experience drought-induced population mortality under climate change, it was remarkably silent on the actual mechanisms of action by which water limitation will impact miombo species. At present,

development of an evidence-based climate-change adaptation plan is hampered by insufficient knowledge about plant-water relations for miombo principal trees.

The importance of water as a growth-limiting factor is evident in miombo ecosystems. For example, the proportion of deciduous tree species increases with increasing aridity southwards away from the equator, suggesting precipitation may be the key factor structuring this ecosystem relative to other factors such as fire (Bond *et al*. 2005; Lawton 1978; Trapnell 1959), geomorphology (Cole 1963), fauna (Guy 1989; Scholes 1993) and anthropogenic disturbances (Gillespie *et al*. 2000). Out of these four factors, fire and anthropogenic disturbances have received more attention than the other two. Lawton (1978) concluded that "the vegetation in miombo woodlands on any one site at any one time depends more on its history of burning than on any other single factor, e.g. any direct effect of climatic or edaphic variables". However, White (1983) and Chidumayo (1997) have both observed a steady reduction in tree species richness with increasing ecosystem aridity, suggesting that there is a climatic influence. The onset of a long seasonal dry spell coincides with significant reductions in canopy cover, again suggesting the importance of water in structuring this ecosystem. Although leaf shedding is strongly correlated with ecosystem water availability, leaf emergence is poorly correlated. Miombo trees flush leaves at the height of the dry season when ecosystem water is most limiting suggesting other factors other stem water status drive this phenophase (Chidumayo 2001). Jeffers and Boaler (1966) attributed dry season leaf flush for miombo tree species to access to deep soil moisture reserves built up during the previous rainy season. On the contrary, Chidumayo (2001) believes that the interaction between minimum and maximum temperatures, determines patterns of leaf phenology in

miombo woodlands. However, the extent to which xylem long distance water transport regulate patterns of leaf phenology in miombo woodlands remains poorly understood. Although many authors have acknowledged the importance of water in structuring miombo woodlands (Chidumayo 1987; Scholes & Walker 1993; White 1983), we know remarkably little about plant-water relations for miombo tree species. Questions regarding the physiology and ecophysiological responses of miombo woodlands tree species to water stress and the extent to which this determines species niche specialisation remain unanswered. Therefore, this thesis focuses on the existing knowledge gap on plant-water relations in miombo woodlands by examining hydraulic properties, xylem vulnerability to cavitation, leaf phenology as it relates to seasonal changes in plant-water relations, and the extent to which branch hydraulics scale with leaf functional traits. In this study, we ask the following principal questions with reference to miombo woodlands:

1. Do differences in ecological niche with respect to species drought-tolerance and to observed patterns of leaf phenology correspond to differences in hydraulic architecture and xylem structure among miombo woodlands' principal trees?
    a. To what extent are the perceived differences in hydraulic architecture, driven by differences in conduit structural dimensions?
    b. Do miombo tree species, which extend over wide ecological amplitudes, show greater plasticity in hydraulic properties and xylem anatomy?
2. Do miombo woodlands' tree species differing in niche specialization show significant variation in xylem cavitation resistance?

   a. To what extent is cavitation resistance coordinated with hydraulic efficiency and is there a functional relationship between conduit size and xylem cavitation vulnerability among miombo tree species?
   b. Do tree species occupying contrasting habitats show plasticity in cavitation resistance and xylem structure?

3. Are seasonal changes in leaf display in miombo woodlands, functionally coordinated with temporal changes in xylem transport?
   a. To what extent do tree species differing in drought tolerance ability differ in native embolism?
   b. Are there significant differences in water potential threshold that triggers leaf shedding and flushing for miombo tree species differing in drought-tolerance?
4. Are branch hydraulic properties strongly coordinated with leaf functional traits associated with drought tolerance ability?
   a. How do stem hydraulic properties and leaf functional traits vary between wet and dry miombo woodlands sites?
   b. How much of this variation is caused by plasticity in wide-ranging species and how much is caused by community turnover?

1.3 RESEARCH OBJECTIVES

The primary goal of this research was to quantify and evaluate the hydraulic properties, xylem cavitation resistance, seasonal changes in hydraulic properties, and leaf functional traits associated with plant drought tolerance. These hydraulic and leaf functional traits

were analyzed in relation to tree species habitat preference in miombo woodlands in order to better our understanding of the mechanisms of action by which water availability structures miombo woodlands. The specific objectives of this thesis were to:

1. Quantify and evaluate the hydraulic properties of miombo woodlands canopy tree species differing in habitat preference and phenology.
2. Examine xylem vulnerability to cavitation for miombo woodlands canopy tree species differing in drought tolerance.
3. Investigate the extent to which seasonal changes in xylem hydraulic properties influence seasonal changes in leaf phenology.
4. Evaluate the relationship between hydraulic properties and leaf functional traits related to plant drought tolerance capability.

In this thesis, I studied the hydraulic architecture and xylem vulnerability to cavitation in miombo woodlands using two gazetted forest reserves in Zambia. This study combines intensive field-based measurements and laboratory experimentation on hydraulic architecture, seasonal changes in leaf display, and leaf functional traits. We selected nine principal miombo woodlands tree species differing in habitat preference and phenology. Four of the nine tree species have a restricted habitat distribution (found only in wetter, mesic sites) [*Brachystegia floribunda* Benth (Fabaceae), *Isoberlinia angolensis* (Benth.)Hoyle & Brenan (Fabaceae), *Julbernardia paniculata* (Benth.)Troupin (Fabaceae), and *Marquesia macroura* Gilg (Dipterocarpaceae)]. These narrow habitat range species range from evergreen to semi-evergreen. The other five are wide ranging (found both in drier and wetter sites) [*Brachystegia boehmii* Benth (Fabaceae), *Brachystegia longifolia* Benth (Fabaceae), *Brachystegia spiciformis* Benth (Fabaceae),

Erythrophleum africanum (Benth.) Harms (fabaceae), and *Pericopsis angolensis* (Baker) Meeuwen (Fabaceae)]. The wide habitat ranging species are fully drought-deciduous. Throughout this thesis, narrow-ranging species are referred to as mesic specialists and wide-ranging species as generalists.

1.4 THESIS OVERVIEW

This thesis is split into seven chapters. The four core chapters are presented in the form of self-contained journal articles, and have all been submitted for peer review. The citation format for the four key chapters follows the standards of the journals to which they have been submitted.

1.4.1 Chapter 1

This chapter has introduced the aims and objectives of this thesis.

1.4.2 Chapter 2

The state of knowledge of key themes in relation to the main objectives of this thesis is reviewed in Chapter 2. Some background on the theoretical and empirical context of this thesis is presented in this chapter.

1.4.3 Chapter 3

Chapter 3 presents a general description of the hydraulic properties and xylem anatomy for the miombo species in this study. The response of these physiological traits to changes in ecosystem water stress is also compared. This chapter has been submitted as a journal article to Tree Physiology.

1.4.4 Chapter 4

In Chapter 4, cavitation vulnerability is investigated and compared across miombo species differing in habitat preference. Some of the hydraulic data in Chapter 3 are combined with cavitation data to examine the trade-off between xylem efficiency and safety. Also the relationship between cavitation resistance and xylem anatomy is examined. This chapter has been submitted as a paper to Plant, Cell and Environment.

1.4.5 Chapter 5

Chapter 5 explores the relationship between seasonal changes in stem water relations and patterns of leaf display in miombo woodlands. This Chapter combines some of the cavitation data to analyze the hydraulic safety margins under field conditions for miombo species. This chapter has been submitted as a paper to Journal of Vegetation Science.

1.4.6 Chapter 6

In Chapter 6, the functional relationship between branch hydraulics and leaf functional traits related to drought tolerance in plants is investigated. This Chapter combines data from Chapters 3 and 4. This chapter has been submitted as a paper to Acta Physiologiae Plantarum.

1.4.7 Chapter 7

Although each Chapter ends with a conclusion, an attempt is made to present some significant findings from this research coherently and put them in the context of theories presented in Chapter 2.

1.5 REFERENCES

Backéus, I., Pettersson, B., Strömquist, L., & Ruffo, C. (2006). Tree Communities and Structural Dynamics in Miombo (*Brachystergia-Julbernardia*) Woodland, Tanzania. *Forest Ecology and Management*, **230**: 171-178.

Boaler, S. B. 1966. Ecology of a miombo site, Lupa north forest reserve, Tanzania: II. plant communities and seasonal variation in the vegetation. *Journal of Ecology* **54**: 465-479.

Bond, W. J., Woodward, F. I., & Midgley, G. F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**: 525-538.

Brodribb, J. T., & Hill, R. S. 1999. The importance of xylem constraints in the distribution of conifer species. *New Phytologist*, **143**: 365-372.

Campbell, B., Frost, P., & Byron, N. 1996. Miombo woodlands and their use: Overview and key issues. In: Campbell B (Ed.), *The Miombo in transition: Woodlands and welfare in Africa*. CIFOR. Bogor: pp. 1-10

Chidumayo, E. N. 1987. Species Structure in zambian miombo woodland. *Journal of Applied Ecology* **3**: 109-118.

Chidumayo, E. N. 1997. *Miombo Ecology and Management: An Introduction*. Stockholm: Stockholm Environment Institute.

Chidumayo, E. N. 2001. Climate and phenology of savanna vegetation in southern Africa. *Journal of Vegetation Science*, **12**: 347-354.

Chidumayo, E. N. 2002. Changes in miombo woodland structure under different land tenure and use systems in central Zambia. *Journal of Biogeography*, **29**: 1619-1626.

Chipika, J. T., & Kowero, G. 2000. Deforestation of woodlands in communal areas of Zimbabwe: is it due to agricultural policies? *Agriculture, Ecosystems and Environment*, **79:** 175–185.

Cole, M. M. 1963. Vegetation and geomorphology in northern Rhodesia: an aspect of the distribution of the savanna of central Africa. *Geographical Journal* **129**: 290-305.

Desankar, V. P. & Prentice, C. 1995. Modelling vegetation dynamics of miombo woodlands of Zambezian Africa under changing climatic conditions. In: Pemetta, J.C. et al. eds. *Impacts of climate change on ecosystems and species: Terrestrial ecosystems*. IUCN, Gland, pp 23-38.

Fanshawe, D. B. 1971. *The Vegetation of Zambia*. Lusaka: Government Printers.

Frost, P. 1996. The Ecology of Miombo Woodlands. In: Campbell, B. ed. *The Miombo in Transition: Woodlands and Welfare in Africa*. CIFOR, Bogor, pp 11-57.

Gentry, A. H. 1998. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* **75**: 1-34.

Gillespie, T. W., Grijalva, A., & Farris, C. N. 2000. Diversity, composition, and structure of tropical dry forest in central America. *Plant Ecology* **147**: 37-47.

Grundy, M. I. 1995. Wood biomass estimation in dry miombo woodland in Zimbabwe. *Forest Ecology and Management* **72**: 109-117.

Guy, P. R. 1989. The influence of elephants and fire on a *Brachystergia-Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology* **54**: 215-226.

IPCC 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, 976 p.

Jeffers, J. N. R. & Boaler, S. B. 1966. Ecology of a miombo site, Lupa north forest reserve, Tanzania: I. weather and plant growth. *Journal of Ecology* **54**: 447-463.

Kanschik, W., & Becker, B. 2001. Dry miombo - ecology of its major plant species and their potential use as bio-indicators. *Plant Ecology,* **155:** 139-146.

Lawton, R. M. 1978. A study of the dynamic ecology of Zambian vegetation. *Journal of Ecology* **66**: 175-198.

Malaisse, F. 1978. The Miombo Ecosystem. In: UNESCO ed. *Tropical Forest Ecosystems: A State-of-knowledge report prepared by UNESCO/ UNEP/ FAO*. UNESCO, Paris, pp. 589-606.

Malimbwi, R. E., Solberg, B., & Luoga, E. 1994. Estimation of biomass and volume in miombo woodland at Kitulangalo Forest Reserve, Tanzania. *Journal of Tropical Forest Science,* **7**: 230-242.

Maseda, P. H., & Fernandez, R. J. (2006). Stay wet or else: Three ways in which plants can adjust hydraulically to their environment. *Journal of Experimental Botany, **57***: 3963-3977.

Murphy, P. G. & Lugo, A. E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* **17**: 67-88.

Olivares, E. & Medina, E. 1992. Water and nutrient relations of woody perennials from tropical dry forests. *Journal of Vegetation Science* **3:** 383-392.

Peel, M. C, Finlayson, B. L & McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrological and Earth System Sciences* **11**: 1633-1644.

Pockman, W. T. & Sperry, J. S. 2000. Vulnerability to xylem cavitation and the distribution of sonoran desert vegetation. *American Journal of Botany* **87**: 1287-1299.

Scholes, R. J. & Walker, B. H. 1993. *An African Savanna: Synthesis of the Nysvley Study*.: Cambridge University Press, Cambridge, 306 p.

Scott, L. (1982). A Late Quaternary Pollen Record from the Transvaal Bushveld, South Africa. *Quaternary Research* **17**: 339-370.

Sithole, A. & Murewi, F. J. C. 2009. Climate variability and change over southern Africa: Impacts and challenges. *African Journal of Ecology* **47**: 17-20.

Storrs, A. E. G. 1979. *Know your Trees: Some Common Trees of Zambia*. Ndola: Forest Department.

Stromgaard, P. 1985. Biomass estimation equations for miombo woodland, Zambia. *Agroforestry Systems*, **3**: 3-13.

Trapnell, C. G. 1959. Ecological results of woodland and burning experiments in Northern Rhodesia. *Journal of Ecology* **47**: 129-168.

Vincens, A., Williamson, D., Thevenon, F., Taieb, M., Buchet, G., Decobert, M., Thouveny, N. 2003. Pollen-based vegetation changes in southern Tanzania during the last 4200 years: climate change and/or human impact. *Palaeogeography, Palaeoclimatology, Palaeoecology* **198**: 321-334.

Walker, M. S., & Desanker, V. P. 2004. The impact of land use on soil carbon in miombo woodlands of Malawi. *Forest Ecology and Management*, **203**, 345-360.

Williams, M., Ryan, C. M., Rees, R. M., Sambane, E., Fernarndo, J., & Grace, J. 2008. Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique. *Forest Ecology and Management* **254**: 145–155

White, F. 1983. *The vegetation of Africa : a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. Unesco, Paris. 356 p.

CHAPTER 2

LITERATURE REVIEW

2

LITERATURE REVIEW

2.1 INTRODUCTION

Seasonally dry tropical forests present some of the most stressful environments in which plant growth and distribution are limited by precipitation (Murphy & Lugo, 1986). There is sufficient evidence from a number of studies linking precipitation to species distribution in these ecosystems (Burke, 2006; Condit, 1998; R. Condit, *et al*, 2004; Condit, Hubbell, & Foster, 1996; Engelbrecht, *et al*, 2006, 2007; Lewis, *et al.* 2004; Merbold *et al*., 2009; Okitsu, 2005; Slot, 2007; Williams, *et al*, 1996). Dry season duration and severe drought appear to be the primary factors limiting species ecological ranges in water-limited ecosystems (Condit, 1998; Condit *et al*., 2004; Gentry, 1998; Scholes & Walker, 1993). A common cause of tree mortality in tropical ecosystems is water stress (Engelbrecht *et al*., 2006). Years of severe droughts have always been characterised by death of the drought-intolerant tree species (Philips *et al.* 2009). The consistence in the reduction in species diversity (Chidumayo, 1987) and an increase in the proportion of deciduous tree species with increasing aridity (Murphy & Lugo, 1986) confirms that water stress is the primary factor structuring tropical ecosystems.

There is growing evidence showing that water stress imposes considerable restrictions on xylem transport (Sperry & Tyree, 1988; Tyree & Sperry, 1989; Tyree & Zimmermann, 2002). Water stress-induced xylem hydraulic limitation has the potential to limit major plant physiological processes such as photosynthesis (Brodribb & Field, 2000; Brodribb, *et al.* 2002; Mencuccini, 2003). Biomechanical processes of leaf

shedding have been linked to water stress-induced hydraulic limitations (Brodribb & Holbrook, 2003, 2006; Sperry, *et al.* 2002; Tyree, *et al*. 1993). However, bud break and eventual leaf emergence is in most cases poorly correlated with ecosystem water availability (Chidumayo, 2001).

On the basis of these studies it would appear that the mechanism of action of how water stress shapes tropical ecosystems may be the limitations it imposes on the xylem long distance water transport pathway. Therefore, studying plant-water relations for tropical ecosystems in relation to species habitat preference would add more insight into how these ecosystems will respond to future climate trends particularly in areas where a reduction in precipitation has been predicted (IPCC, 2007). Although plant water relations have been studied for a number of tropical forests, seasonally dry tropical forests remain the least studied in this aspect. Specifically, tropical forests in Africa have not received as much attention as their counterparts in Australia, Asia, and America.

In this review I examine tree hydraulic properties, and xylem vulnerability to cavitation, in relation to species habitat selection in water-limited ecosystems. The functional relationship between leaf phenology and temporal changes in xylem long distance water transport pathway is reviewed. I also review the possible functional coordination between xylem transport properties and leaf morphological traits linked to water stress management in water limited ecosystems.

2.2 HYDRAULIC ARCHITECTURE AND SPECIES NICHE SPECIALISATION

These are parameters that quantify some aspects of hydraulic architecture: (a) hydraulic conductivity (K_H – kg s^{-1} MPa^{-1} m), which measures the xylem capacity to conduct water; (b) stem-area specific hydraulic conductivity (K_S – kg s^{-1} $m^{-1}MPa^{-1}$), defines the porosity

of the xylem conduits and is derived by dividing K_H with the conducting sapwood cross-section area; (c) Huber value (*HV*- cm^2 cm^{-2}) is the sapwood cross-section area per unit leaf area supplied by the stem (cm^2/ cm^2), and; (d) leaf specific hydraulic conductivity (K_L – kg $s^{-1}MPa^{-1}m^{-1}$) defines the sufficiency with which the xylem supplies its aerial parts (mathematically K_L is a product of *HV* x K_S) (Tyree & Ewers, 1991). Hydraulic architecture plays a crucial role in plant's ecological adaptive strategy (Brodribb & Hill 1999; Engelbrecht, *et al* 2000; Mencuccini 2003). Several authors have presented the adaptive response of tree hydraulic architecture to ecosystem water availability (Engelbrecht, *et al*. 2000; Jacobsen *et al*. 2007; Preston & Ackerly, 2003; Tissier *et al*. 2004; van der Willigen, *et al.* 2000).

Engelbrecht *et al*. (2000) investigated hydraulic properties for two neo-tropical tree species differing in habitat preference. They reported higher stem area hydraulic conductivity and leaf specific conductivity in tree species adapted to mesic habitat than tree species with an arid habitat adaptation. Similar findings have also been reported by van der Willigen *et al*. (2000) who compared the hydraulic properties of tropical trees coming from contrasting habitats. Tyree & Ewers (1991) describe differences in plant hydraulic properties as an adaptation meant to enhance species' fitness under a given set of biophysical environment. In general, some species are better adapted to water stressed environments, while others show a strong adaptation for wetter habitats (Tyree & Zimmermann, 2002).

While a number of studies have reported high conductivities in plants growing in mesic than arid habitats, there are also studies that have reported the opposite (Cornwell *et al*. 2007; Maherali & Delucia 2000). Cornwell *et al*. (2007) examined hydraulic

properties of Hawaiian *Metrosideros polymorpha* coming from contrasting habitats. They observed trees at the dry sites displayed higher K_L and K_S values than trees at the wet sites. They attributed increase in K_L to significant adjustments in leaf area to sapwood area. Although these studies seem to have generated contradictory findings, they highlight the importance of inter-species analyses as opposed to community-wide comparisons.

In addition to habitat differences, hydraulic properties have also been demonstrated to occur along the lines of leaf phenology (Choat *et al*. 2005; Goldstein, *et al*. 1989; Machado & Tyree, 1994). Goldstein *et al*. (1989) investigated water relations of evergreen and deciduous-tropical savanna trees. They reported higher hydraulic efficiency among evergreen than deciduous species. Goldstein *et al*. (1989) reasoned that the relatively high hydraulic conductance among evergreen species was designed to buffer the high-evaporative demands prevalent in tropical ecosystems. From the functional point of view, high leaf specific conductivity enables plants to sustain high evaporative demands and thus permits high stomatal conductance (Tyree *et al*. 1991). In general the adaptive significance of high hydraulic conductance is to maintain a long-term positive plant carbon balance (Mencuccini 2003). Similar findings have been reported by Machado & Tyree (1994) who compared the water-relations of two tropical trees differing in leaf phenology. However, a recent study from north eastern Australia by Choat *et al*. (2005) reported higher specific hydraulic conductivity and leaf specific conductivity (LSC) among deciduous than evergreen tree species. Villar-Salvador *et al*. (1997) investigated differences in stem hydraulic features in three *Quercus* species on a

climatic gradient in Spain. They also reported higher hydraulic conductivities for deciduous species than evergreen tree species.

While differences in methodological approaches may account for much of the seemingly contradictory observations, it is clear that there is no simple correlation between ecosystem water availability and plant hydraulic characteristics. Therefore, the extent to which stem hydraulic architecture is an important factor influencing the distribution of tree species in water-limited ecosystems remains ambiguous. Furthermore, although tree hydraulic properties have been analyzed for many tropical forest trees, most of these studies have come from Neotropical forests and less has emerged from seasonally dry tropical forests. In particular, there are no known studies that have comprehensively analysed the distribution of miombo woodlands tree species in relation to tree hydraulic architecture, making this study the first of its kind to quantify and evaluate the hydraulic properties of miombo trees differing in leaf phenology and niche specialisation.

2.3 CAVITATION RESISTANCE AND SPECIES DROUGHT TOLERANCE ABILITY

According to the cohesion-tension theory, evaporating water at sub-stomatal level generates a large negative hydrostatic pressure (tension) which pulls up long water columns in the xylem. The large negative hydrostatic pressure is supported by the cohesive properties of water (Hopkins & Huner, 1995; Taiz & Zeiger, 1998). The continuous water column from the soil through the plant out to the atmosphere is known as the soil-plant-atmosphere continuum (SPAC). Therefore, the driving force behind water movement in the xylem is the transpiration-pull and water moves from the soil to

the atmosphere in response to water potential difference (bulk flow). Transporting water through the xylem under tension creates potential problems for the plant. Because water is transported under high tension, it is always in a physically metastable condition and this predisposes the xylem to air entry in a process known as cavitation (Zimmerman 1983). Cavitation is the rapid phase change by xylem water under tension from liquid to vapour thereby breaking the SPAC. There is sufficient evidence indicating that air entry into the xylem compromises the integrity of the xylem (Sperry & Tyree, 1988; Tyree & Sperry, 1989; Tyree & Zimmermann, 2002; Tyree & Ewers, 1991; Zimmermann, 1983). As the xylem tension increases, the probability of an air bubble being drawn into the xylem via the microscopic pores in the xylem cell wall increases (Zimmermann, 1983). This phenomenon is known as air-seeding. Therefore, the stability of xylem water under high tension is dependent upon the exclusion of air bubbles of a critical size from the xylem conduits (Zimmermann, 1983; Zimmermann *et al*., 2004)). Ability to withstand cavitation has often been linked to plant drought tolerance ability.

The water potential causing 50% (Ψ_{50}) reduction in hydraulic conductivity has often been taken as an index representing plant drought-tolerance capability (Martinez-Vilalta, *et al.* 2002; Sperry & Saliendra, 1994; Tyree & Sperry, 1989). Therefore, high cavitation resistance implies high-drought tolerance. Many studies have demonstrated that plants coming from arid environments tend to be more resistant to cavitation than those coming from wet habitats (Brodribb & Hill, 1999; Jacobsen, *et al*., 2007; Lopez *et al.* 2005; van der Willigen, *et al*., 2000). Van der Willigen *et al*. (2000) investigated xylem hydraulic characteristics of sub tropical tree species with contrasting habitat preference. They reported higher cavitation resistance for tree species coming from a dry

habitat than those from a riparian habitat. While examining the role of xylem constraints on the distribution of conifer species, Brodribb and Hill (1999), found species from wet forests to be more vulnerable to cavitation than those from arid ecosystems. Jacobsen *et al* (2007) compared cavitation resistance among three arid Californian plant communities. The less arid chaparral community were remarkably more resistant than the more arid Mojave community.

Differences in cavitation vulnerability have also been reported to vary considerably between evergreen and deciduous tree species (Bucci *et al*. 2004). Choat *et al*. (2005) investigated hydraulic architecture of deciduous and evergreen tree species from North-Eastern Australia. The findings of this study demonstrated that, evergreen tree species were more resistant to xylem cavitation than deciduous ones. They attributed the low-cavitation resistance in deciduous trees to low wood density.

From an ecological point of view, cavitation resistance may be one of the decisive factors influencing tree species habitat preference in water-limited ecosystems (Maseda & Fernandez, 2006; Swift, *et al.* 2008). The distribution of the Sonoran desert vegetation in North America, highlights the major restrictions that water stress exerts on species niche specialisation (Pockman & Sperry, 2000). The functional dependence of plant drought tolerance ability on xylem cavitation resistance has also been demonstrated by Lopez et al. (2005) who investigated cavitation vulnerability for tropical trees and shrubs in central Panama. Using a large data set comprising of 167 species, Maherali, *et al.* (2004) observed xylem cavitation resistance to increase in the direction of increasing ecosystem aridity.

One of the principal reasons attributed to these observed significant variations in xylem vulnerability to cavitation is the proposed evolutionary trade-off between hydraulic efficiency and xylem safety in terrestrial plants (Tyree & Zimmermann, 2002). Evidence of this trade-off has been reported in a number of studies (Lovisolo & Schubert, 1998; Martinez-Vilalta, *et al*., 2002; Pockman & Sperry, 2000; Sperry & Saliendra, 1994). The potential for large trade-off between hydraulic efficiency and safety increases with increasing conduit diameter. Because wider conduits are hydraulically more efficient than narrow ones, the origins of cavitation have controversially been linked to conduit size (Hacke, *et al.* 2000). However, evidence has been growing in support of the air-seeding hypothesis suggesting that the origins of water stress induced xylem cavitation lies at pit pore diameter level and not conduit diameter (Domec, *et al.*, 2006; Lewis, 1988; Wheeler, *et al*., 2005; Zimmermann, 1983). It is, therefore, not surprising that the trade-off between hydraulic efficiency and xylem security has failed to materialise in other studies (Brodribb & Hill, 1999; Froux, *et al*. 2005).

Regardless of the conclusions from these studies, the relationship between hydraulic efficiency and xylem safety appear to have both physiological and ecological relevance in water-limited ecosystems. Despite what appears to be a general acceptance of the correlation between cavitation resistance and species habitat preference, there are scanty studies coming from seasonally dry tropical forests. For some ecosystems such as miombo forests in southern Africa, there is no empirical data on xylem cavitation vulnerability, making this thesis the first of its kind to provide such data. The relationship between cavitation resistance and hydraulic efficiency is critically analyzed in relation to species habitat preference in Chapter IV.

2.4 LEAF PHENOLOGY AND WATER STRESS

The intensity and severity of seasonal droughts in tropical ecosystems necessitates a number of adaptive responses to mitigate its potential impact. Among many strategies deciduousness is of adaptive significance in water-limited ecosystems (Murphy & Lugo, 1986; Williams, *et al*. 1997). Although precipitation is one of the key drivers influencing seasonal patterns of leaf display in water-limited ecosystems, the interaction between water stress and leaf phenology is poorly understood (Holbrook, *et al.* 1995). Available evidence suggests that patterns of leaf display are strongly regulated by plant xylem transport (Brodribb & Holbrook, 2003; Tyree, *et al*., 1993). Zimmermann's (1983) segmentation theory proposes that, in times of water stress, plants will forfeit the most marginal and less-expensive-to-replace aerial organs (leaves and twigs) in order to protect the most expensive down-stream organs (branches, stems, roots). Tyree and Ewers (1991) proposed the vulnerability segmentation hypothesis. According to the vulnerability-segmentation hypothesis, the plant organs that are more vulnerable to cavitation are the peripheral ones (leaves) and are, therefore, expected to cavitate at less negative xylem tensions than the downstream organs.

Many studies have provided ample evidence in support of these theories (Lo Gullo, *et al*. 2004; Tyree, *et al*., 1993; Tyree & Sperry, 1988). Tyree *et al*. (1993) demonstrated in walnut trees that prior to leaf shedding, petioles had lost close to 87% of conductance compared to 14% lost by stems. The concept of runaway embolism proposes that a pattern of shedding less costly and easy to replace distal organs is closely related to species xylem pressure (Tyree & Sperry 1988). The line of reasoning of this idea is that plants drop the expendable distal organs at times of water stress. They then remain

leafless until such a time that plant water balance attains a favourable level. From a physiological point of view, leaf area adjustment is a fundamental process that enhances plant fitness in water-limited ecosystems. Therefore, on the basis of the segmentation and vulnerability segmentation theories we should expect that plants will respond to water stress according to their hydraulic designs and patterns of leaf phenology should differ along similar lines.

It has been proposed that patterns of leaf phenology are influenced by seasonal dynamics in the xylem long distance water transport pathway (Borchert, 1994b). Many studies have demonstrated functional dependence of leaf phenology on plant water status (Borchert, 1994a, 1994b; Chapotin, *et al.* 2006; Reich & Borchert, 1984; Wang, *et al.* 1992; Williams, *et al*., 1997). Borchert (1994b) observed patterns of leaf phenology to be strongly correlated with seasonal changes in stem water status in a Costa Rican seasonally dry tropical forest. Similar findings have been reported by Williams, *et al*., (1997) who monitored leaf phenology for woody species in an Australian tropical Savanna. Experimental evidence supports the functional dependence theory of leaf phenology on stem water status (Borchert, 1994a). Though many studies show support for the functional dependence theory, there are some studies showing conflicting findings (Chidumayo, 2001; Duff *et al*., 1997; Filho & Filho, 2000; Wright & Cornejo, 1990). Thus, the validity of the stem water status functional dependence hypothesis remains a subject for further research.

Wright & Cornejo (1990) carried out an irrigation study on Barro Colorado Island (BCI) to test the validity of the functional dependence theory of leaf phenology on plant water status. The results of this study though not highly consistent demonstrated leaf

shedding to be independent of stem water status. While Wright and Cornejo's (1990) study highlighted the dependence of leaf phenology on stem water status for some species, they were quick to point out the various species-specific response-behaviours of tropical plants to environmental cues. Filho & Filho (2000) showed changes in canopy cover in a Brazilian forest to be more strongly correlated to atmospheric drying than seasonal changes in soil water deficit. Given that plant water status at pre-dawn approximates soil water status (Williams & Araujo, 2002), Filho and Filho's findings seem to question the validity of the functional dependence theory of leaf phenology on stem water status. The inconsistence in findings require that similar studies be undertaken in other less researched ecosystems such as the ones in Africa.

To the best of my knowledge, there have been no rigorous studies that have examined the relationship between leaf phenology and seasonal changes in plant water relations in miombo woodlands. This thesis tests the validity of the functional dependence theory of leaf phenology on stem water status in miombo woodlands.

2.5 LEAF ATTRIBUTES AND DROUGHT TOLERANCE

Plants respond to water stress at both morphological and physiological levels (Preston & Ackerly, 2003). Although knowledge for both morphological (Wright *et al*., 2004) and physiological (Tyree & Zimmermann, 2002) responses has increased over time, we still do not fully understand the basic relationship between the two sets of water stress responses. The consistent trend of shifts in both hydraulic conductivities and leaf functional traits from wet to arid ecosystems suggests that the two responses may be functionally coordinated. The hydraulic limitation hypothesis proposes an increase in path resistance with increasing tree height, constrains plant photosynthetic activity,

thereby leading to a reduction in overall height growth (Ryan & Yoder, 1997). On the basis of this theory, we expect that the size of the photosynthesizing structure (leaf) should scale with xylem transport characteristics. There is growing evidence demonstrating considerable coordination between hydraulic supply and photosynthetic rate (Brodribb & Field, 2000; Santiago *et al*., 2004). It has also been demonstrated that hydraulic supply scales positively with stomatal conductance (Nardini & Salleo, 2000). Remarkably, specific leaf area (ratio of leaf area to its mass – $cm^2\ g^{-1}$) and mass based photosynthetic rate are substantially coordinated (Mencuccini, 2003; Niinemets, 1999; Reich, *et al.* 1998; Reich, *et al*., 1995). If photosynthesis strongly correlates with both hydraulic efficiency and specific leaf area, then one would expect that SLA and hydraulic efficiency must be coordinated.

Pressure for selection under arid environments selects plants with small, hard and leathery leaves (Niinemets, 2001). As expected there has been a trend towards reduced specific leaf area and leaf size with declining average annual precipitation (Fonseca, *et al*., 2000; Pickup, et al. 2005; Preston & Ackerly, 2003; Westoby, *et al*., 2002; Wilson, *et al.* 1999; Wright, *et al*., 2004; Wright, *et al.* 2002). Specific leaf area (SLA) is an essential functional trait that not only describes the transpiring leaf surface area (O'Grady *et al*., 2009) but to a large extent also describes a plant's photosynthetic capacity (Niinemets, 1999).

The prevailing view is that SLA represents plant resource (water, light, nutrients) exploitation capability and reflects the expected returns on previously invested resources (Wilson, *et al*. 1999). Theoretically, high-SLA leaves are expected to be extremely productive in resource-rich environments (Williams, *et al*., 1996). In contrast, low SLA

leaves work better in resource-poor environments where retention of captured resources is a higher priority (Wilson *et al*, 1999). Fonseca, *et al* (2000) observed SLA and leaf width marched together in the direction towards decreasing rainfall. Equally Cunningham, *et al*. (1999) demonstrated the existence of a repeated reduction in SLA across 10 species pairs in an Australian forest in the direction of drier environments. Several other pieces of evidence have confirmed these observations (Ackerly, *et al.*, 2002; Magnani, *et al.* 2002; Preston & Ackerly, 2003; Warren, *et al*., 2006). Differences in SLA have also been demonstrated to occur along leaf phenological lines (Ackerly, *et al*., 2002).

In addition to SLA, there has also been an observed trend towards high leaf dry matter content under arid habitats (Ryser, 1996). Leaf dry matter content reflects plant's resource acquisition strategies under a given set of environmental variables (Wilson, *et al.*, 1999). Prior *et al* (2003) demonstrated that both specific leaf area and dry matter content were lower for deciduous trees than evergreen tree species. They reasoned that differences in these leaf attributes reflected differences in species habitat selection, thus suggesting that leaf attributes play a pivotal role in defining species ecology (Westoby *et al.* 2002).

The adjustable response of both morphological and physiological traits to varying water stress suggests that these plant functional traits may exert some fundamental influence on each other. Though there is a possible interaction between hydraulic properties and leaf functional traits associated with plant drought-tolerance, there are only a handful of studies that have attempted to critically analyze this functional coordination, and all these studies are outside miombo ecosystem. Therefore, a critical examination of

this relationship will be made in this thesis. Though SLA, DMC, and other leaf attributes have been studied in most of the tropical biomes, African biomes are under-represented (Niinemets, 2001). In particular, there is a conspicuous absence of leaf attribute data for miombo woodlands in southern Africa. This thesis attempts to fill this apparent knowledge gap that exists on miombo species.

2.5 CONCLUSIONS

The extent to which hydraulic architecture influences species habitat selection in water-limited ecosystems remains unclear and appears to vary across ecosystems. Although water stress is one of the primary factors controlling leaf display in water-limited ecosystems, there is ample evidence suggesting the opposite. Therefore, the extent to which water stress controls patterns of seasonal leaf display in tropical ecosystems still remains unresolved. Although plants display both morphological and physiological responses to water stress, the interaction between hydraulic properties and leaf functional traits associated with drought tolerance are poorly understood. In general, there is a conspicuous absence of physiological and ecophysiological data for some of the most prominent global ecosystems. The miombo forests in southern Africa are case in point where information on tree hydraulic architecture and influential leaf attributes are lacking.

2.6 REFERENCES

Ackerly, D. D., Knight, C. A., Weiss, S. B., Barton, K., & Starmer, K. P. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia,* **130**: 449-457.

Borchert, R. (1994a). Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees,* **8:**198-204.

Borchert, R. (1994b). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology,* **75**: 1437-1449.

Brodribb, J. T., & Field, T. S. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell Environ.,* **23**: 1381-1388.

Brodribb, J. T., & Hill, R. S. 1999. The importance of xylem constraints in the distribution of conifer species. *New Phytologist,* **143**: 365-372.

Brodribb, J. T., & Holbrook, N. M. 2003. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytologist,* **158**: 295-303.

Brodribb, J. T., & Holbrook, N. M. 2006. Declining hydraulic efficiency as transpiring leaves desiccate: two types of response. *Plant, Cell Environment,* **29**: 2206-2215.

Brodribb, J. T., Holbrook, N. M., & Gutierrez, M. V. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant, Cell Environment,* **25:** 1435-1444.

Bucci, S. J., Goldstein, G., Meinzer, F. C., Scholz, F.G., Franco, A. C., & Bustamante, M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology,* **24**: 891-899.

Burke, A. 2006. Savanna trees in Namibia - factors controlling their distribution at the arid end of the spectrum. *Flora,* **201:** 189-201.

Chapotin, M. S., Razanameharizaka, H. J., & Holbrook, M. N. 2006. Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytologist,* **169:** 549-559.

Chidumayo, E. N. 1987. Species structure in Zambian miombo woodland. *Journal of Applied Ecology,* **3**: 109-118.

Chidumayo, E. N. (2001). Climate and phenology of savanna vegetation in southern Africa. *Journal of Vegetation Science,* **12**: 347-354.

Choat, B., Ball, M. C., Luly, G. J., & Holtum, M. A. J. 2005. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from North-eastern Australia. *Trees,* **19**: 305-311.

Choat, B., Sack, L., & and Holbrook, N. M. 2007. Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytologist,* **175**: 686-698.

Condit, R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climate Chaange,* **39**: 413-427.

Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbel, S. P., & Foster, R. B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of El Nino Dry Season. *Journal of Tropical Ecology,* **20**: 51-72.

Condit, R., Hubbell, S.P., & Foster, B.R. 1996. Changes in tree species abundance in a neotropical forest: impact of climate change. *Journal of Tropical Ecology,* **12:** 231-256.

Cornwell, W. K., R. Bhaskar, L. Slack, S. Cordell, and C.K. Lunch. 2007. Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs low precipitation. *Funct. Ecol.* 21:1063-1071.

Cunningham, S. A., Summerhayes, B., & Westoby, M. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecology,* **69**: 569-588.

Domec, J., Lachenbruch, B., & Meinzer, F. C. 2006. Bordered pit structure and function determine spatial patterns of air-seeding thresholds in xylem of Douglars-fir (*Pseudotsuga menziesii*; Pinaceae) trees. *American Journal of Botany*, **93**: 1588-1600.

Duff, G. A., Myers, B. A., Williams, R. J., Eamus, D., O'Grady, A., & Fordyce, I. R. (1997). Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a Northern Autralian savanna. *Australian Journal of Botany,* **45**: 211-224.

Engelbrecht, B. M. J., Dalling, J. W., Pearson, T. R. H., Wolf, R. L., Gálvez, D. A., Koehler, T., Tyree, M. T. & Kursar, T. A. 2006. Short dry Spells in the Wet Season Increase Mortality of Tropical Pioneer Seedlings. *Oecologia,* **148**: 258-269.

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A, Tyree, M. T., Turner, B. L., & Hubbell, S. P. 2007. Drought sensitivity shapes species distribution patterns in tropical Forests. *Nature,* **447**: 80-83.

Engelbrecht, B. M. J., Velez, V., & Tyree, M. T. (2000). Hydraulic conductance of two co-occuring neotropical understorey shrubs with different habitat preferences. *Annals of Forest Science,* **57:** 201-208.

Filho, L. J. P., & Filho, C. V. M. 2000. Seasonal changes in the water status of three woody legumes from the Atlantic forest, Caratinga, Brazil. *Journal of Tropical Ecology* **16**: 21-32.

Fonseca, C. R., Overton, J. M., Collins, B., & Westoby, M. 2000. Shifts in Trait-Combination Along Rainfall and Phosphorus Gradients. *Journal of Applied Ecology,* **88**: 964-977.

Froux, F., Ducrey, M., Dreyer, E., & Huc, R. 2005. Vulnerability to embolism differs in roots and shoots and among three Mediterranean conifers: consequences for stomatal regulation of water loss? *Trees*, **19**: 137-144.

Gentry, A. H. 1998. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden,* **75**: 1-34.

Goldstein, G., Rada, F., Rundel, P., Azocar, A., & Orozco, A. 1989. Gas exchange and water relations of evergreen and deciduous tropical savanna trees. *Annals of Forest Science,* **46**: 448s-453s.

Hacke, U. G., Sperry, J. S., & Pittermann, J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology,* **1**, 31-41.

Holbrook, M., Whitbeck, J. L., & Mooney, A. H. 1995. Drought responses of neotropical dry forest trees. In Bullock, H. S., Mooney, A. H. & Medina, E. Eds. *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge, pp 243-276

Hopkins, W., & Huner, P. A. N. 1995. *Introduction to Plant Physiology*. John Wiley & Sons, New Jersey. 503 p

IPCC. (2007). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Jacobsen, A. L., Pratt, R. B., Davis, D. S., & Ewers, W. F. 2007. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell and Environment,* **30**: 1599-1609.

Lewis, A. (1988). A test of the air-seeding hypothesis using *Sphagnum hyalocysts*. *Plant Physiology,* **87**: 577-582.

Lewis, S. L., Malhi, Y., and Phillips, O.L. 2004. Fingerprinting the Impacts of global change on tropical forests. *Philosophycal Transactions of the Royal Society* **359**: 437-462.

Lo Gullo, M. A., Noval, L. C., Salleo, S., & Nardini, A. 2004. Hydraulic architecture of plants of *Helianthus annuus* L. cv. Margot: evidence for plant segmentation in herbs. *Journal of Experimental Botany, **55***: 1549–1556.

Lopez, O., Kursar, T. A., Cochard, H., & Tyree, M. 2005. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology,* **25**: 1553-1562.

Lovisolo, C., & Schubert, A. 1998. Effects of water stress on vessel size and xylem hydraulic conductivity in Vitis vinifera L. *Journal of Experimental Botany,* **49**: 693-700.

Machado, J., & Tyree, T. M. 1994. Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. *Tree Physiology*, **14**: 219-240.

Magnani, F., Grace, J., & Borghetti, M. 2002. Adjustment of tree structure in response to the environment under hydraulic constraints. *Functional Ecology,* **16**: 385-393.

Maherali, H., & DeLucia, E. H. (2000). Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiology,* **20**: 859-867.

Maherali, H., Pockman, T. W., & Jackson, B. R. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology,* **85**: 2184-2199.

Martinez-Vilalta, J., Prat, E., & Oliveras, J. P. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia,* **133**, 19-29.

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J. F. J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U., & Zweife, R. 2009. Hydraulic adjustment of Scots pine across Europe. *New Phytologist*, **184**: 353–364.

Maseda, P. H., & Fernandez, R. J. 2006. Stay wet or else: Three ways in which plants can adjust hydraulically to their environment. *Journal of Experimental Botany,* **57**: 3963-3977.

Mencuccini, M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell and Environment,* **26**: 163-182.

Mencuccini, M., & Grace, J. (1995). Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology,* **15**: 1-10.

Merbold, L., Ardo, J., Arneth, A., Scholes, R. J., Nouvellon, Y., De Grandcourt, A., Archibald, S., Bonnefond, J. M., Boulain, N., Bruemmer, *et al.* (2009). Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosciences,* **6**: 1027–1041.

Murphy, P. G., & Lugo, A. E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics, 17*, 67-88.

Nardini, A., & Salleo, S. 2000. Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? *Trees,* **15**: 14–24.

Niinemets, U. 1999. Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist,* **144**: 35-47.

Niinemets, U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology,* **82**: 453-469.

O'Grady, A. P., Cook, P. G., Eamus, D., Duguid, A., Wischusen, J. D. H., Fass, T., & Worldege, D. 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia,* **160**: 643-655.

Okitsu, S. 2005. Factors Controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs, 30,* 135-151.

Philips, O. L., Aragao, C. O. L., Lewis, L. S., Fisher, J., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., van der Heijden, G. et al. 2009. Drought sensitivty of the Amazon rainforest. *Science,* **323**: 1344-1347.

Pickup, M., Westoby, M., & Basden, A. 2005. Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology,* **19**: 88-97.

Pittermann, J., Sperry, J. S., Wheeler, J. K., Hacke, U. G., & Sikkema, E. H. 2006. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant, Cell and Environment,* **29**: 1618-1628.

Pockman, W. T., & Sperry, J. S. (2000). Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany,* **87**: 1287-1299.

Preston, A. K., & Ackerly, D. D. 2003. Hydraulic architecture and the evolution of shoot allometry in contratsing climates. *American Journal of Botany*, **90**: 1502-1512.

Prior, L. D., Eamus, D. & Bowman, D. M. J. S. 2003. Leaf attributes in the seasonally dry tropics: a comparison of four habitats in Northern Australia. *Functional Ecology*, **17**: 504-515

Reich, P. B., & Borchert, R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **72**: 61-74.

Reich, P. B., Ellsworth, D. S., & Walters, M. B. 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology*, **12**: 948-958.

Reich, P. B., Kloeppel, B. D., Ellsworth, D. S., & Walters, M. B. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia*, **104**: 24-30.

Ryan, M. G., & Yoder, B. J. 1997. Hydraulic limits to tree height and tree growth: What keeps trees from growing beyond a certain height? *BioScience*, **47**: 235-242.

Ryser, P. (1996). The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology*, **10**: 717-723.

Santiago, L. S., Goldstein, G., Meinzer, F., C., Fisher, J. B., Machado, K., Woodruff, D., et al. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**: 543-550.

Scholes, R. J., & Walker, B. H. 1993. *An African Savanna: Synthesis of the Nysvley Study*. Cambridge: Cambridge University Press.

Shumway, D. L., Steiner, K. C., & Kolb, T. E. 1993. Variation in seedling hydraulic architecture as a function of species and environment. *Tree Physiology*, **12**: 41-54.

Slot, M., and Poorter, L. 2007. Diversity of tropical tree seedling responses to drought. *Biotropica*, **39**: 683-690

Sperry, J. S., Hacke, G. U., & Wheeler, K. J. 2005. Comparative analysis of end wall resistivity in xylem conduits. *Plant, Cell and Environment*, **28**: 456-465.

Sperry, J. S., Hacke, U. G., Oren, R., & Comstock, J. P. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment*, **25**: 251-263.

Sperry, J. S., & Saliendra, N. Z. 1994. Intra- and inter-plant variation in xylem cavitation in Betula occidentalis. *Plan, Cell and Environment,* **17**: 1233-1241.

Sperry, J. S., & Tyree, T. M. 1988. Mechanism of water stress induced xylem embolism. *Plant Physiology,* **88**: 581-587.

Swift, C. C., Jacobs, S. M., & Esler, K. J. 2008. Drought induced xylem embolism in four riparian trees from the Western Cape Province: Insights and implications for planning and evaluation of restoration. *South African Journal of Botany,* **74**: 508-516.

Taiz, L., & Zeiger, E. 1998. *Plant Physiology*. Massachusetts: Sinauer Associates, Inc.792 p

Tissier, J., Lambs, L., Peltier, J., & Marigo, G. 2004. Relationship between hydraulic traits and habitat preference for six Acer species occurring in the French Alps. *Annals of Forest Science,* **61**: 81-86.

Tyree, M. T., Cochard, H., Cruiziat, P., Sinclair, B., & Ameglio, T. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell and Environment,* **16**: 87-882.

Tyree, M. T., & Ewers, F. W. 1991. Tansley Review No.34. The Hydraulic architecture of trees and other woody plants. *New Phytologist,* **119**: 345-360.

Tyree, M. T., Snyderman, D. A., Wilmot, T. R., & Machado, J. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*). *Plant Physiology*, **96**: 1105-1113

Tyree, M. T., & Sperry, J. S. 1988. Do Woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology,* **88**: 0574-0580.

Tyree, M. T., & Sperry, J. S. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology, 40*, 19-38.

Tyree, M. T., & Zimmermann, M. H. (2002). *Xylem structure and the ascent of sap* (2nd ed.). Berlin: Springer. 283 p

van der Willigen, C., Sherwin, H. W., & Pammenter, N. W. 2000. Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. *New Phytologist,* **145**: 51-59.

Villar-Salvador, P., Castro-Diez, P., Perez-Rontome, C., & Montserrat-Marti, G. 1997. Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees,* **12**: 90-96.

Wang, J., Ives, N. E., & Lechowicz, M. J. 1992. The relation of foliar phenology to xylem embolism in trees. *Functional Ecology*, **6**: 469-475.

Warren, C. R., Dreyer, E., Tausz, M., & Adams, M. A. 2006. Ecotype adaptation and acclimation of leaf traits to rainfall in 29 species of 16 year old *Eucalyptus* at two common gardens. *Functional Ecology*, **20**: 929-940.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, A. P., & Wright, J. I. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annul Review of Ecology and Systematics*, **33**: 125-159.

Wheeler, K. J., Sperry, S. J., Hacke, G. U., & Hoang, N. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell and Environment*, **28**: 800-812.

Williams, L. E., & Araujo, F. J. 2002. Correlations among predawn leaf, midday leaf, and midday stem water potential and their correlations with other measures of soil and plant water status in *Vitis vinifera*. *Journal of American Society of Horticulture Science*, **127**: 448-454.

Williams, R. J., Duff, G. A., Bowman, D. M. J. S., & Cook, D. G. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography*, **23**: 747-756.

Williams, R. J., Myers, B. A., Muller, W. J., Duff, G. A., & Eamus, D. 1997. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology*, **78**: 2542-2558.

Wilson, P. J., Thompson, K., & and Hodgson, G. J. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, **143**: 155-162.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature*, **428**: 821-827.

Wright, I. J., Westoby, M., & Reich, P. B. 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology*, **90**: 534-543.

Wright, S. J., & Cornejo, H. F. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology*, **71**: 1165-1175.

Zimmermann, M. H. 1983. *Xylem Structure and the Ascent of Sap*. Berlin: Springer-Verlag.

Zimmermann, U., Schneider, H., Wegner, L. H., & Haase, A. (2004). Water ascent in tall trees: Does evolution of land plants rely on a highly metastable state? *New Phytologist*, **162**: 575-615.

CHAPTER 3

Hydraulic architecture, xylem anatomy and plasticity for nine miombo woodlands canopy tree species with contrasting habitat preferences and leaf phenologies

OVERVIEW

Knowledge of tree hydraulic architecture for miombo woodland tree species is lacking. Studying hydraulic properties in relation to tree species habitat preference and how these hydraulic traits shift in response to increasing ecosystem aridity is vital for understanding the various ecological strategies that enhance plant competitive ability under a given set of biophysical variables. This chapter addresses the first research objective and tests the hypotheses that 1) narrow habitat ranging tree species with mesic specialisation have a vascular system that is more efficient than broad ranging habitat generalists and 2) that drought tolerant tree species extend their habitat range into the drier sites as a result of plasticity in hydraulic architecture and structural adjustments in vessel anatomy.

This work highlights the importance of hydraulic properties in influencing species habitat preference and the responsiveness of these hydraulic properties to variations in precipitation. The study provides the quantified range of hydraulic properties for nine principal miombo tree species (these results will be used in Chapter 4 to evaluate the relationship between cavitation resistance and hydraulic efficiency and in Chapter 6 to examine the relationship between hydraulic efficiency and leaf functional traits associated with plant drought tolerance). Findings from other tropical ecosystems which have shown tree hydraulic properties to vary along the lines of ecological niche specialisation are confirmed in this chapter.

The article was written by Royd Vinya with major comments coming from co-authors. This paper has been submitted to Tree Physiology and at the time of submitting this thesis was undergoing peer review.

Hydraulic architecture, xylem anatomy and plasticity for nine miombo woodland canopy tree species with contrasting habitat preferences and leaf phenologies

Authors: Royd Vinya[1], Yadvinder Malhi[1], Nick D. Brown[2], Timothy Brodribb[3],

1 Environmental Change Institute, Oxford University Centre for the Environment,
2 Department of Plant Sciences, University of Oxford,
3 School of Plant Sciences, University of Tasmania

SUMMARY

Africa's Miombo woodlands constitute one of the most important dry tropical forests on earth, yet the hydraulic function of these forests is unknown. Given the current predictions of increased aridity by the end of this century in the miombo ecoregion, knowledge of the likely response of miombo woodlands tree species is important in planning adaptation strategies. Tree hydraulic architecture is central to this understanding. In this study, the hydraulic properties of nine tree species differing in habitat preference and leaf phenology were investigated. The hydraulic efficiency and allometry of stems were analysed to determine whether differences in species habitat preference could be explained by tree hydraulic architecture. The hydraulic properties analyzed were stem-area-specific hydraulic conductivity (K_S), Huber value (*HV*), and leaf specific conductivity (K_L). The xylem anatomical structures analysed were conduit length and diameter. The results show that mesic specialised tree species displayed significantly ($P < 0.05$) higher K_S, and K_L values than co-occurring generalists. We found no significant variations in *HV* between the two miombo woodlands ecological groups. Our results show a significant ($P < 0.05$) trend towards declining K_S and K_L from wet to dry miombo woodland sites in three out of four broad ranging tree species. We found very

marginal but statistically significant ($P < 0.05$) differences in conduit diameter among the nine species studied. However, conduit lengths were significantly ($P < 0.05$) longer among tree species with wet miombo woodlands specialisation than among broad ranging miombo species. Both conduit diameter and length varied insignificantly between the two generalists' populations growing on the wet and dry miombo woodland sites. Our results suggest that tree hydraulic architecture influences the range of habitats any given species can occupy competitively. Hydraulic plasticity is a prerequisite for species ability to extend its habitat range from wet to dry environments in water-limited ecosystems.

Key words: Huber value; Hydraulic architecture; Leaf specific conductivity; Miombo woodlands; Specific hydraulic conductivity.

3.1 INTRODUCTION

In seasonally dry tropical forests the greatest impact of predicted climate change is likely to be in the magnitude and frequency of drought (IPCC 2007). Climate change predictions for most sub-tropical regions, point in the direction of decreasing mean annual precipitation. In particular, the current climatic prediction for the miombo ecoregion is for a reduction in mean annual precipitation by more than 20% (Sithole and Murewi 2009). Previous studies have established that droughts in the miombo eco-region were highly prevalent in the 20th Century, and may intensify under climate change (Nicholson 2001). There is little doubt that future climate trends pose some considerable challenges to the survival of the miombo woodlands (Desankar and Prentice 1995). Plant drought response is therefore, key to adaptation planning for the miombo eco-region.

Africa's miombo woodlands are vast, of high conservation value and important for human well-being (Frost 1996).

Although it has long been recognised that precipitation is the principal determinant of tree species composition in miombo woodlands (Chidumayo 1987, White 1983), knowledge of plant-water relations for this biome remains poor. In particular, there is a conspicuous absence of data for miombo woodlands in Africa on the hydraulic designs of the key tree species. It would be valuable to know more for the following reasons: Hydraulic response of a tree is the result of interactions between a suite of traits and properties including leaf phenology, architecture and xylem conduit structural properties. However, little is known scientifically about the relationship between these components for miombo species: Rapid environmental change requires a management response that should be informed by sound knowledge of miombo tree species ecophysiology. At present insufficient is known to permit development of an evidence-based climate-change adaptation plan; restoration of degraded miombo woodland is being promoted to combat widespread deforestation. Once again, a robust understanding of the relationship between tree hydraulic architecture and ecological habitat preference would allow suitable species to be selected for reforestation.

Hydraulic properties have been studied for a number of tropical and neo-tropical ecosystems and results appear to be inconsistent (Brodribb and Holbrook 2003, Choat et al. 2005, Hao et al. 2008). While several studies have reported higher xylem hydraulic efficiency for those tree species restricted to mesic habitats than for widely distributed tree species (Engelbrecht et al. 2000, Lovisolo and Schubert 1998), others have reported

the opposite (Cornwell et al. 2007, Maherali and DeLucia 2000). However, other studies have found no clear pattern in hydraulic properties of trees with contrasting habitat preference (Hao et al. 2008). Furthermore, the reported correlation between leaf phenology and hydraulic properties has equally generated different trends for different forest ecosystems. For example, some studies have reported higher specific hydraulic and leaf specific conductivities among evergreen than deciduous tree species (Goldstein et al. 1989, Machado and Tyree 1994). Other studies have found deciduous species to be more hydraulically efficient than evergreen ones (Choat et al. 2005, Villar-Salvador et al. 1997). While differences in methodological approaches may account for much of the disparities observed among these studies, it only serves to confirm that globally derived conclusions do not apply at a local scale, hence the need to gain a clear insight into how these properties vary within individual ecosystems.

We chose the miombo woodlands in Zambia to study xylem hydraulic properties and anatomy. In this study we aim to answer the following questions: 1) Do differences in ecological niche with respect to species drought-tolerance and to observed patterns of leaf phenology correspond to differences in hydraulic architecture and xylem anatomy? 2) To what extent, are the perceived differences in hydraulic architecture, driven by differences in conduit structural dimensions? 3) Do tree species, which extend over, wide ecological amplitudes, show greater plasticity in hydraulic properties and anatomy? We addressed these questions by evaluating xylem hydraulic properties and anatomy of nine miombo woodlands canopy tree species with contrasting habitat preference and leaf phenology.

Our hypotheses were that; 1) narrow habitat ranging tree species with mesic specialisation have a vascular system that is more efficient than broad ranging habitat generalists; 2) differences in hydraulic architecture are driven by differences in conduit structural dimensions and; 3) drought tolerant tree species extend their habitat range into the drier sites as a result of greater plasticity in hydraulic architecture and structural adjustments in vessel anatomy.

3.2 MATERIALS AND METHODS

3.2.1 Study sites

In this study we chose two gazetted forest reserves to represent the wet and dry miombo woodlands. The two selected forest reserves had known forest management histories, (less than 10 years) soil-vegetation surveys and are reasonably uniform in geology, although small local variations may have been present. The two forest reserves experienced weather patterns in which summer rains fall between November and April followed by a long seasonal drought lasting from May to October. The wet site was located in Mwekera National Forest No. 6 on the outskirts of Kitwe City (12˚ 49′ S and 28˚ 22′ E; elevation of 1295m above sea level). The vegetation of the wet site is predominantly *Brachystegia-Julbernardia* woodlands with the genera *Brachystegia, Isoberlinia, Julbernardia* and *Marquesia* as common canopy co-dominants (Chidumayo 1987). The wet site received an average annual precipitation of 1,200 mm with mean annual temperatures ranging from 14 to 28 ^{o}C. The dry site is located in Choma district at 16^{o} 50’ S and 27^{o} 03’ E with an average elevation of 1266 m above sea level. The long-term climate for the two sites is presented in Figure 3.1.

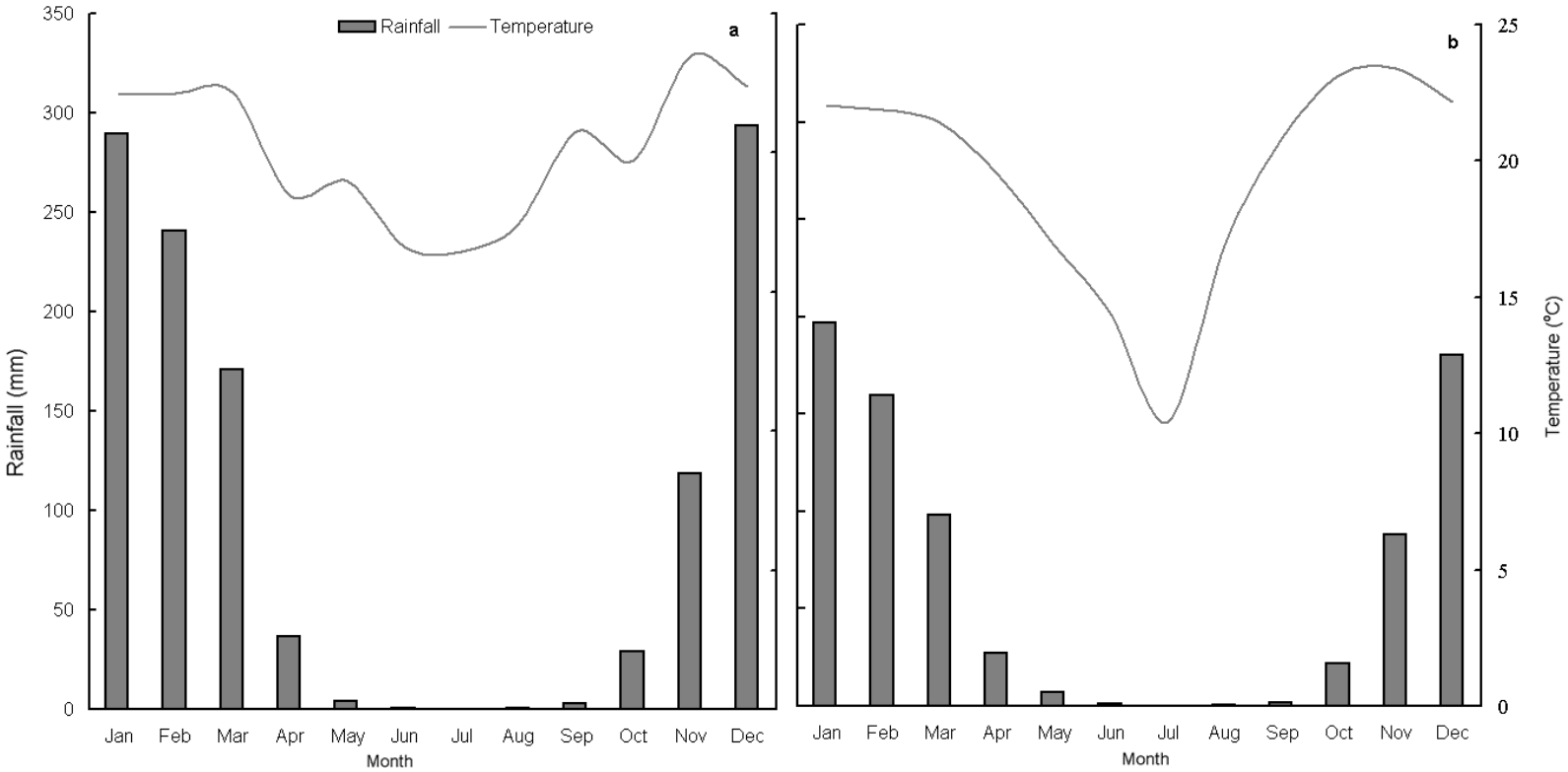


Figure 3.1: Long-term (1960 – 2005) mean rainfall and temperature for the (a) wet (b) dry miombo woodland sites.

The vegetation of the dry site has *Brachystegia boehmii*, *Brachystegia spiciformis*, and *Julbernardia globiflora* as the common canopy co-dominants. The dry site received 800 mm of mean annual precipitation with mean annual temperatures ranging between 12 and 27 ^{o}C.

3.2.2 Sampling

In this study we examined nine co-dominant miombo woodland tree species.. Four of the nine species [*Brachystegia floribunda* Benth (Fabaceae), *Isoberlinia angolensis* (Benth.)Hoyle & Brenan (Fabaceae), *Julbernardia paniculata* (Benth.)Troupin (Fabaceae), and *Marquesia macroura* Gilg (Dipterocarpaceae)] display a narrow habitat range with distribution mainly confined to wet miombo sites and are referred to as mesic specialists in this study. The other five species [*Brachystegia boehmii* Benth (Fabaceae), *Brachystegia longifolia* Benth (Fabaceae), *Brachystegia spiciformis* Benth (Fabaceae), *Erythrophleum africanum* (Benth.) Harms (Fabaceae), and *Pericopsis angolensis* (Baker) Meeuwen (Fabaceae)] exhibit wide habitat ranges with distributions throughout the miombo eco-region and are referred throughout this study as generalists. The average diameter at breast height for the sample trees ranged from 30 to 39 cm on the wet site and from 18 to 25 cm on the dry site (Appendix 5.1)

The nine tree species were selected on the basis that: (1) they differed substantially in habitat preferences (Chidumayo 1987, Smith and Allen 2004), (2) they had contrasting leaf phenology and, (3) they form much of the canopy throughout the miombo woodlands. Twenty five trees per species (giving a total of 225 trees on the wet and 100 trees on the dry sites) were selected based on the criteria that they were healthy,

actively growing, and at least 100 m apart. On the dry site 100 trees were sampled due to the absence of *Brachystegia longifolia*. On both the dry and wet sites we controlled for local environmental variability by sampling individuals that co-occurred.

3.2.3 Anatomic measurements

Three fresh twigs were harvested from each replicate individual tree under study for maximum vessel length determination. Conduit length determination involved forcing air (pressure = 100 kPa) through the basal end of the twig while at the same time keeping the distal end dipped into a bucket of water (Ewers and Fisher 1989, Zimmermann and Jeje 1981). The submerged distal end of an intact twig was continuously cut back in sections of 1 cm until bubbles were seen forming at the cut end. Once bubbles appeared, the procedure was stopped and the total length of the remaining segment measured to the nearest millimeter. This was then recorded as the maximum vessel length for that particular twig.

For vessel diameter measurement, samples were prepared by initially being soaked for 3 weeks in a solution of ethanol, distilled water, and glycerol mixed in equal proportions (Beikircher and Mayr 2008). Cross-sections were cut between 15 and 30 μm thick using a sliding microtome. The micro slides were stained with Safranin and mounted with Canada Balsam. The micro slides were thereafter dried in an oven at 80^{o}C for 8 – 12 hrs. Micro slides were photographed using a digital camera mounted on a microscope. The photographs were prepared and analyzed using the software Image J (freely available from www. http://rsb.info.nih.gov/ij/). Using the function, 'Analyze particles' in Image J, the minimum threshold for analysis was set at 10 μm. The images were analysed for vessel diameters and density. Three different types of vessel diameters

were thereafter derived, following the procedures of Tyree and Zimmermann (2002). Vessel diameters analysed were: Mean vessel diameter (*D*); hydraulic mean diameter (D_H) and; mean vessel diameter accounting for 95% conductivity (D_{95}).

Mean vessel diameter (*D*) was calculated by averaging all vessels above 10 μm. Mean hydraulic diameter was calculated as:

$$D_H = \left[\frac{\sum D^4}{N} \right]^{1/4} \qquad \textbf{[Eqn. 1]}$$

Mean diameter accounting for 95% conductance was calculated by ranking all the diameters raised to the fourth power in ascending order. These D^4 diameters were then summed up until their sum was equivalent to 95% of the total conductance (Tyree and Zimmermann 2002). An arithmetic average was then calculated for diameters accounting for this conductance.

3.2.4 Hydraulic conductivity

From April to May 2008, hydraulic properties for the nine miombo woodlands canopy tree species were determined. This period was chosen specifically because it was at the end of the rainy season and soils were therefore well hydrated. Hydraulic properties are known to vary considerably with branch diameter and unless measurements are made at the same diameter, comparisons become difficulty to make (van der Willigen et al. 2000). One way of going round this problem is by taking measurements from morphologically-identical branch diameters (Patino et al. 1995). We therefore, confined our hydraulic property measurement to only second-order branches. Since plant hydraulic properties are known to display substantial vertical variations within an individual tree (Tyree and

Zimmermann 2002), care was taken to minimize this effect by sampling from approximately the same crown height. Three healthy second-order leaf-bearing twigs were harvested in the early hours of the morning (between 05:30 and 07:30hrs) from each of the replicate individuals for each species giving a total of 675 twigs on the wet site and 300 twigs on the dry site. The diameter underbark for the harvested twigs ranged from 4 to 10 mm. The harvested twigs were immediately covered in wet towels and sealed in plastic sample bags in order to minimize air entry through the exposed cut vessels. Samples were then transported to the nearby laboratory for conductivity determination. At the laboratory, the twigs were trimmed approximately equal to the length as the determined species maximum vessel length plus 10% allowance in order to avoid open vessels. Throughout the process of sample preparation twigs were always kept completely immersed in water. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. A water-tight connection between the segment and the reservoir was achieved using drilled laboratory rubber corks. The water reservoir was constantly refilled in order to maintain the same delivery pressure. The segments were perfused with degassed, filtered (to 0.2 μm) and acidified (with HCl, pH = 2) distilled water (Kolb et al. 1996, Sperry et al. 1988). Each segment was allowed to equilibrate before initial flow rate was measured. Sap flow was measured by attaching a pre-weighed cotton wool covered in a plastic onto the free distal end of the segment. Covering the wool with plastic ensured that evaporation losses were kept to a bare minimum. Prior to sap flow determination all segments were flushed at a constant pressure of 150 *kPa* for periods ranging from 20 to 30 minutes depending on species and extent of native xylem

air blockage. Therefore, the figures reported here are maximum conductivities. At the end of each flow determination, segment underbark diameter (using a digital micro calliper - accuracy 0.01mm) and length were accurately measured. For segments where pith was very pronounced (exceeding 10% of sapwood diameter) the pith diameter was also measured and subtracted from the total diameter. Maximum hydraulic conductivity (K_H) was calculated as:

$$K_H = \left(\frac{J_V}{(\Delta P / l)}\right) \qquad (\text{kg m s}^{-1}\ \text{MPa}^{-1}) \qquad \textbf{[Eqn. 2]}$$

Where K_H is the maximum hydraulic conductivity, J_V is the flow rate (kg s^{-1}); ΔP is the delivery pressure (MPa) and; l is segment length (m).

Stem-area specific conductivity (K_S, kg s^{-1} m^{-1} MPa^{-1}) was derived by dividing hydraulic conductivity with the effective sapwood cross-sectional area (A_W, m^2).

3.2.5 Huber value

Three healthy and fully expanded leaves were harvested from each of the 25 replicate trees per species for leaf area estimation. Total number of leaves supported by each twig was physically counted. The leaves were scanned using a flat bed scanner (Packard Bell Diamond 1200Plus) and leaf areas estimated using the image analysis software Image J (freely available from www. http://rsb.info.nih.gov/ij/). Huber value (*HV*) was calculated as the ratio of the twig area to total leaf area supported by that twig:

$$HV = \frac{A_W}{A_L} \qquad \textbf{[Eqn. 3]}$$

where; A_L (m^2) is the total leaf area supported by the twig

Leaf specific conductivity (K_L, kg s^{-1} m^{-1} MPa^{-1}) was derived as: $K_L = K_S$ x HV

3.2.6 Statistics

In order to answer the question whether significant differences in hydraulic and xylem anatomic properties were more pronounced at functional type (generalists versus specialists) species or within-species levels, we used a mixed-effects ANOVA (Zar, 2010). Functional type was treated as a fixed factor, species and individual tree within-species were as a random factor. Linear regression analysis allowed us to explore the relationship between hydraulic properties and xylem anatomy. We also developed series of general linear models (GLM) to answer the question whether most of the variations in hydraulic properties and xylem anatomy occur from site to site or species to species (Hofmann and Franco, 2003). Site, species, and the interaction factor (site x species) were treated as independent factors. Since our interest was to derive general conclusions about the difference between wet and dry miombo woodlands sites species was treated as a random factor. Site was the fixed factor. Each of the hydraulic properties and xylem dimension were treated as dependent variables. Data were subjected to logarithmic transformations in order to meet normality and variance homogeneity requirements for both ANOVA and linear regression. All statistical analysis was carried out in Minitab (version 15, Pennsylvania, USA).

3.3 RESULTS

3.3.1 Variations in hydraulic property and conduit anatomy

The mean stem hydraulic properties for the nine miombo woodland tree species are summarised in Figure 3.2.

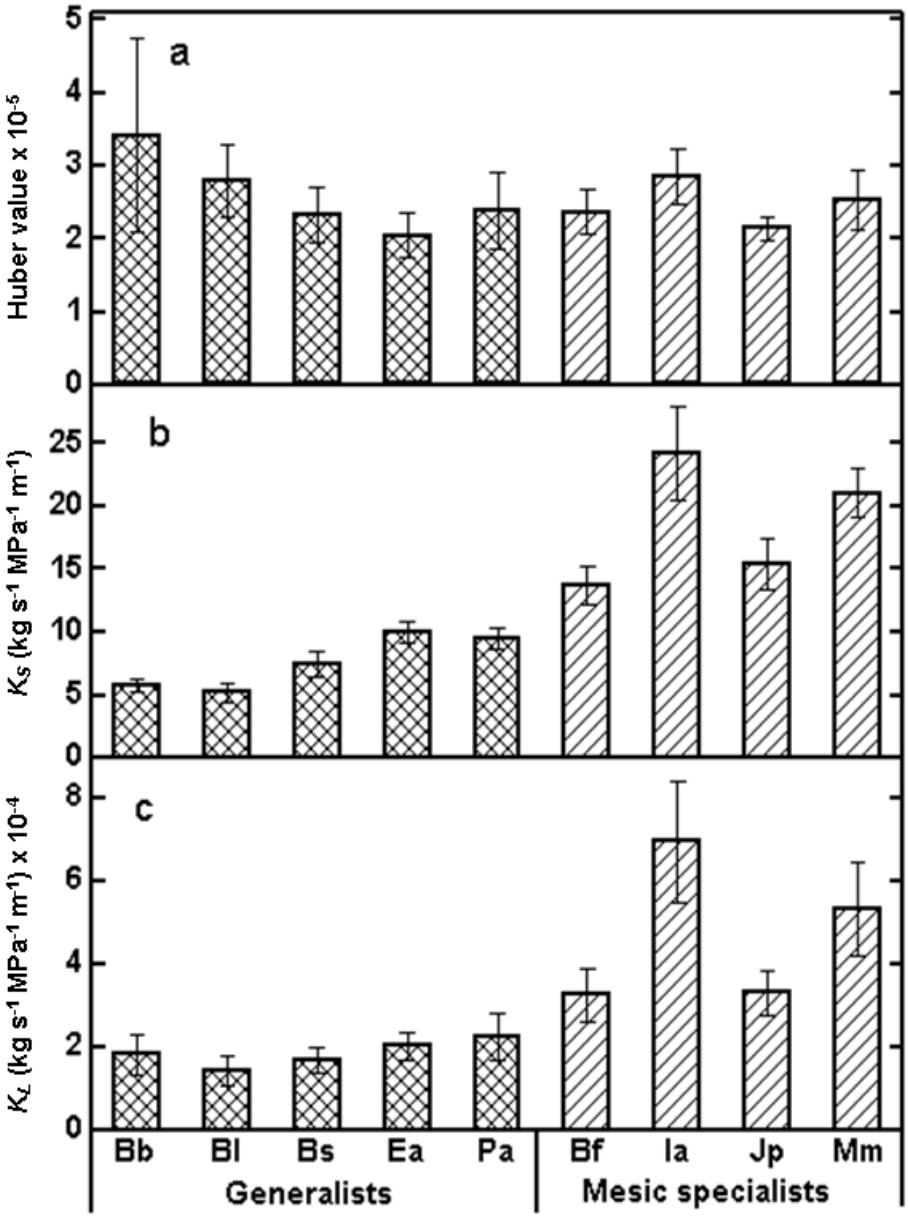


Figure 3.2: Hydraulic properties for the nine miombo woodlands canopy tree species co-occurring on the wet site; (a) Huber value, (b) specific hydraulic conductivity (K_S), (c) leaf specific conductivity (K_L). Error bars are at 95% confidence level. Chart abbreviations are: Bb = *Brachystegia boehmii*, Bl = *Brachystegia longifolia*, Bs = *Brachystegia spiciformis*, Ea = *Erythrophleum africanum*, Pa = *Pericopsis angolensis*, Bf = *Brachystegia floribunda*, Ia = *Isoberlinia angolensis*, Jp = *Julbernardia paniculata*, Mm = *Marquesia macroura*.

Species mean specific hydraulic conductivity (K_S) for wet site generalists ranged between 5.17 ± 0.37 and 9.97 ± 0.41 kg s^{-1} MPa^{-1} m^{-1} (Appendix 3.1). Mesic specialists showed K_S values ranging from 13.73 ± 0.74 to 24.19 ± 1.82 kg s^{-1} MPa^{-1} m^{-1}. Leaf specific conductivity (K_L) among mesic specialists varied from 3.32 ± 0.27 to 6.86 ± 0.05 x 10^{-4} kg s^{-1} MPa^{-1} m^{-1} whereas among generalists it ranged from 1.41 ± 0.12 to 2.27 ± 0.22 x 10^{-4} kg s^{-1} MPa^{-1} m^{-1}. Values of Huber value (*HV*) ranged from 2.1 ± 0.01 to 2.8 ± 0.01 x 10^{-5} among mesic specialists and 2.0 ± 0.01 to 2.9 ± 0.02 x 10^{-5} for generalists.

Among mesic specialists mean vessel diameter (*D*) ranged from 25 ± 0.7 to 27 ± 0.8 μm; mean hydraulic diameter (D_H) varied between 28 ± 0.9 and 34 ± 1.0 μm, and; mean diameter accounting for 95% flow (D_{95}) from 29 ± 1.0 to 38 ± 1.8 μm. Average vessel diameters among generalists varied between 20 ± 0.5 and 26 ± 0.7 μm for *D*; 23 ± 0.7 and 32 ± 0.9 μm for D_H and; 24 ± 0.8 and 37 ± 1.4 μm for D_{95}. Mean conduit length among specialists ranged from 0.25 ± 0.00 to 0.52 ± 0.01 m and between 0.22 ± 0.0 and 0.31 ± 0.0 among generalists.

There was significant variability in specific hydraulic conductivity (K_S) and leaf specific conductivity (K_L) between functional types (generalists versus mesic specialists), species nested within-functional type and individuals nested within-species (Table 3.1). However, most of the variability in K_S and K_L was more pronounced between functional types than species nested within-functional type. Huber value varied insignificantly ($P > 0.05$) between functional types but was significant ($P < 0.05$) both between species and within-species though variability was more pronounced within-species than between them (Table 3.1).

Table 3.1 Results of linear mixed-effects analysis of variance for the nine miombo woodlands tree species. K_S = stem-area-specific hydraulic conductivity; *HV* = Huber value; K_L = leaf specific conductivity; *D* = mean diameter; D_H = mean hydraulic diameter; D_{95} = Mean hydraulic diameter accounting for 95% flow; V_D = Vessel density; V_L = vessel length; *VC* = variance component.

Variable	**Source**	***df***	***MS***	***F-ratio***	***P***	***VC***
K_S (kg s^{-1} MPa^{-1} m^{-1})	Functional Type	1	25.4633	661.33	< 0.001	49.72
	Species (Functional Type)	7	1.1289	29.32	< 0.001	15.43
	Individual (Functional Type Species)	216	0.0385	1.82	< 0.001	16.24
HV	Functional Type	1	0.0125	0.66	0.417	0.14
	Species (Functional Type)	7	0.0678	3.58	0.001	5.40
	Individual (Functional Type Species)	216	0.0189	2.02	< 0.001	46.52
K_L (kg s^{-1} MPa^{-1} m^{-1})	Functional Type	1	6.9027	234.3	< 0.001	32.07
	Species (Functional Type)	7	0.2375	8.06	< 0.001	7.72
	Individual (Functional Type Species)	216	0.0295	2.01	< 0.001	29.57
D (µm)	Functional Type	1	0.0076	0.29	0.591	0.12
	Species (Functional Type)	7	0.1100	4.16	< 0.001	11.62
	Individual (Functional Type Species)	216	0.0265	88.09	< 0.001	86.23
D_H (µm)	Functional Type	1	0.1443	11.19	0.001	3.25
	Species (Functional Type)	7	0.2055	15.93	< 0.001	32.43
	Individual (Functional Type Species)	216	0.0129	86.03	< 0.001	62.80
D_{95} (µm)	Functional Type	1	0.3412	25.15	< 0.001	5.00
	Species (Functional Type)	7	0.2618	19.3	< 0.001	26.81
	Individual (Functional Type Species)	216	0.0136	3.53	< 0.001	42.88
V_D (vessels/ mm^2)	Functional Type	1	0.2603	3.51	0.062	0.85
	Species (Functional Type)	7	2.0622	27.81	< 0.001	46.97
	Individual (Functional Type Species)	216	0.0742	1713.64	< 0.001	52.12
V_L (m)	Functional Type	1	2.5168	6022.46	< 0.001	32.45
	Species (Functional Type)	7	0.7130	1706.08	< 0.001	64.36
	Individual (Functional Type Species)	216	0.0004	1.2	0.058	1.16

The variability in conduit length was more significant between functional types and species nested within-functional types than within-species (Table 3.1). Mean hydraulic diameter (D_H) and D_{95} both varied significantly ($P < 0.05$) at all levels though most of the variability was more pronounced at species and within-species than between functional types. Differences between and within-species accounted for a total of 99% of variability in vessel density (V_D).

3.3.2 Relationship between hydraulic properties and xylem anatomy

When all data points were pooled together ($n = 225$), specific hydraulic conductivity was significantly correlated ($P < 0.05$) to xylem anatomical properties. Specific hydraulic conductivity (K_S) was significantly ($r = 0.39$; $P < 0.001$) and positively correlated to maximum vessel length; was negatively correlated to both mean hydraulic diameter (D_H, $r = 0.19$, $P < 0.004$) and mean hydraulic diameter accounting for 95% flow (D_{95}, $r = -0.25$, $P < 0.001$). There was an insignificant (D, $r = 0.06$, $P = 0.41$) negative correlation between K_S and mean vessel diameter.

These correlations were also significant at inter-species level ($n = 9$) (Figure 3.3b, c, d), suggesting that tree species with high hydraulic efficiency had narrow and longer xylem conduits.

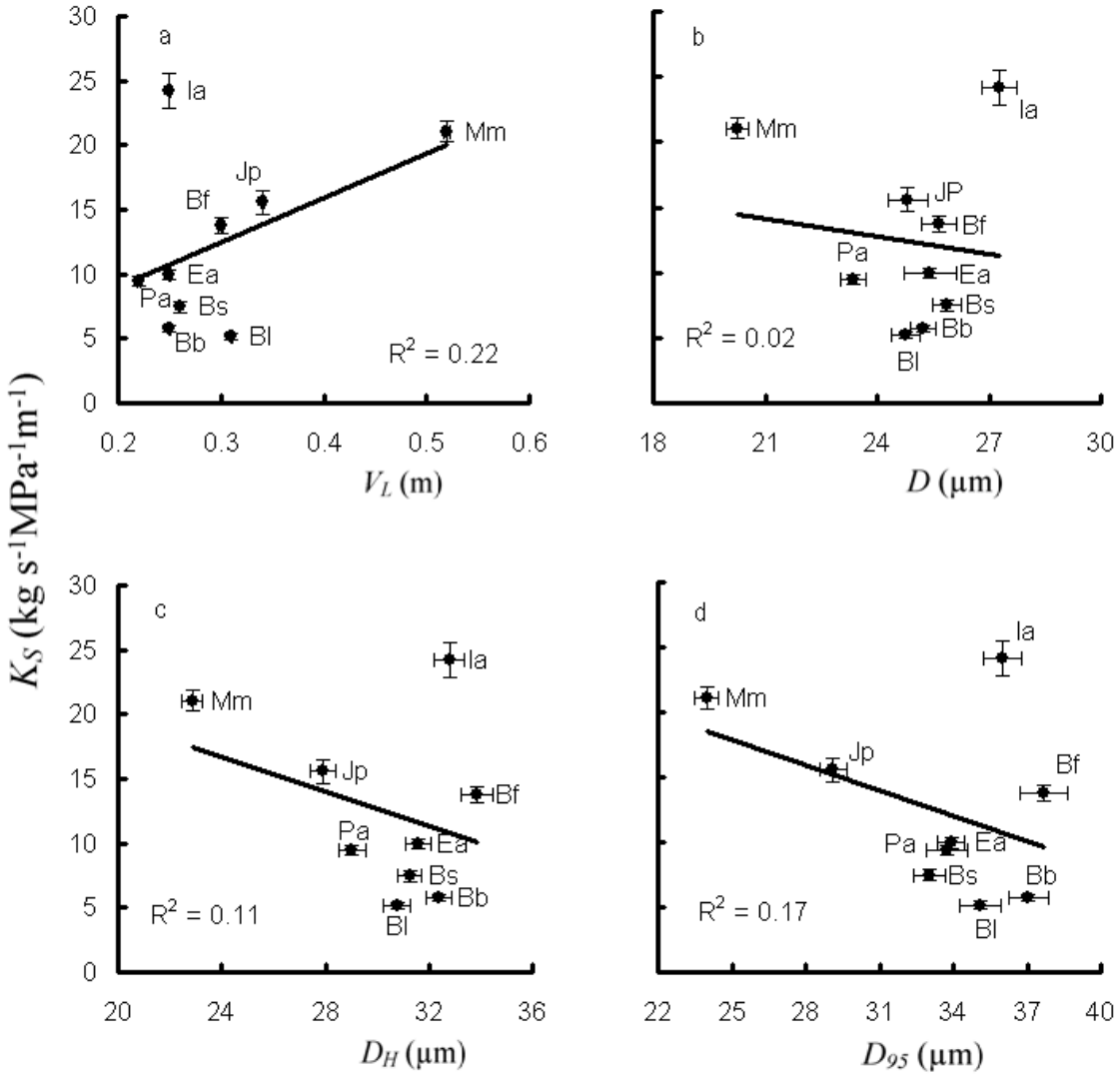


Figure 3.3: Relationships between specific hydraulic conductivity and xylem anatomical properties; (a) Vessel length (V_L), (b) mean diameter (D), (c) mean hydraulic diameter (D_H), (d) mean hydraulic diameter accounting for 95% flow (D_{95}). Each point is species mean ± SE (n = 25 trees per species). The regression coefficients for V_L, D_H, and D_{95} were significant ($P < 0.05$). The regression coefficient for D was insignificant ($P > 0.05$). The regression models describing the relationships were: $K_S = 1.52 + 0.927\ V_L$; $K_S = 1.22 - 0.139\ D$; $K_S = 1.90 - 0.597\ D_H$; $K_S = 2.12 - 0.724\ D_{95}$. Chart abbreviations are as before.

For the entire data set (n = 225 trees), specific leaf conductivity (K_L) was significantly and positively correlated to V_L (r = 0.33; $P < 0.001$), negatively correlated to both D_H (r = 0.15, P = 0.025), and D_{95} (r = 0.19, P = 0.005), not correlated to D (r = 0.06, P = 0.38).

At inter-species level (n = 9), K_L was significantly ($P < 0.05$) correlated with V_L, and not with vessel diameters (D, D_H, and D_{95}) (Figure 3.4). Tree species with high hydraulic efficiency had on average long and narrow vessels.

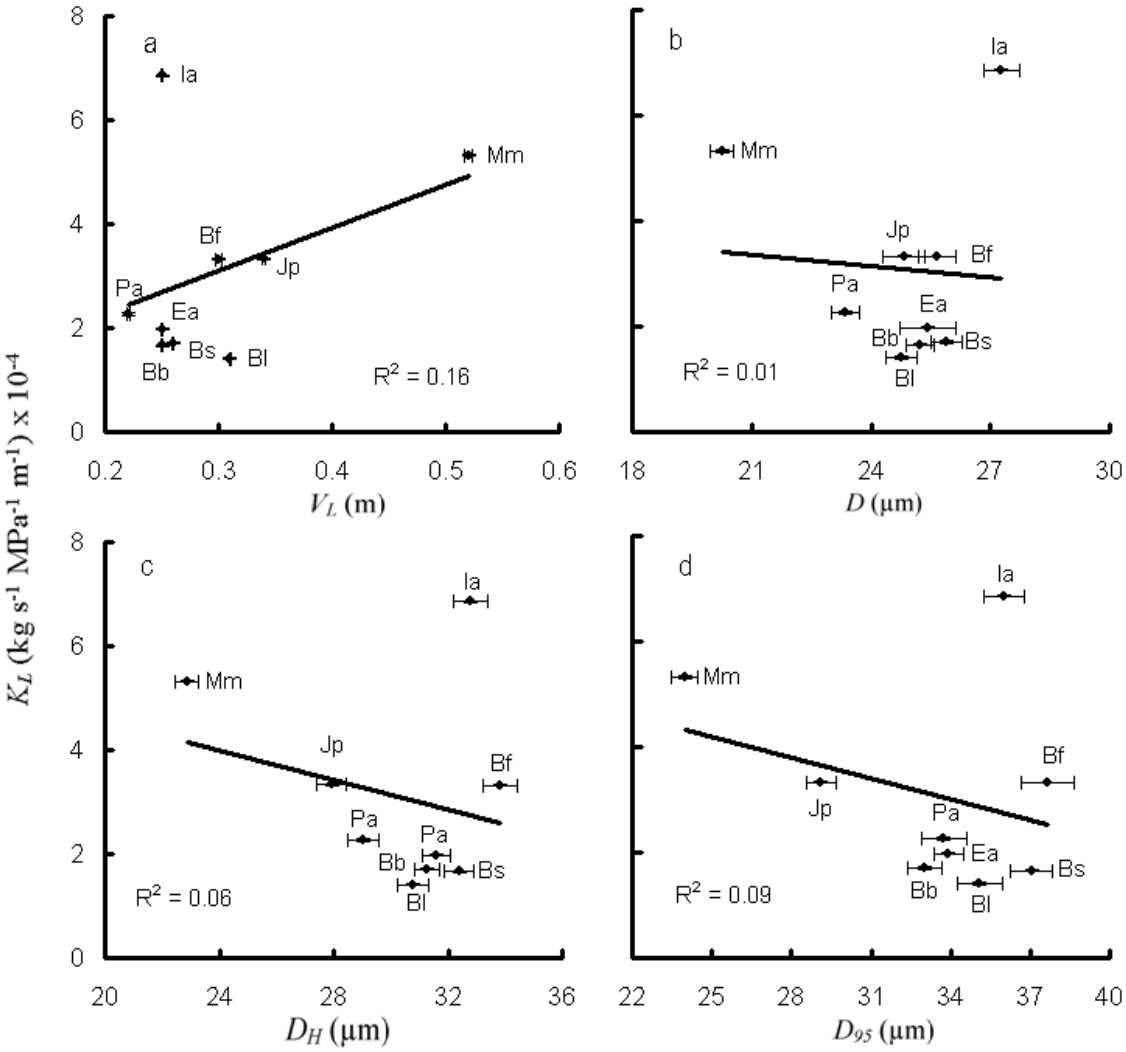


Figure 3.4: Relationships between leaf specific conductivity (K_L) and conduit parameters for the nine miombo woodlands tree species; (a) Vessel length (V_L), (b) mean diameter (D), (c) mean hydraulic diameter (D_H), (d) mean hydraulic diameter accounting for 95% flow (D_{95}). Each point is species mean ± SE (n = 25 trees per species). The regression coefficients for V_L, was significant ($P < 0.05$). The regression coefficients for vessel diameters (D, D_H, *and* D_{95}) were insignificant ($P > 0.05$). The regression models describing the relationships were: $K_L = 0.201 + 0.468\ V_L$; $K_L = 0.073 - 0.089\ D$; $K_L = 0.357 - 0.276\ D_H$; $K_L = 0.435 - 0.321\ D_{95}$.

3.3.3 Hydraulic and anatomic plasticity

There were significant (ANOVA, $P < 0.05$) variations in K_S, HV and K_L both between sites and species nested within sites (Table 3.2).

Table 3.2: Results of general linear model comparing hydraulic properties and conduit dimensions for wet and dry site generalists. Table abbreviations are as before.

Variable	**Scale**	***df***	***ms***	***F-ratio***	***P*-value**
HV	site	1	0.23144	11.23	0.001
	species	3	0.16530	8.02	< 0.001
	site x species	3	0.11823	5.74	0.001
K_S (kg s^{-1} MPa^{-1} m^{-1})	site	1	1.89255	84.78	< 0.001
	species	3	4.84983	217.27	< 0.001
	site x species	3	0.78715	35.26	< 0.001
K_L (kg s^{-1} MPa^{-1} m^{-1})	site	1	1.36652	62.06	< 0.001
	species	3	1.07042	48.61	< 0.001
	site x species	3	0.49055	22.28	< 0.001
D (μm)	site	1	37.18	1.88	0.263
	species	3	277.76	14.06	0.028
	site x species	3	19.75	1.38	0.251
D_H (μm)	site	1	83.89	0.81	0.436
	species	3	945.12	9.06	0.052
	site x species	3	104.34	5.39	0.001
D_{95} (μm)	site	1	196.02	1.00	0.391
	species	3	1768.85	9.00	0.052
	site x species	3	196.51	5.97	0.001
V_L (mm)	site	1	16.4	0.60	0.494
	species	3	14647.7	537.79	< 0.001
	site x species	3	27.2	0.03	0.994

Conduit diameters did not vary significantly (ANOVA, $P < 0.05$) between sites or species nested within sites. Vessel length did not vary significantly between sites but varied significantly between species nested within sites.

On average wet site generalists had significantly (Two-sample *t*-test assuming equal variances, $P < 0.05$) higher specific conductivity (K_S) and leaf specific conductivity (K_L) values than dry site generalists. A trend towards low K_S and HV from wet to dry miombo woodlands habitats was noticeable in *Brachystegia boehmii* (K_S, 5.7 ± 0.3 to 2.8 ± 0.07 kg s^{-1} MPa^{-1} m^{-1}; *HV*, 2.9 ± 0.02 to 2.2 ± 0.1), *Brachystegia spiciformis* (K_S, 7.5 ± 0.5 to 5.3 ± 0.18 kg s^{-1} MPa^{-1} m^{-1}; *HV*, 2.3 ± 0.02 to 1.4 ± 0.1) and *Erythrophleum africanum* (K_S, 10 ± 0.4 to 8.2 ± 0.3 kg s^{-1} MPa^{-1} m^{-1}; *HV*, 2.0 ± 0.01 to 2.1 ± 0.2) (Figure 3.5).

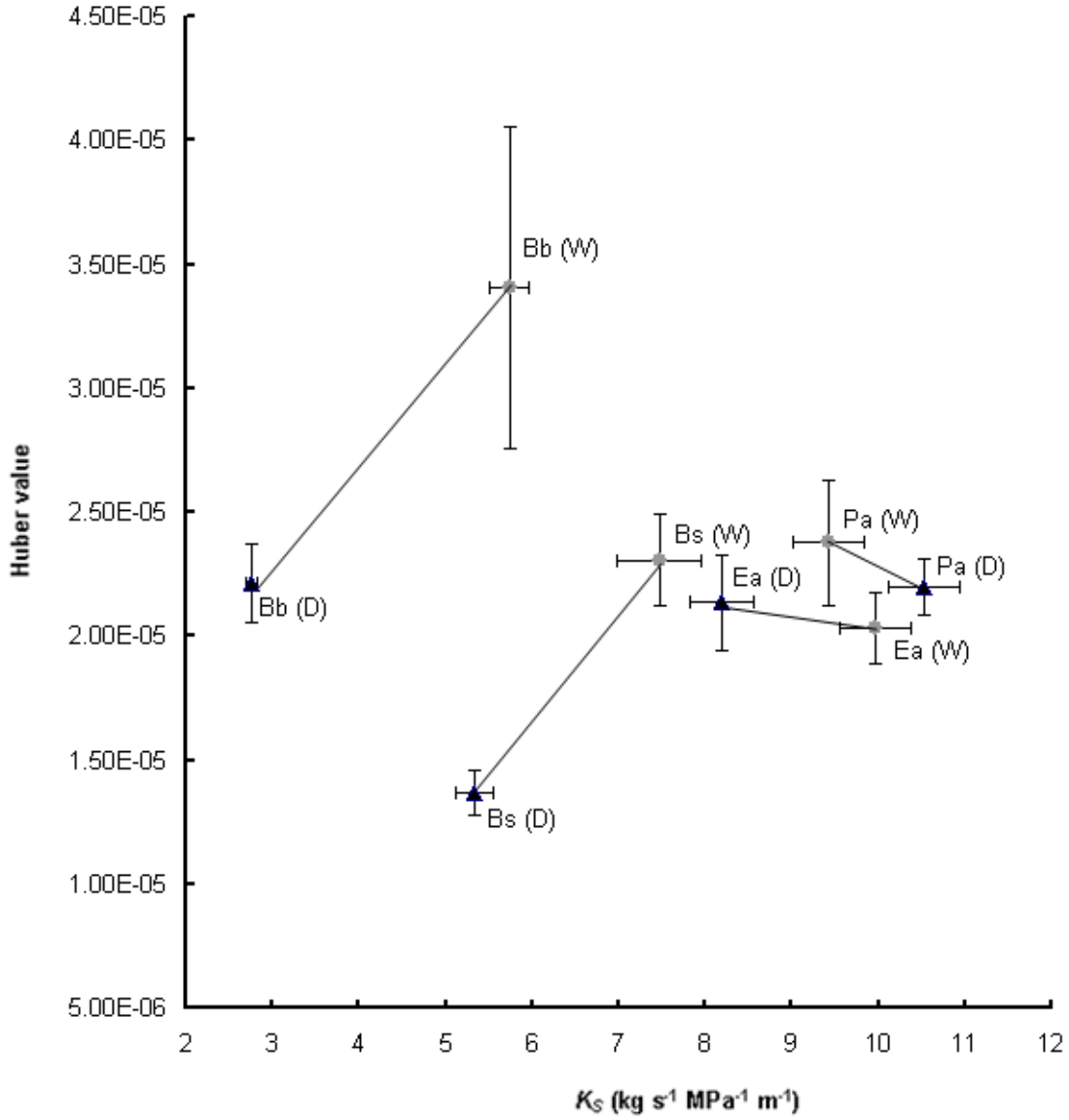


Figure 3.5: Plot of stem area specific hydraulic conductivity and Huber value (*HV*) showing changes in the two properties from wet to dry miombo woodlands site for the four broad ranging tree species. Each point is species mean ± SE (n = 25 trees per species). Chart abbreviations are as above. Letters *D* and *W* in parenthesis are abbreviations for dry and wet miombo sites.

Pericopsis angolensis showed significantly ($P < 0.05$) higher K_S on the dry (10.5 ± 0.4 x kg s^{-1} MPa^{-1} m^{-1}) than wet site (9.4 ± 0.4 x 10^{-4} kg s^{-1} MPa^{-1} m^{-1}). There was an insignificant ($P > 0.05$) difference in *HV* in *Pericopsis angolensis* between the wet and dry sites. There was a wet-dry site declining trend in leaf specific conductivity in *Brachystegia boehmii* (1.66 ± 0.12 to 0.59 ± 0.03 x 10^{-4} kg s^{-1} MPa^{-1} s^{-1}), *Brachystegia spiciformis* (1.71 ± 0.15 to 0.7 ± 0.04 x 10^{-4} kg s^{-1} MPa^{-1} s^{-1}), and *Erythrophleum africanum* (1.98 ± 0.15 to 1.59 ± 0.09 x 10^{-4} kg s^{-1} MPa^{-1} s^{-1}).

3.4 DISCUSSION

3.4.1 Variations in hydraulic properties among co-occurring species

Miombo woodlands canopy tree species showed substantial variations in hydraulic properties despite growing under similar climatic conditions (Table 3.1; p 59). We hypothesized that narrow habitat ranging tree species with mesic specialisation have a vascular system that is more efficient than broad ranging habitat generalists. Our results are in agreement with the hypothesis. There is a clear trend towards higher stem-area-specific (K_S) and leaf specific conductivities (K_L) in tree species adapted to wet miombo habitats than those with wide habitat distribution (Figure 3.2; p 57). Our hydraulic properties values for both mesic specialists and generalists fall within the range summarized by (Tyree and Zimmermann 2002) for most tropical trees around the world. The results from this study are consistent with many studies that have also reported similar trends towards higher stem-area-specific and leaf specific conductivities in tree species from wet ecosystems than ones from dry sites (Canham et al. 2009, Engelbrecht et al. 2000).

High specific conductivity and leaf specific conductivity among mesic specialists suggests an adaptation for supporting high transpiration rates. Leaf specific conductivity tends to be coordinated with stomatal conductance, such that tree species with high K_L have high stomatal conductance (Hubbard et al. 2001, Ripullone et al. 2007) and tend to have high photosynthetic rate (Brodribb et al. 2002). Low K_S and K_L among drought-deciduous habitat generalists suggests an adaptation towards increased cavitation resistance. This is consistent with the notion that tree species with low hydraulic supply are more resistant to water-stressed xylem cavitation than ones with efficient hydraulic systems (Tyree and Zimmermann 2002). Differences in both hydraulic conductivity and specific leaf conductivity between co-occurring miombo woodlands canopy tree species with substantial differences in habitat preference suggest that tree hydraulic architecture influences species habitat preference in this ecosystem.

3.4.2 Relationship between stem-area-specific hydraulic conductivity and conduit dimensions

We hypothesized that differences in hydraulic architecture are driven by differences in conduit structural dimensions. In a very consistent way, tree hydraulic architecture varied proportionally with conduit allometry among the nine miombo woodlands tree species differing in habitat preference. Generally, there is a strong relationship between hydraulic efficiency and conduit allometry among miombo species such that tree species with high hydraulic efficiency have long and narrow xylem conduits (Figure 3.3; p 61 and 3.4; p 63). Traditionally it has been concluded that individuals with wide conduits are more hydraulically efficient than ones with narrow conduits (Tyree and Zimmermann 2002). Our results are inconsistent with this notion as the more hydraulically efficient

individuals possessed narrow and long conduits. There are several reasons for this seemingly contradictory observation. Key among several reasons is that rate of water flow in the xylem is controlled by many other structural arrangements such as pits (frequency, size) in addition to conduit diameter. Available evidence suggest that lumen resistivity to flow tends to scale inversely with conduit length (Pittermann et al. 2006, Sperry et al. 2005). Therefore, the resistance for a stem of given length should be higher for species with short vessels, because of the reduced number of pits. Therefore, the high hydraulic conductivity among mesic specialists maybe attributed to their possession of average longer xylem vessels than co-occurring generalists. This conclusion is supported by our findings which show tight coordination between vessel length and stem hydraulic efficiency (Figure 3.3; p 61 and 3.4; p 63).

3.4.3 Hydraulic plasticity among broad ranging habitat generalists

Shifts in hydraulic properties in response to ecosystem water availability has been reported in a number of studies (Martínez-Vilalta et al. 2009, Preston and Ackerly 2003). Towards dry ecosystems plants tend to prevent the development of damaging water potential gradients by reducing the leaf-to-sapwood-area ratio as a compensatory strategy for increased transpiration (McDowell et al. 2002, Mencuccini and Bonosi 2001). Plants are also known to develop xylem structures with a distinct characteristic of narrow and short conduits towards arid ecosystems (Tyree and Zimmermann 2002) resulting in low hydraulic supply for plants in such ecosystems. We predicted that greater plasticity in xylem hydraulic properties and anatomic dimensions confers the ability for generalists to extend their distribution into drier miombo woodlands habitats. Our results are in agreement with the hypothesis as hydraulic properties among the four generalists shifted

in response to changing ecosystem aridity. However, vessel dimensions did not vary significantly either between the two sites or between species, suggesting non plastic response in this parameter (Table 3.2; 64). We believe that the reductions in K_S and K_L towards dry ecosystem among miombo generalists reflect their water use efficiency in dry habitats.

These differential hydraulic adjustments in response to ecosystem water availability reflect the long-term adaptation of these miombo trees to water stress. In Western Australia, Canham et al. (2009) surveyed four *Banksia* species growing in contrasting ecohydrological habitats. They reported a tendency for plants at wet sites to have higher K_S and K_L than those in dry sites. Experimental evidence in the case of *Vitis vinifera* demonstrated that plant hydraulic traits are very responsive to soil water dynamics (Lovisolo and Schubert 1998). The variations in hydraulic shifts among miombo generalists suggests that response to changing ecosystem water availability is species-specific and that different tree species employ diverse structural mechanisms to deal with water stress. This conclusion is strengthened by our results which show substantial differential shifts in sapwood to leaf area ratio and stem area specific hydraulic conductivity (Figure 3.5; p 66).

3.4.5 Conclusions

In conclusion our data show that miombo woodlands tree species adapted to wet habitats have higher hydraulic conductivities than tree species adapted to drier habitats. These variations are driven by differences in both the conduit diameter and length. The hydraulic architecture for mesic specialists appears to be suited to wet environments to

support presumably high transpiration rate. On the other hand generalists display hydraulic architectures which enable them to be very successful under water-limiting environments where the need to resist cavitation is more important than supporting high transpirational rates. Towards drier miombo habitats generalists employ diverse hydraulic strategies to improve fitness under drier miombo habitats. The most dominant generalists extend into the drier habitats by reducing both hydraulic conductivity and leaf specific conductivity. The other two species employ a combination of reducing specific conductivity and increased leaf specific conductivity. We can conclude that hydraulic architecture controls the range of habitats a species can colonize successfully and that the ability to attain wide habitat distribution among broad ranging tree species may be attributed to their greater hydraulic plasticity.

Acknowledgements

We wish to thank Milimo Miyoba, Metson Kasowe, Japhet Kabonso, and Kennedy Kayuma who helped with field and laboratory work. Zambia Forestry College and Choma district Forestry Department offices are thanked for providing laboratory spaces where all experimental work was conducted. The Zambia Meteorological Department is deeply appreciated for providing long-term climate data for Ndola and Choma.

Funding

Field work for this research was fully funded by the Association of Commonwealth Universities and the Copperbelt University.

3.5 REFERENCES

Beikircher, B. and S. Mayr. 2003. The hydraulic architecture of *Juniperus communis* L. ssp. communis: shrubs and trees compared. *Plant Cell and Environment* **31**:1545-1556.

Brodribb, J.T. and N.M. Holbrook. 2003. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytologist* **158**:295-303.

Brodribb, T.J., N.M. Holbrook, and M.V. Gutiĕrrez. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell and Environment* **25**:1435-1444.

Canham, A.C., R.H. Froend, and W.D. Stock. 2009. Water stress vulnerability of four Banksia species in contrasting ecohydrological habitats on the Gnangara Mound, Western Australia. *Plant Cell and Environment* **32**, 64–72.

Chidumayo, E. N. 1987. Species Structure in Zambian Miombo Woodland. *Journal of Applied Ecology* **3**:109-118.

Choat, B., M.C. Ball, J.G. Lully, and J.A.M. Holtum. 2005. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from North-eastern Australia. *Trees* **19**:305-311.

Cornwell, W. K., R. Bhaskar, L. Slack, S. Cordell, and C.K. Lunch. 2007. Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs low precipitation. *Functional Ecology* **21**:1063-1071.

Desankar, V. P. and C. Prentice. 1995. Modelling vegetation dynamics of miombo woodlands of Zambezian Africa under changing climatic conditions. In: Pemetta, J.C. et al. eds. *Impacts of Climate Change on Ecosystems and Species: Terrestrial Ecosystems*. IUCN, Gland, pp. 23-38.

Engelbrecht, B. M. J., V. Velez, and M.T.Tyree. 2000. Hydraulic conductance of two co-occuring neotropical understorey shrubs with different habitat preferences. *Annals of Forest Science* **57**:201-208.

Ewers, W. F. and J.B. Fisher. 1989. Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal Botany* **76**:645-656.

Frost, P. 1996. The Ecology of Miombo Woodlands. In *The Miombo in Transition: Woodlands and Welfare in Africa:* Ed B. Campbell. CIFOR, Bogor, pp. 11-57.

Goldstein, G., F. Rada, P. Rundel, A. Azocar, and A. Arozco. 1989. Gas exchange and water relations of evergreen and deciduous tropical savanna trees. *Annals of Forest Science* **46**:448s-453s.

Hao, G. Y., W. A. Hoffmann, F. G. Scholz, S. J. Bucci, F. C. Meinzer, A. C. Franco, K. Cao and G. Goldstein. 2008. Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. *Oecologia* **155**:405-415.

Hofmann, W.A. and A.C. Franco. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology* **91**:475-484

Hubbard, R. M., M.G. Ryan, V. Stiller, and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell and Environment* **24**:113-121.

IPCC 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, 976 p.

Kolb, K. J., J.S. Sperry and B.B. Lamont. 1996. A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. *Journal of Experimental Botany* **47**:1805-1810.

Lovisolo, C. and A. Schubert. 1998. Effects of water stress on vessel size and xylem hydraulic conductivity in Vitis vinifera L. *Journal of Experimental Botany* **49**:693-700.

Machado, J. and T.M. Tyree. 1994. Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. *Tree Physiology* **14**:219-240.

Maherali, H. and E. H. DeLucia. 2000. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiology* **20**:859-867.

Martínez-Vilalta, J., H. Cochard, M. Mencuccini, F. Sterck, A. Herrero, J. F. J. Korhonen, P. Llorens, E. Nikinmaa, A. Nolè, R. Poyatos, F. Ripullone, U. Sass-Klaassen and R. Zweifel. 2009. Hydraulic adjustment of Scots pine across Europe. *New Phytologist* **184**:353–364.

McDowell, N., H. Barnard, B.J. Bond, T. Hinckley, R.M. Hubbard, H. Ishii, B. Köstner, F. Magnani, J.D. Marshall, F.C. Meinzer, N. Phillips, M.G. Ryan and D. Whitehead. 2002. The relationship between tree height and leaf area: sapwood area ratio. *Oecologia* **132**:12–20.

Mencuccini, M. and L. Bonosi. 2001. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. *Canadian Journal of Forest Research* **31**:442–456.

Nicholson, E. S. 2001. Climatic and environmental change in Africa during the last two centuries. *Climate Change* **17**:123-144.

Patino, S., M.T. Tyree and E.A. Herre. 1995. Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic Ficus species from Panama. *New Phytologist* **129**:125-134.

Pittermann, J., J. S. Sperry, J.K. Wheeler, U.G. Hacke, and E.H. Sikkema. 2006. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant Cell and Environment* **29**:1618-1628.

Preston, A. K. and D.D. Ackerly. 2003. Hydraulic architecture and the evolution of shoot allometry in contratsing climates. *American Journal of Botany* **90**:1502-1512.

Ripullone, F., M.R. Guerrieri, A. Nole, F. Magnani and M. Borghetti. 2007. Stomatal conductance and leaf water potential responses to hydraulic conductance variation in *Pinus pinaster* seedlings. *Trees* **21**:371-378.

Sithole, A. and F.J.C. Murewi. 2009. Climate variability and change over southern Africa: Impacts and challenges. *African Journal of Ecology* **47**:17-20.

Smith, P. and Q. Allen. 2004. *Field Guide to The Trees and Shrubs of the Miombo Woodlands*. Royal Botanic Gardens Kew, London, 176 p.

Sperry, J. S., J.R. Donnelly, and M.T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell and Environment* **11**:35-40.

Sperry, J. S., U. G. Hacke, and J. K. Wheeler. 2005. Comparative analysis of end wall resistivity in xylem conduits. *Plant Cell and Environment* **28**:456-465.

Tyree, M. T. and M.H. Zimmermann. 2002. *Xylem Structure and the Ascent of Sap*. 2nd Edn. Springer, Berlin, 283 p.

van der Willigen, C.., H.W. Sherwin and N.W. Pammenter. 2000. Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. *New Phytologist* **145**:51-59.

Villar-Salvador, P., P. Castro-Diez, C. Perez-Rontome, G. Montserrat-Marti. 1997. Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees* **12**:90-96.

White, F. 1983. *The Vegetation of Africa : A Descriptive Memoir to Accompany the Unesco/AETFAT/UNSO Vegetation Map of Africa*. Unesco, Paris: 356 p.

Zar, J. H. (2010) *Biostatistical Analysis*. 5th Edn. Pearson Education International, London, 944 p.

Zimmermann, M. H. and A.A. Jeje. 1981. Vessel length in stems of some American woody species. *Canadian Journal of Botany* **59**:1882–1892.

CHAPTER 4

Xylem cavitation vulnerability influences tree species habitat preference in miombo woodlands

OVERVIEW

Cavitation in plants significantly alters the rate of water flow through the xylem. Xylem dysfunction has been linked to vegetation distribution in many ecosystems (Brodribb & Hill 1999; Pockman & Sperry 2000). The ability to resist cavitation varies with species hydraulic architecture. Miombo ecoregion is predicted to experience increased ecosystem aridity under future climate scenarios. Water stress may induce cavitation related species mortalities. Although miombo woodlands in Africa have long been identified as a water-limited ecosystem where tree species distribution is limited by water stress, we know very little about the physiology of its principal species in relation to drought resistance. This Chapter addresses this knowledge gap by examining xylem vulnerability to cavitation for nine miombo principal tree species (objective 2; p 12).

Here I test whether difference in habitat preference among miombo principal trees is as a result of significant variation in cavitation resistance. I also test the extent to which cavitation resistance varies between similar tree populations growing in habitats with contrasting soil moisture availability.

This paper has been submitted to Plant, Cell and Environment. This article was written by Royd Vinya with valuable comments coming from Yadvinder Malhi, Nick Brown, Timothy Brodribb, Joshua Fisher and Luis Aragao.

Title: Xylem cavitation vulnerability influences tree species habitat preference in miombo woodlands

Authors: Royd Vinya[1, 2], Yadvinder Malhi[1], Joshua B Fisher[1], Luiz Aragao[5], Nick Brown[3], Timothy Brodribb[4],

1 School of Geography and the Environment, Oxford University Centre for the Environment,
2 School of Natural Resources, Copperbelt University,
3 Plant Sciences Department, University of Oxford,
4 School of Plant Sciences, University of Tasmania

ABSTRACT

Cavitation vulnerability studies are central to understanding the potential response of miombo woodlands tree species to predicted future drying under global climate change. In this study, we investigated xylem vulnerability to cavitation for nine miombo woodlands canopy tree species differing in habitat preference and leaf phenology. We used the standard bench drying technique to induce cavitation in twigs. We measured cavitation vulnerability (Ψ_{50}), stem-area specific hydraulic conductivity (K_S), and xylem anatomic parameters (mean hydraulic diameter - D_H; mean hydraulic diameter accounting for 95% flow - D_{95} and; conduit length - V_L) that influence xylem transport. Results show that tree species with a narrow habitat range (mesic specialists) are more vulnerable to cavitation than habitat wide ranging species (generalists). The water potential at 50% loss in hydraulic conductivity for mesic specialists ranged between − 1.5 and − 2.2 MPa and that for generalists between − 2.5 and − 3.6 MPa. We observed a strong trade-off

between K_S and Ψ_{50}. While vessel diameters were insignificantly ($P > 0.05$) correlated with Ψ_{50}, V_L was significantly ($P < 0.05$) and negatively correlated to Ψ_{50}. Our results suggest that xylem cavitation vulnerability might be one of the decisive factors setting ecological boundaries for principal miombo species.

Key words: Cavitation; Climate change; Leaf specific conductivity; Miombo woodlands; xylem transport

4.1 INTRODUCTION

The likelihood that stability of the soil-plant-atmospheric-continuum (SPAC) will be compromised as a result of air entering a conducting xylem conduit increases with increasing water stress (Tyree & Sperry 1988). This hydraulic dysfunction occurs when air is pulled into xylem conduits and expands rapidly to limit fluid transport of water in plants in a process called cavitation. Cavitation in plants disrupts long distance xylem water transport leading to a decrease in hydraulic conductivity (Tyree & Sperry 1989). Therefore, the ability to withstand cavitation and continue to conduct water under high-water stress defines a plant's drought tolerance capability and the range of habitats it can successfully colonise (Brodribb & Hill, 1999; Pockman & Sperry 2000). The most common measure of xylem vulnerability to cavitation is the water potential causing 50% (Ψ_{50}) reduction in hydraulic conductivity. High cavitation susceptibility is closely correlated with lower tolerances to water deficit (Edwards & Diaz, 2006, Kolb & Davis, 1994, Stratton, Goldstein & Meinzer, 2000, Tyree & Zimmermann, 2002). Given the negative impact of cavitation on plants xylem long distance water transport pathway (Zimmermann, 1983), one would expect that the relationship between reduction in

hydraulic conductivity and cavitation resistance may play a pivotal role in defining a species ecological limits in water-limited ecosystems. From a functional point of view, this relationship is expected to play some crucial role in influencing species extinction rates under global climate change.

As regards Africa's miombo ecoregion, future climate prediction is for a reduction in mean annual precipitation by more than 20% (Sithole & Murewi 2009). The magnitude of this predicted climatic shift suggests that the miombo biome might be at risk of experiencing increased drought-stress related species mortality. There is evidence suggesting that water stress can lead to cavitation-induced plant mortality (Tyree et al. 2003). Therefore, the predicted rapid environmental change requires a management response that should be informed by sound knowledge of tree species' physiology. At present our knowledge about the relationships between xylem cavitation vulnerability and species habitat preference for the miombo woodlands in Africa is insufficient.

Therefore, the main objective of this study was to study under field conditions xylem cavitation vulnerability and the extent to which this physiological property controls tree species habitat preference in Zambia's miombo woodlands. In this study, we ask the following questions:

- Do miombo woodlands tree species differing in niche specialization show significant differences in xylem cavitation resistance and to what extent do they differ in xylem anatomy related to hydraulic conductance? This question was answered by studying the hydraulic properties, and xylem structure in co-occurring miombo woodlands canopy tree species differing in habitat preference and leaf phenology.

- To what extent is cavitation resistance coordinated with hydraulic efficiency and is there a functional relationship between conduit size and cavitation vulnerability among miombo tree species? This is consistent with the proposed trade-off between xylem efficiency and safety (Zimmermann 1983).
- Do tree species occupying miombo woodlands habitats with contrasting precipitation show plasticity in cavitation resistance and xylem structure? This was answered by comparing the hydraulic properties and xylem anatomy of naturally occurring habitat wide ranging conspecific tree populations growing in wet and dry miombo woodlands sites.

4.2 MATERIALS AND METHODS

4.2.1 Site

Using the 1000 mm isohyet, White (1983) subdivided the miombo into wet (above 1000 mm mean annual precipitation) and dry (less than 1000 mm mean annual precipitation) woodlands. The wet northern miombo woodlands are species rich and support both drought-tolerant wide habitat-ranging and drought-intolerant narrow-habitat-ranging tree species (Chidumayo 1987). Consistent with the subdivision of the miombo into wet and dry woodlands, we chose two gazetted forest reserves representative of the wet and dry miombo vegetation types. The two selected forest reserves had known forest management histories, current soil-vegetation surveys and were reasonably similar in geology, although some minor local variations may have been present. The two forest reserves experience weather pattern in which summer rains occur between November and April followed by an extensive seasonal drought lasting from May to October. The wet site forest reserve was Mwekera National Forest No. 6 located on the outskirts of Kitwe City

(12˚ 49´ S and 28˚ 22´ E; elevation 1295m above sea level). The vegetation of the wet site is predominantly *Brachystegia-Julbernardia* woodlands with the genera *Brachystegia*, *Isoberlinia*, *Julbernardia* and *Marquesia* as common canopy co-dominants (Chidumayo 1987). The area received an average annual precipitation of 1,200 mm with mean annual temperatures ranging from 14 to 28 ^{o}C (data from Ndola Airport, located 35 km from the study site). The location of the dry site was Choma district at 16^{o} 50' S and 27^{o} 03' E with an average elevation of 1266 m above sea level.

The vegetation of the dry site has *Brachystegia boehmii*, *Brachystegia spiciformis*, and *Julbernardia globiflora* as the common canopy co-dominants. The dry site receives 800 mm of mean annual precipitation with mean annual temperatures ranging between 12 ^{o}C and 27 ^{o}C (data collected 20 km from the study site).

4.2.2 Sampling

In this study, we examined nine co-dominant miombo woodlands tree species. Four of the nine species [*Brachystegia floribunda* Benth (Fabaceae), *Isoberlinia angolensis* (Benth.) Hoyle & Brenan (Fabaceae), *Julbernardia paniculata* (Benth.) Troupin (Fabaceae), and *Marquesia macroura* Gilg (Dipterocarpaceae)] display a narrow habitat range with distribution mainly confined to wet miombo sites and are referred to as mesic specialists in this study. The other five species [*Brachystegia boehmii* Benth (Fabaceae), *Brachystegia longifolia* Benth (Fabaceae), *Brachystegia spiciformis* Benth (Fabaceae), *Erythrophleum africanum* (Benth.) Harms (Fabaceae), and *Pericopsis angolensis* (Baker) Meeuwen (Fabaceae)] exhibit wide habitat ranges with distributions throughout the miombo eco-region and are referred throughout this study as generalists. The full botanical and ecological descriptions of these trees have been adequately presented by

Palgrave (2002) and Smith and Allen (2004). We selected the nine tree species on the basis that: (1) they differed substantially in habitat preference (Chidumayo 1987; Smith & Allen 2004), (2) they had contrasting leaf phenology, and (3) they form much of the canopy throughout the miombo woodlands.

We sampled twenty five (25) trees per species (giving a total of 225 trees on the wet and 100 trees on the dry sites). Selection of trees was based on the criteria that they were healthy, actively growing, and at least 100 m apart. On the dry site, 100 trees were sampled due to the absence of *Brachystegia longifolia*. On both the dry and wet sites, we controlled for local environmental variability by sampling individuals that co-occurred. Co-occurring individual trees were tagged, and their GPS coordinates recorded to facilitate repeat measurements. To avoid confounding effects of soil characteristics and water variability we avoided sampling species on hill slopes (Trapnell et al. 1976) and riparian zones, respectively. The average diameter at breast height for the sample trees ranged from 30 to 39 cm on the wet site and from 18 to 25 cm on the dry site (Appendix 5.1).

4.2.3 Anatomical measurements

We determined maximum vessel length by forcing air at a pressure of between 60 – 100 kPa through the basal end of the twig while at the same time keeping the distal end dipped into a bucket of water (Choat et al., 2005; Ewers & Fisher, 1989; Zimmermann & Jeje, 1981). The distal end of a twig was continuously cut back in sections of 1 cm until bubbles formed at the cut end. Once bubbles appeared, the total length of the remaining portion measured. This was then recorded as the maximum vessel length for the twig.

We measured vessel diameter on twig samples similar in diameter as the ones used for conductivity determination (samples ranged in lengths from 5 to 6 cm). Sample preparation prior to vessel diameter determination involved soaking them for 3 weeks in a solution of ethanol, distilled water, and glycerol mixed in equal proportions (Beikircher & Mayr, 2008). This procedure ensured that the woody samples were soft enough to produce smooth cuts as well as prolonging the life span of the microtome blade. Cross-sections were cut between 15 and 30 µm thick using a manual sliding microtome. We flushed the micro sections with Xylene to check for the presence of water and further promote dehydration. The micro sections were, thereafter, stained with Safranin and mounted with Canada balsam. They were immediately dried in an oven at 80^{o}C for 8 – 12 hrs. Micro slides were photographed using a digital camera mounted on a microscope. The photographs were prepared and analyzed using the software Image J (freely available from www. http://rsb.info.nih.gov/ij/). Using the analyze function in Image J, minimum vessel thresholds were set at 10 μm. Three different types of vessel diameters were analyzed, following the procedures of Tyree & Zimmermann, (2002). The three vessel diameters analyzed were mean vessel volume (D), hydraulic mean diameter (D_H), and mean vessel diameter accounting for 95% conductivity (D_{95}).

Arithmetic mean vessel diameter (D_H) was calculated by averaging all vessels. Mean hydraulic diameter was calculated as:

$$D_H = \left[\frac{\sum D^4}{N} \right]^{1/4} \qquad \text{[Eqn 1]}$$

Mean diameter accounting for 95% conductance was calculated by ranking all the diameters raised to the fourth power in ascending order. These D^4 diameters were then

summed up until their sum was equal to 95% of the total conductance (Tyree & Zimmermann, 2002). An arithmetic mean was then calculated for diameters accounting for this conductance.

4.2.4 Hydraulic properties

We sampled only second-order branches in order to minimize confounding effects arising from differences in branch diameters (Patino, Tyree, & Herre 1995; Van der Willigen, Sherwin, & Pammenter 2000). Given that plant hydraulic properties show strong vertical variations within an individual tree (Tyree & Zimmermann 2002), we minimized this effect by sampling from roughly the mid-crown. We harvested three healthy second-order leaf-bearing twigs in the early hours of the morning (between 05:30 and 07:30hrs) from each of the replicate individuals for each species (giving a total of 675 twigs on the wet site and 300 twigs on the dry site). The diameter underbark for the harvested twigs ranged from 4 to 10 mm. The harvested twigs were immediately covered in wet towels and sealed in plastic sample bags in order to minimize dehydration through the exposed cut vessels. Samples were then transported to the nearby laboratory for conductivity determination. At the laboratory, we trimmed the twigs to approximately equal to the length as the determined species maximum vessel length plus 10% allowance in order to avoid open vessels. Throughout sample preparation, twigs were always kept totally immersed in distilled water. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Laboratory rubber corks gave a water-tight connection between the segment and water reservoir. The water reservoir was constantly refilled in order to maintain the same delivery pressure. Segments were perfused with degassed,

filtered (to 0.2 μm) and acidified (with HCl, pH = 2) distilled water. Previous studies have established that failure to acidify the perfusion solution, may promote growth of microbes in the water reservoir thereby leading to a decline in conductivity (Kolb, Sperry & Lamont 1996; Sperry, Donelly & Tyree 1988). We, therefore, acidified the perfusion solution with HCl acid in order to prevent microbial growth in the water reservoir. We allowed each segment to equilibrate for between 15 to 30 minutes before initial flow rate determination. Sap flow measurement involved attaching a pre-weighed cotton wool covered in a plastic onto the free distal end of the segment to reduce evaporation losses. Prior to measuring sap flow, we flushed all segments at a constant pressure of 150 kPa. Flushing times ranged from 20 to 30 minutes depending on species and degree of xylem air blockage. Therefore, the figures reported here are maximum conductivities. At the end of each flow determination, segment underbark diameter and length were accurately measured (using a digital micro caliper - accuracy 0.01mm). Segments where pith was exceedingly pronounced (exceeding 10% of sapwood diameter) the pith diameter was also measured and subtracted from the total diameter. Maximum hydraulic conductivity (K_H) was calculated as:

$$K_H = \left(\frac{J_V}{(\Delta P / l)}\right) \qquad (\text{kg s}^{-1}\ \text{MPa}^{-1}\ \text{m}) \qquad \text{[Eqn 2]}$$

where K_H is the maximum hydraulic conductivity, J_V is the flow rate (kg s^{-1}); ΔP is the delivery pressure (MPa) and; l is segment length (m).

Stem-area specific hydraulic conductivity (K_S, kg s^{-1} m^{-1} MPa^{-1}) was derived by dividing hydraulic conductivity with the effective sapwood cross-sectional area (m^2).

4.2.5 Cavitation induction

The standard bench drying technique was employed to generate cavitation in twigs (Cochard, Cruiziat & Tyree 1992). We harvested three twigs per sample tree for cavitation vulnerability experiment. Samples were left to dehydrate naturally on laboratory benches and their water potentials periodically monitored. We dehydrated the samples to varying range of water potentials corresponding to 0 - >80% loss of hydraulic conductance. Depending on species, the drying periods ranged from 6 – 48 hrs. Samples for the conductivity experiment were the control samples, and we took the necessary steps to ensure that they remained hydrated as explained in the previous section. The harvested twigs were long enough to allow for excision of small samples for water potential determination. Small sample twigs for water potential measurements were initially sealed in plastic bags for 30 minutes to allow for equilibration of water potential. Thereafter, water potential of the segment was determined using a pressure chamber (SKPM 1405, Skye Instruments, Llandrindod Wells, UK).

For construction of vulnerability curves, hydraulic conductivity (K_H minimum) was initially determined on dehydrated segments using the gravimetric method already described above. This was followed by flushing out emboli as described above and re-measurement of K_H to obtain K_H maximum. Percent reduction in hydraulic conductivity (PLC) was then calculated as:

$$PLC = \frac{K_{H\,\max} - K_{H\,\min}}{K_{H\,\max}} \times 100 \qquad \text{[Eqn 3]}$$

where K_H max is the maximum hydraulic conductivity without emboli and; K_H min is initial hydraulic conductivity with emboli. To confirm that the segments had thoroughly

been freed of emboli, they were perfused with Safranin dye at the end of each experiment.

Vulnerability curves were constructed by plotting the water potential versus percent loss in hydraulic conductivity. The vulnerability curves were fitted with the following sigmoid function:

$$PLC = 100 / (1 + \exp (a (\Psi - \Psi_{50}))) \quad \text{[Eqn 4]}$$

where Ψ_{50} is the water potential associated with 50% loss in hydraulic conductance, and *a* represents the slope of the vulnerability curve. Sigmoid function provided the best fit for the miombo tree species. The use of the sigmoid function is justified by its vital relationship with the air seeding theory (Pammenter & van der Willigen 1998). Zimmermann's (1983) air-seeding hypothesis predicts that the pressure needed to generate cavitation in a conducting xylem is inversely proportional to the diameter of the pit membrane pore. Therefore, the Ψ_{50} on the vulnerability curve relates to the rare largest pit pore, whereas *a* relates to the air entry point on the vulnerability curve, over which conductivity loss begins to rise (Domec & Gartner 2001; Meinzer et al. 2009).

4.2.6 Statistics

Statistical analyses were performed in Minitab (version 14 Minitab Inc., State College, Pennsylvania, USA). We used mixed-effects ANOVA model to compare differences in hydraulic properties and xylem anatomy for the nine miombo woodlands canopy tree species co-occurring on a wet site. We used a general linear model ANOVA to test for the effects of site and species between generalists' populations growing on the wet and dry miombo woodlands sites. In this mixed model, site was a fixed factor and the random

factor was species. Specific hydraulic conductivity, cavitation resistance, and xylem dimensions (diameter and length) were each treated as dependent variable while site and species were independent variables. This mixed model allowed us to answer the question whether most of the variations in hydraulic properties and xylem anatomy occur from site to site or species to species (Zar 2010). The relationship between cavitation resistance, hydraulic efficiency and xylem anatomy, was analysed using linear regression analysis. Prior to any statistical analysis, data was log transformed to achieve normality and variance constant.

4.3 RESULTS

4.3.1 Variations in cavitation resistance, hydraulic efficiency, and conduit parameters

Mean specific hydraulic conductivity and xylem conduit parameters are presented in Table 4.1.

Table 4.1: Vessel diameters and length among the examined nine miombo woodlands canopy tree species. Table abbreviations are: K_S = specific hydraulic conductivity; D = mean vessel diameter; D_H = mean hydraulic diameter; D_{95} = mean hydraulic diameter accounting for 95% flow and; V_L = vessel length

Site	Species	K_S (kg s^{-1} MPa^{-1} m^{-1})	Conduit diameters (μm)			V_L (mm)
			D	D_H	D_{95}	
	Brachystegia boehmii	5.74 ± 0.3	25 ± 0.6	32 ± 0.9	37 ± 1.4	247 ± 1.0
	Brachystegia longifolia	5.17 ± 0.3	26 ± 0.7	31 ± 0.8	34 ± 1.1	309 ± 1.0
	Brachystegia spiciformis	7.47 ± 0.5	25 ± 1.2	32 ± 0.9	34 ± 1.0	260 ± 1.0
	Erythrophleum africanum	9.97 ± 0.4	24 ± 0.6	29 ± 1.0	33 ± 1.4	251 ± 1.0
Wet	*Pericopsis angolensis*	9.43 ± 0.4	20 ± 0.5	23 ± 0.7	24 ± 0.8	220 ± 1.0
	Brachystegia floribunda	13.73 ± 0.6	25 ± 0.7	31 ± 1.0	35 ± 1.6	295 ± 2.0
	Isoberlinia angolensis	24.19 ± 1.3	26 ± 0.8	34 ± 1.0	38 ± 1.8	254 ± 1.0
	Julbernardia paniculata	15.58 ± 0.9	27 ± 0.8	33 ± 1.0	37 ± 1.1	340 ± 2.0
	Marquesia macroura	21.07 ± 0.8	25 ± 1.0	28 ± 0.9	29 ± 1.0	524 ± 5.0
Dry	*Brachystegia boehmii*	2.77 ± 0.07	25 ± 0.7	34 ± 1.4	39 ± 1.7	245 ± 11.0
	Brachystegia spiciformis	5.33 ± 0.18	25 ± 0.8	29 ± 1.0	31 ± 1.3	259 ± 8.0
	Erythrophleum africanum	8.19 ± 0.28	21 ± 0.9	25 ± 0.5	26 ± 0.5	253 ± 9.0
	Pericopsis angolensis	10.53 ± 0.35	21 ± 0.5	23 ± 0.7	24 ± 0.7	221 ± 8.0

The vulnerability curves for the nine Miombo woodlands canopy tree species are presented in Fig 4.1.

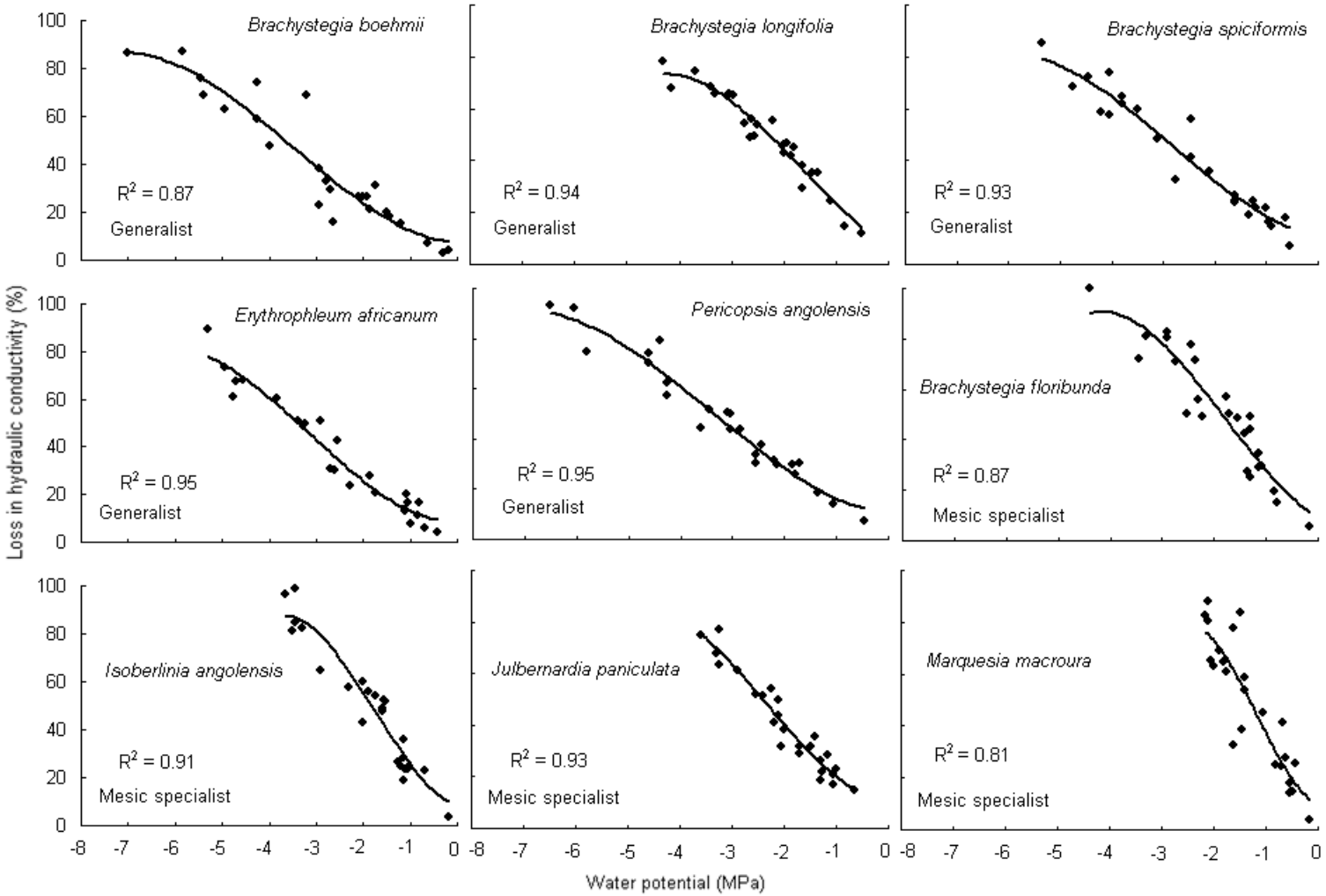


Figure 4.1: Cavitation vulnerability curves for nine co-occurring miombo forest tree species co-occurring on a wet site.

There were clear differences in vulnerability curves between mesic specialists and habitat generalists. Generalists displayed significantly (ANOVA, $P < 0.05$) higher cavitation resistance than mesic specialists (Fig 4.2).

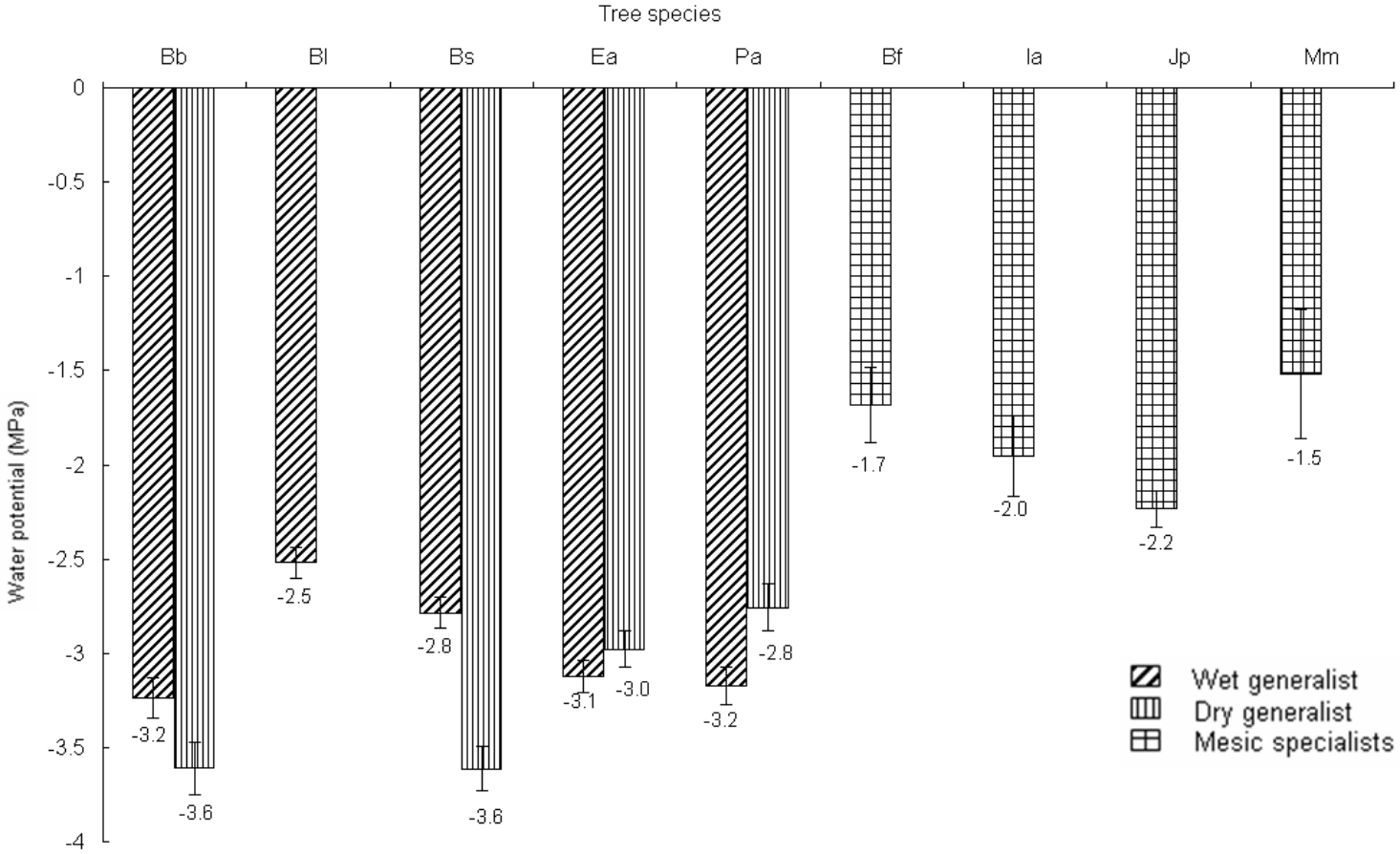


Figure 4.2: Average water potential at 50% (Ψ_{50}) loss in hydraulic conductivity for nine miombo woodland tree species growing on both dry and wet sites. Tree species averages were determined from the vulnerability curves in fig. 1 and 3. Bars are species means ± SE (*n* = 25 trees per species). Error bars are at 95% confidence interval. Chart abbreviations are: Bb = *Brachystegia boehmii*; Bl = *Brachystegia longifolia*; Bs = *Brachystegia spiciformis*; Ea = *Erythrophleum africanum*; Pa = *Pericopsis angolensis*; Bf = *Brachystegia floribunda*; Ia = *Isoberlinia angolensis*; Jp = *Julbernardia paniculata*; Mm = *Marquesia macroura*.

Overall, miombo woodlands generalists were significantly more resistant to xylem cavitation than mesic specialists. The two mesic specialists, *Marquesia macroura* and *Brachystegia floribunda* displayed highest vulnerability, with both species losing 50% of conductivity at less negative xylem pressures than the rest. The least cavitation resistant generalist was *Brachystegia longifolia* with 50% loss of conductivity at water potential less than 3 MPa.

There was significant ($P < 0.05$) variability in hydraulic conductivity (K_S) and xylem vulnerability to cavitation (Ψ_{50}) for the nine miombo woodlands canopy tree species differing in habitat preference. Functional type explained almost 50% of the variance, while species nested within-functional type and individual nested within species explained a total of 31%. By contrast, functional type explained only 8% of the variances in Ψ_{50}, whereas species nested within functional type explained 4% with individual trees nested within-species explaining 42% of the variance (Table 4.2).

Table 4.2: Results of linear mixed effects analysis of variance for nine miombo woodlands tree species studied. Ψ_{50} = water potential causing 50% loss in conductivity; K_S = stem-area-specific hydraulic conductivity; V_L = vessel length; D = Mean vessel diameter; D_H = mean hydraulic diameter; D_{95} = mean hydraulic diameter accounting for 95% flow; V_D = vessel density; *MS* = mean square; *VC* = variance component.

Variable	**Source**	***df***	***MS***	***F-ratio***	***P***	***VC***
Ψ_{50} (MPa)	Functional Type	1	65.3256	12.18	0.01	7.63
	Species (Functional Type)	7	5.3625	3.10	0.004	4.18
	Individual (Functional (Type Species))	216	1.7298	1.84	< 0.001	41.58
K_S (kg s^{-1} MPa^{-1} m^{-1})	Functional Type	1	25.463	661.33	< 0.001	49.72
	Species (Functional Type)	7	1.1289	29.32	< 0.001	15.43
	Individual (Functional Type Species)	216	0.0385	1.82	< 0.001	16.24
V_L (m)	Functional Type	1	2.5169	6022.46	< 0.001	32.45
	Species (Functional Type)	7	0.7130	1706.08	< 0.001	64.36
	Individual (Functional Type Species)	216	0.0004	1.2	0.058	1.16
D (µm)	Functional Type	1	0.0077	0.29	0.591	0.12
	Species (Functional Type)	7	0.1100	4.16	< 0.001	11.62
	Individual (Functional Type Species)	216	0.0265	88.09	< 0.001	86.23
D_H (µm)	Functional Type	1	0.1443	11.19	0.001	3.25
	Species (Functional Type)	7	0.2055	15.93	< 0.001	32.43
	Individual (Functional Type Species)	216	0.0129	86.03	< 0.001	62.80
D_{95} (µm)	Functional Type	1	0.3412	25.15	< 0.001	5.00
	Species (Functional Type)	7	0.2618	19.3	< 0.001	26.81
	Individual (Functional Type Species)	216	0.0136	3.53	< 0.001	42.88
V_D (vessels/ mm^2)	Functional Type	1	0.2603	3.51	0.062	0.85
	Species (Functional Type)	7	2.0622	27.81	< 0.001	46.97
	Individual (Functional Type Species)	216	0.0742	1713.64	< 0.001	52.12

More of the variations in conduit length were explained by differences between functional types and species nested within-functional type than differences between individual trees nested-within species. Functional type and species explained more than

90% of variances in conduit length in comparison to less than 2% accounted for by individual trees nested within-species (Table 4.2). Both mean hydraulic diameter (D_H) and hydraulic diameter accounting for 95% flow varied significantly between functional type, species and individuals nested within-species, whereas mean diameter (D) did not vary significantly between functional types (Table 4.2).

4.3.2 Relationships among hydraulic efficiency, xylem anatomy, and cavitation resistance

Cavitation resistance was significantly ($P < 0.05$) negatively correlated with specific hydraulic conductivity. A linear regression explained 54% of the variations in specific hydraulic conductivity (Fig 4.3). The relationship between K_S and Ψ_{50} remained significant even after removing the influential species (*Marquesia macroura*) from the analysis.

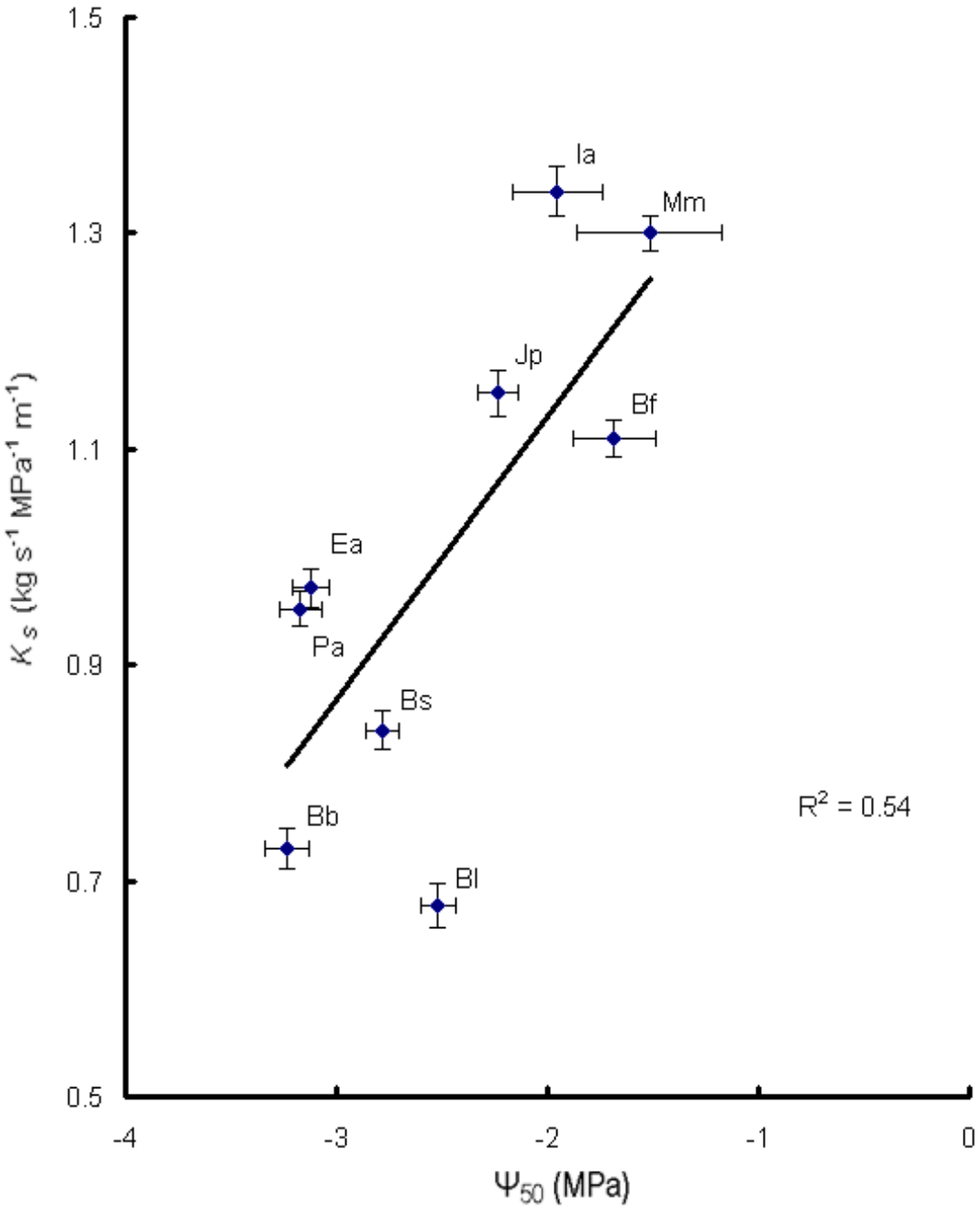


Figure 4.3: Stem specific hydraulic conductivity (K_S) versus stem water potential threshold causing 50% loss in hydraulic conductivity. Points are species means ± SE (n = 25 trees per species). Error bars are at 95% confidence interval. Chart abbreviations are as before.

There was a positive and significant correlation between cavitation resistance and conduit length. A linear regression explained 53% of the variations in cavitation resistance (Fig 4.4). The relationship between conduit length and Ψ_{50} remained significant even after removing the influential species (*Marquesia macroura*) from the analysis.

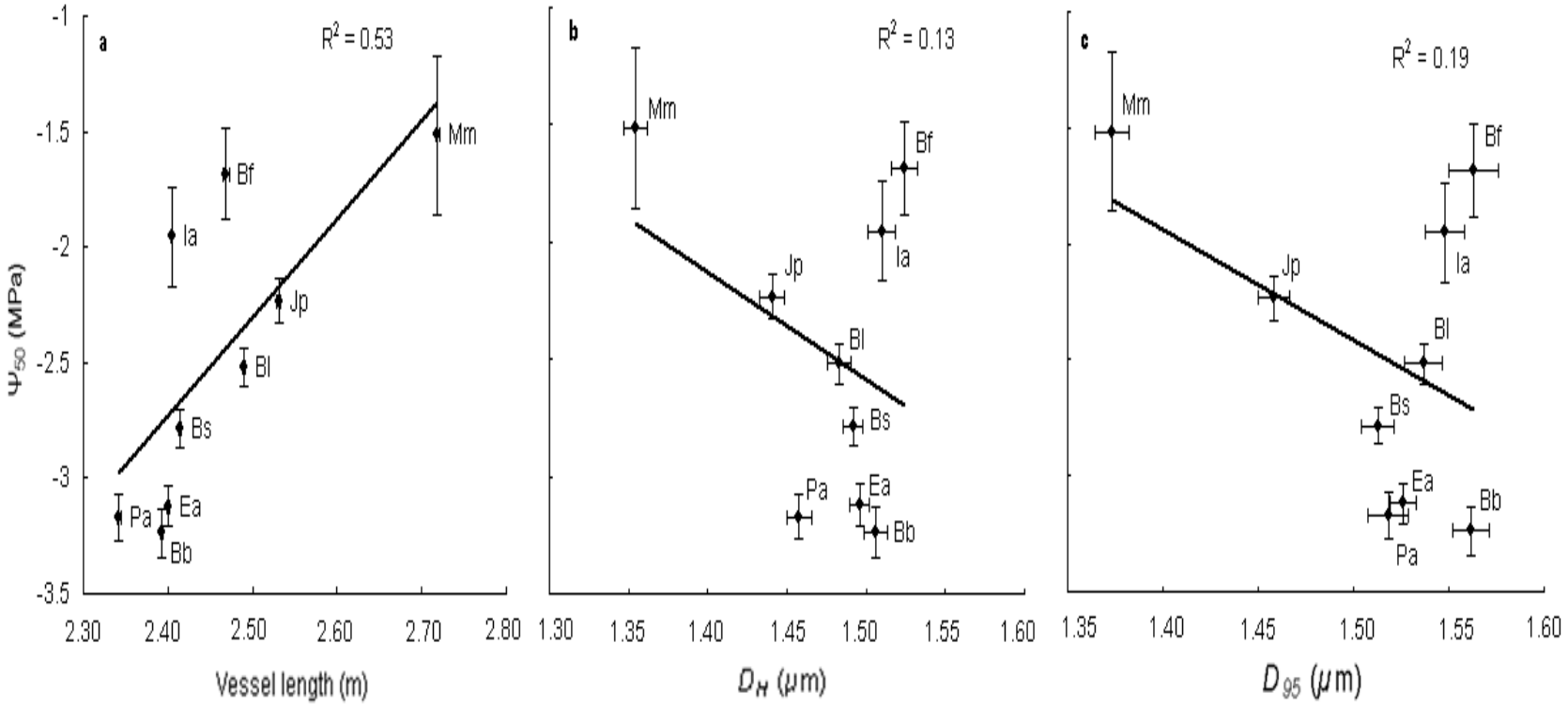


Figure 4.4: Relationship between average conduit parameter and water potential at 50% (Ψ_{50}) loss in hydraulic conductivity (a) Vessel length (V_L) (b) mean hydraulic diameter (D_H) (c) mean hydraulic diameter accounting for 95% flow (D_{95}). Points are species means ± SE (n = 25 trees per species). Error bars are standard errors at 95% confidence interval. Data is transformed as explained in the methods section.

Hydraulic mean diameter (D_H) and D_{95} were not significantly correlated ($P > 0.05$) with Ψ_{50} (Fig 4.5).

4.3.3 Comparisons between wet and dry site miombo generalists

There were no clear differences in vulnerability curves among the four generalists co-occurring on a dry miombo woodlands site (Fig 4.5).

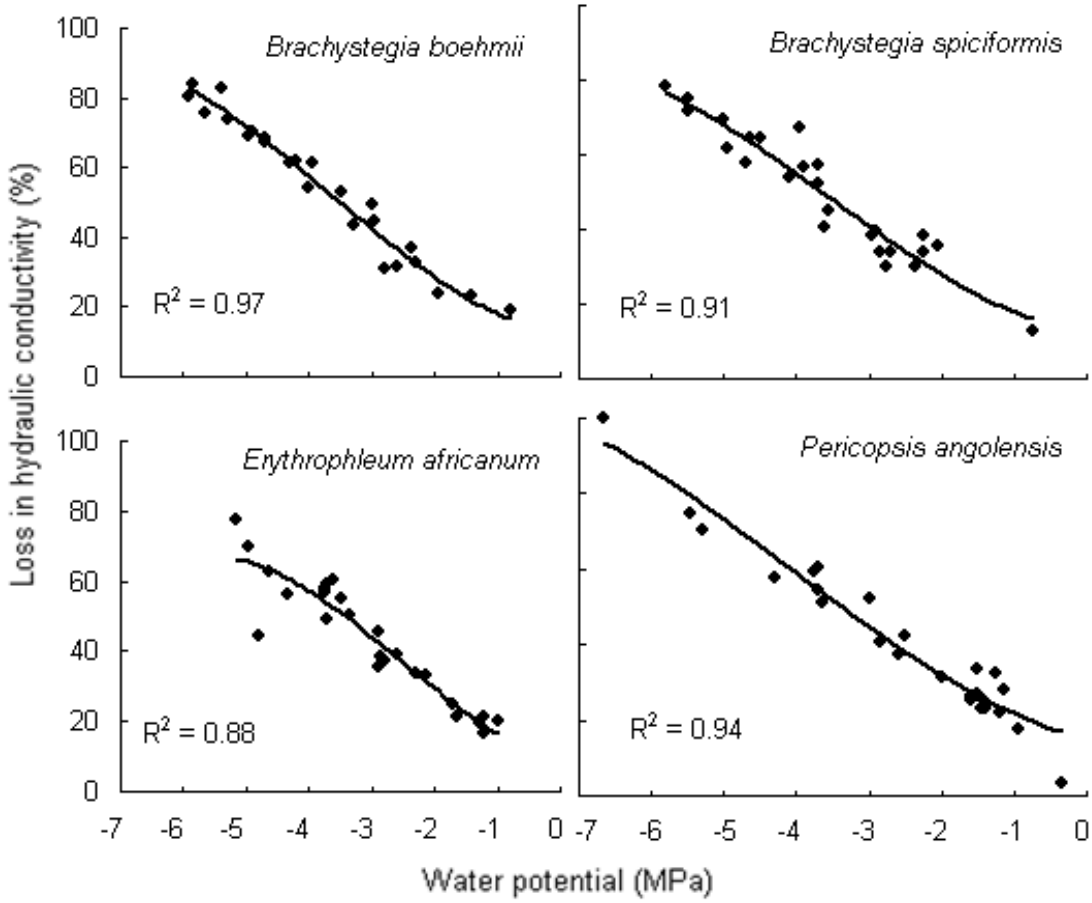


Figure 4 5: Cavitation vulnerability curves for four miombo woodlands generalist tree species growing on a dry site

Stem area specific hydraulic conductivity varied significantly both between sites and species nested within site (Table 4.3).

Table 4.3: Fraction of total variance (r^2) explained by site, species nested within site and the interaction variable (site x species). The r^2 values were calculated from the ANOVA sum of squares. Original trait values were transformed as outlined in the data analysis section. Table abbreviations for traits are as before.

Trait	r^2 Site	r^2 Species	r^2 Site x Species
Ψ_{50} (MPa)	0.01	0.03	0.06*
K_S (kg s^{-1} MPa^{-1} m^{-1})	0.06*	0.49*	0.08*
D (μm)	0.01	0.23*	0.02
D_H (μm)	0.01	0.45*	0.05
D_{95} (μm)	0.02	0.46	0.05
V_L (mm)	0.00	0.85*	0.001

* denotes statistically significant ($P < 0.05$) variation across either site, species or their interaction.

However, site explained only 5% of the variance in K_S in comparison to species nested within site which explained close to 50% of the variances. Cavitation resistance and conduit parameters did not vary significantly between the two miombo sites. However, species nested within site varied significantly for all traits except for D_{95}.

4.4 DISCUSSION

4.4.1 Variations in cavitation resistance, hydraulic efficiency, and conduit parameters

There were clear differences in cavitation resistance between generalists and mesic specialists (Table 4.2; p 95 and Fig 4.1; 91). In spite of growing under relatively homogenous environmental conditions, miombo woodlands tree species differing in habitat preference did not converge to a common cavitation resistance threshold. Tree species with broad habitat preference converged to higher resistance to xylem cavitation whereas those with mesic specialisation were the least resistant to cavitation. The range

of cavitation resistance values reported in this study falls within the same range reported for drought deciduous and evergreen species from other ecosystems (Choat et al 2005; Maherali, Pockman & Jackson 2004; Mencuccini & Comstock 1997). Many studies have linked cavitation vulnerability to ecosystem water stress (Brodribb and Hill 1999; Van der Willigen et al 2000). Pockman and Sperry (2000) proposed that xylem vulnerability to cavitation imposes considerable restrictions on vegetation distribution. These findings render further support to this hypothesis as tree species with wide habitat distribution (occurring in both wet and dry habitats) reached lower stem water potentials before losing 50% of conductivity than co-occurring tree species with natural habitat distribution confined to the relatively wet miombo woodlands (Fig 4.2; p 93).

We believe that the ability to compete and establish across wide miombo habitats by generalists (Chidumayo 1987; Frost 1996) can be attributed to their hydraulic architecture which has low hydraulic efficiency and at the same time is much more resistant to cavitation. The hydraulic architecture of the mesic specialists is more vulnerable to cavitation and, therefore, limits their competitive advantage to the mesic miombo habitats. On the other hand, the hydraulic architecture of generalists confers competitive advantages in both mesic and water-limited dry miombo ecosystem. Our findings suggest that cavitation vulnerability could be one of the decisive factors determining the ecological boundaries for miombo tree species. If, as our results suggest, mesic specialists are more vulnerable to cavitation than generalists, then some of the principal miombo tree species might be at risk of experiencing cavitation-induced population mortality under future climate shift. Available evidence has shown that xylem embolism can result in plant species mortality (Tyree et al. 2003). On the basis, of our

results we are confident to say that future droughts as predicted under global climate change may promote increased population mortality among mesic specialists. Dominance may significantly shift in favour of the drought deciduous generalists. This is consistent with the conclusions drawn by Desankar and Prentice (1995) from a climate envelope modelling study.

4.4.2 Relationships among cavitation resistance, hydraulic efficiency and conduit parameters

We found a significant correlation between hydraulic efficiency and cavitation vulnerability for the nine miombo woodlands canopy tree species. These results are consistent with other studies (Martinez-Vilalta, Prat & Piñol 2002; Pockman & Sperry 2000) and Zimmerman's (1983) proposed trade-off between xylem safety and hydraulic efficiency. In general, an increase in cavitation comes at the cost of related decrease in conductivity and vice-versa (Fig 4.3; p 97). The results of this study show no correlation between conduit diameters (D_H and D_{95}) and Ψ_{50}, though maximum conduit length was significantly correlated with cavitation vulnerability (Fig 4.4; p 99). This suggests that cavitation vulnerability among miombo woodlands canopy tree species is independent of conduit size. Van der Willigen et al (2000) investigated cavitation vulnerability in five subtropical species coming from contrasting habitats growing under similar conditions. They also found no significant correlation between Ψ_{50} and conduit diameter. The findings, which have shown, a lack of correlations between cavitation resistance and conduit size for miombo woodlands canopy tree species reinforce the idea that the origins of xylem cavitation are related to the pit membrane pore size (Zimmerman 1983). The air-seeding hypothesis proposes that the pressure required to generate cavitation in a

conducting xylem conduit is inversely proportional to the pit pore diameter (Zimmermann 1983). If the air-seeding hypothesis is accepted in its current form the, low Ψ_{50} thresholds among generalists in comparison to co-occurring mesic specialists suggest that generalists' posses significantly smaller pit membrane pores than specialists. From a physiological point of view, the hydraulic architecture of generalists is well adapted to withstand droughts in comparison to that of specialists.

4.4.3 Comparisons between wet and dry site miombo generalists

It has been proposed that pressure for selection under arid ecosystems favour plants with high resistance to cavitation (Tyree & Zimmermann 2002). Choat, Slack and Holbrook (2007) surveyed diversity of hydraulic traits in *Cordia* species growing in sites with contrasting precipitation. They observed significant intra and interspecific shifts in cavitation resistance. Apart from substantial reduction in hydraulic efficiency we found no difference in cavitation resistance and conduit parameters between wet and dry miombo woodlands conspecific populations (Table 4.3; p 101). There is a growing body of evidence pointing in the direction of xylem vulnerability being genetically determined rather than being responsive to environmental heterogeneity (Van der Willigen et al 2000, Van der Willigen & Pammenter 1998). Cornwell et al (2007) investigated plasticity in structure and function, in Hawaiian *Metrosideros polymorpha* growing in habitats with contrasting precipitation. They too observed inflexibility in xylem cavitation vulnerability. Canham, Froend and Stock (2009) observed a mixed adaptive response in *Banksia* species in Western Australia growing in contrasting ecohydrological habitats. While one species displayed shifts in cavitation resistance in response to microhabitat variation one did not. Reduction in specific hydraulic conductivity has been previously

linked to exploitation of low-soil moisture under arid ecosystems (Engelbrecht, Velez, & Tyree 2000). Taken together, these results suggest that plasticity in specific hydraulic conductivity between wet and dry sites coupled with inflexibility in cavitation resistance enables generalists to exploit low-soil moisture prevalent in dry miombo woodlands.

4.4.4 Conclusions

Xylem cavitation vulnerability sets the ecological boundaries for miombo woodlands tree species. On the basis of present findings we believe that resistance to cavitation could be one of the key factors that may determine which miombo woodlands tree species would experience higher extinction rates than the other under global climate change. This study makes a contribution towards the growing body of literature on plant-water relations in seasonally dry tropical forests. It has also contributed towards a better understanding of how cavitation vulnerability influences tree species habitat preference in miombo woodlands. This study has demonstrated that deciduous drought tolerant tree species are more resistant to xylem cavitation than the evergreen mesic specialists. The study has also demonstrated the existence of a strong trade-off between cavitation resistance and xylem efficiency, suggesting that stem hydraulic architecture may impose limitations on tree species habitat preference in miombo ecosystem. While broad ranging tree species display greater plasticity in hydraulic efficiency from wet to dry miombo habitats, cavitation resistance and xylem anatomy remain unresponsive. Results from this study emphasise the need to incorporate tree physiology in predicting species response to future climate change for miombo woodlands. Given that cavitation vulnerability differs across plant organs with downstream organs (roots) being more vulnerable than upstream organs (Mencuccini & Comstock 1997); future studies should focus on cavitation vulnerability

in roots for miombo tree species in order to improve our understanding of the full spectrum of drought response in these trees. In this study we did not look at other factors that influence plant drought tolerance ability, such as mycorrhizal association (Ruiz-Lozano, Azcon & Gomez 1995). Miombo trees have been shown to form mycorrhizal associations (Högberg & Piearce 1986). Unravelling the relationship between mycorrhizal associations and cavitation resistance for miombo species would add more insight into the ecology of this biome.

Acknowledgement

The lead author is funded by a scholarship from the Association of Commonwealth Universities; Copperbelt University provided financial support during field work. We wish to thank the Principal for Zambia Forestry College, the late Mr Saxon N Siame who provided laboratory work space at the wet miombo site. The District Forestry Officer for Choma district Jones Mulomba is greatly appreciated for his logistical support during our stay on the dry site. Lab assistants in Zambia, Milimo Miyoba and Metson Kasowe are also acknowledged.

4.5 REFERENCES

Beikircher B. & Mayr S. (2008) The hydraulic architecture of *Juniperus communis* L. ssp. communis: shrubs and trees compared. *Plant, Cell and Environment*, **31**, 1545-1556.

Brodribb T. & Hill R.S. (1999) The importance of xylem constraints in the distribution of conifer species. *New Phytologist*, **143**, 365-372.

Canham A.C., Froend R.H. & Stock W.D. (2009) Water stress vulnerability of four Banksia species in contrasting ecohydrological habitats on the Gnangara Mound, Western Australia. *Plant, Cell and Environment*, **32**, 64–72.

Chidumayo E. N. (1987) Species Structure in Zambian Miombo Woodland. *Journal of Applied Ecology*, **3**, 109-118.

Choat B., Ball M. C., Luly G. J. & Holtum M. A. J. (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from North-eastern Australia. *Trees*, **19**, 305-311.

Choat B., Sack L. & and Holbrook N. M. (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytologist*, **175**, 686-698.

Cochard H., Cruiziat P. & Tyree M. T. (1992) Use of positive pressure to establish vulnerability curves. *Plant Physiology*, **100**, 205-209.

Cornwell W. K., Bhaskar R., Slack L., Cordell S. & Lunch C.K. (2007) Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs low precipitation. *Functional Ecology*, **21**,1063-1071.

Desankar, V. P. & C. Prentice. 1995. Modelling vegetation dynamics of miombo woodlands of Zambezian Africa under changing climatic conditions. In *Impacts of climate change on ecosystems and species: Terrestrial ecosystems* (eds Pemetta, J.C., Leemans, R., Elde, D., & Humphrey, S.), pp. 23-38. IUCN, Gland.

Domec J. & Gartner B. L. (2001) Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees* **15**, 204-214

Edwards J. E. & Diaz M. (2006) Ecological physiology of *Pereskia guamacho*, a cactus with leaves. *Plant Cell and Environment*, **29**, 247-256.

Engelbrecht B. M. J., Velez V. & Tyree M. T. 2000. Hydraulic conductance of two co-occuring neotropical understorey shrubs with different habitat preferences. *Annals of Forest Science,* **57**, 201-208.

Ewers W. F. & Fisher J. B. (1989) Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany,* **76**, 645-656.

Frost P. (1996) The Ecology of Miombo Woodlands. In *The Miombo in Transition: Woodlands and Welfare in Africa (e*ds B. Campbell), CIFOR, Bogor, pp. 11-57.

Högberg P. & Piearce G. D. (1986) Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns. *Journal of Ecology*, **74**, 775-785

Kolb K. J. & Davis D. S. (1994) Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology*, **75**, 648-659.

Kolb K. J., Sperry J.S. & Lamont B.B. (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. *Journal of Experimental Botany*, **47**, 1805-1810.

Maherali H., Pockman T. W. & Jackson B. R. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184-2199.

Martínez-Vilalta J., Prat E., & Piñol I. O. J. (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia*, **133**, 19-29

Meinzer F. C., Johnson D. M., Lachenbruch B. & McCulloh A. K. (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology,* **23**, 922 - 930

Mencuccini M. & Comstock J. (1997) Vulnerability to cavitation in populations of two desert species, *Hymenoclea salsola* and *Ambrosia dumosa*, from different climatic regions. *Journal of Experimental Botany*, **48**, 1323-1334.

Palgrave K. C. 2002. *Trees of Southern Africa*. 3rd ed. Struik Publishers, Cape Town.

Pammenter N. W. & van der Willigen C. V. (1998) A mathematical and statistical analysis of the curves illustrating vulnerability to xylem to cavitation. *Tree Physiology*, **18**, 589-593.

Patino S., Tyree M. T. & Herre E. A. (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic Ficus species from Panama. *New Phytologist,* **129**, 125-134.

Pockman W. T. & Sperry J. S. (2000) Vulnerability to xylem cavitation and the distribution of sonoran desert vegetation. *American Journal of Botany*, **87**, 1287-1299.

Ruiz-Lozano J. M., Azcon R. & Gomez M. (1995) Effects of arbuscular-mycorrhizal glomus species on drought tolerance: physiological and nutritional plant responses. *Applied Environmental Microbiology*, **61**, 456-460

Sithole A. & Murewi F. J. C. (2009) Climate variability and change over southern Africa: Impacts and challenges. *African Journal of Ecology*, **47**, 17-20.

Smith P. & Allen, Q. 2004. *Field Guide to The Trees and Shrubs of the Miombo Woodlands*. Royal Botanical Gardens Kew, London.

Sperry J. S., Donnelly J. R. & Tyree M.T. (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell and Environment*, **11**, 35-40.

Stratton L., Goldstein G. & Meinzer F. C. (2000) Stem water storage capacity and efficiency of water transport: Their functional significance in a Hawaiian dry forest. *Plant Cell and Environment*, **23**, 99-106.

Trapnell C. G., Friend M. T., Chamberlain G. T., & Birch H. F. (1976) The effects of fire and termites on a Zambian woodland soil. *Journal of Ecology* **64**, 577-588.

Tyree M. T. & Sperry J. S. (1988) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19-38.

Tyree M. T. & Zimmermann M. H. (2002) *Xylem Structure and the Ascent of Sap*. (2nd ed.). Springer, Berlin.

Tyree M. T., Engelbrecht B. M. J. Vargas G. & Kursar T. A. (2003) Desiccation tolerance of five tropical seedlings in Panama: relationship to a field assessment of drought performance. *Plant Physiology*, **132**, 1439 –1447.

Tyree M. T. & Sperry J. S. (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology*, **88**, 0574-0580.

Van der Willigen C. & Pammenter N. W. (1998) Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites. *Tree Physiology*, **18**, 595-600.

Van der Willigen C. V., Sherwin H. W. & Pammenter N. W. (2000) Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. *New Phytologist*, **145**, 51-59.

White F. (1983) *The Vegetation of Africa : a Descriptive Memoir to Accompany the Unesco/AETFAT/UNSO Vegetation Map of Africa*. Unesco, Paris.

Zar, J. H. (2010) *Biostatistical Analysis*. 5th Edn. Pearson Education International, London.

Zimmermann M. H. (1983) *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin.

Zimmermann M. H. & Jeje A. A. (1981) Vessel length in stems of some American woody species. *Canadian Journal of Botany*, **59**, 1882–1892.

CHAPTER 5

Seasonal changes in plant-water relations influence patterns of leaf shedding and flushing in miombo woodlands

OVERVIEW

Future decreases in ecosystem water availability for most of the tropical regions where seasonally dry tropical forests occur under global climate change may alter patterns of leaf display in these biomes. Borchert (1994) proposed that soil and stem water storage determine phenology and distribution of tropical dry forest trees. Although leaf phenology has received considerable attention in miombo woodlands, all studies have mainly been by observation (merely recording timing of leaf fall and emergence), paying very little attention to the role of seasonal dynamics in stem water as it relates to patterns of leaf display in this biome. The extent to which seasonal changes in plant-water relations control patterns of leaf display in miombo woodlands remains poorly understood. Therefore, work presented in this chapter tries to fill this conspicuous knowledge gap on the mechanisms of action by which water stress controls patterns of leaf phenology in miombo woodlands. In this chapter we test the functional dependence hypothesis of leaf phenology on stem water status. This chapter addresses main objective 3 (p 12) of this thesis by focusing on the relationship between leaf phenology and seasonal changes in tree hydraulic architecture. We combined both field observations and laboratory based experimentation.

This chapter has been submitted as a journal article to Journal of Vegetation Science. The paper was authored by Royd Vinya. Yadvinder Malhi, Nick Brown, Luis Aragao, and Timothy Brodribb made comments.

Seasonal changes in plant-water relations influence patterns of leaf shedding and flushing in miombo woodlands

Authors: Royd Vinya[1], Yadvinder Malhi[1], Nick D. Brown[2], Timothy Brodribb[3], Luiz E. O.C. Aragão[4]

Authors addresses:

1 Environmental Change Institute, Oxford University Centre for the Environment,
2 Department of Plant Sciences, University of Oxford,
3 School of Plant Sciences, University of Tasmania,
4 School of Geography, University of Exeter

ABSTRACT

Question: Do seasonal changes in xylem long distance water transport pathway control patterns of leaf display in seasonally dry tropical forests?

Location: Mwekera national forest number 6 in Kitwe, Zambia (12˚ 51´ S, 28˚ 22´ E 1295m above sea level).

Methods: We examined the relationship between seasonal changes in plant-water relations and seasonal patterns of leaf display in Africa's miombo woodlands, a seasonally dry tropical forest. For a period of nine months, we monitored timing of leaf shedding and flushing for nine miombo woodland canopy tree species differing in habitat preference and phenology. Seasonal changes in pre-dawn stem water potential (Ψpd) and stem hydraulic conductivity (K_H) were also measured.

Results: Results show that seasonal patterns of leaf phenology were strongly related to changes in stem-water relations among miombo woodlands canopy tree species. Leaf shedding coincided with the attainment of seasonal minimum Ψpd. Drought-tolerant species suffered significantly ($P < 0.05$) higher seasonal losses in hydraulic conductivity

than drought-intolerant trees. Xylem safety margins were significantly ($P < 0.05$) wider among drought deciduous species than among semi-evergreen and evergreen drought-intolerant species. The water potential triggering leaf shedding and flushing varied significantly ($P < 0.05$) among tree species differing in habitat preference and phenology.

Conclusions: Seasonal changes in plant water status control timing of leaf shedding and flushing in miombo woodlands. This study renders further support to the functional dependence hypothesis of leaf phenology on plant water status.

Key words: Climate change; hydraulic conductivity; leaf phenology, miombo woodlands, plant-water relations, xylem safety margin.

5.1 INTRODUCTION

Miombo woodland, the most widely distributed biome in east and southern Africa (White 1983), has a characteristically strong seasonal dry tropical climate in which summer rains fall between November and April (Malaisse 1978). This is followed by a long seasonal drought lasting between 5 to 6 months (Frost 1996). As is the case with many other seasonally dry tropical forests, leaf phenology is closely related to water availability (Borchert 1994a, b; Chapotin et al. 2006; Filho & Filho 2000; Reich & Borchert 1984; Williams et al. 1997). In this biome, leaf shedding occurs at the onset of the long dry spell, suggesting that water availability maybe the primary factor controlling patterns of leaf phenology (Malaisse 1978). Intriguingly, leaf flush for miombo trees occurs at the very peak of the dry season, approximately two months before the onset of summer rain (Chidumayo & Frost 1996). This may suggest that other factors rather than precipitation exert some control on some aspects of leaf phenology (Chidumayo 2001). Although many studies have acknowledged the importance of precipitation in controlling leaf

shedding in miombo woodlands (Chidumayo 1994; Fuller & Prince 1996; Fuller 1999; Malaisse 1978), this biomechanical process has never been analyzed in terms of seasonal dynamics of plant-water relations.

The relationship between seasonal pattern of plant-water relations and leaf phenology is of special scientific interest in the case of miombo woodlands because predictions of future climate trends for this ecoregion imply increased overall water stress (IPCC 2007; Sithole & Murewi 2009). If drought exerts some considerable influence on leaf phenology in miombo ecosystems, then the predicted increase in ecosystem water stress may alter patterns of leaf display and overall ecosystem productivity.

Water stress promotes cavitation-induced xylem embolisms in plants, leading to air-filled xylem conduits and subsequent reduction in xylem hydraulic conductance (Sperry & Tyree 1988; Tyree & Zimmermann 2002). Many studies have demonstrated that progressive impairment of the long distance xylem hydraulic pathway induces leaf shedding (Brodribb & Holbrook 2003; Salleo et al. 2002; Tyree et al. 1993; Wang et al., 1992). Available evidence suggests that plant ability to cope with water stress will depend on its ability to withstand strongly negative xylem tensions without allowing air entry (Cochard et al, 1992; Sperry & Tyree 1988; Wheeler et al. 2005). The water potential causing 50% (Ψ_{50}) loss in hydraulic conductivity has often been used as a measure of species' ability to withstand xylem cavitation (Kolb & Davis 1994; Lopez et al. 2005). Although Ψ_{50} has found considerable use in defining drought-tolerance capability, its relevance to plant water loss regulation is undermined by its poor relationship with stomatal regulation (Brodribb et al. 2003).

Another useful measure for describing plant water stress management is the xylem pressure coinciding with a rapid increase in loss in hydraulic conductivity on the vulnerability curve (Domec & Gartner 2001; Meinzer, et al. 2009). Available evidence suggests that plants prevent the development of runaway embolisms by limiting xylem pressures below the air entry pressure (Ψ_e) while at the same time maximizing stomatal conductance (Brodribb et al. 2003; Tyree & Sperry, 1988). If this is true, one would infer some functional coordination between species' leaf phenology and xylem security. However, little is known about this relationship in water-limited ecosystems.

In this paper, we evaluate the relationship between seasonal changes in plant-water relations and patterns of leaf display for nine miombo woodlands canopy tree species. Four species [*Brachystegia floribunda* Benth (Fabaceae), *Isoberlinia angolensis* (Benth.)Hoyle & Brenan (fabaceae), *Julbernardia paniculata* (Benth.)Troupin (Fabaceae) and *Marquesia macroura* Gilg (Dipterocarpaceae) range from evergreen to semi-evergreen and are mainly confined to the wet miombo woodlands. The other five species [*Brachystegia boehmii* Benth (Fabaceae), *Brachystegia longifolia* Benth (Fabaceae), *Brachystegia spiciformis* Benth (fabaceae), *Erythrophleum africanum* (Benth.) Harms (Fabaceae) and *Pericopsis angolensis* (Baker) Meeuwen (Fabaceae)] are drought-deciduous and are distributed throughout the dry and wet miombo woodlands. Throughout this paper they are referred to as mesic specialists. We ask the following questions: 1) Are seasonal changes in leaf display in miombo woodlands, functionally coordinated with changes in xylem transport? 2) To what extent do tree species differing in leaf phenology and drought tolerance ability differ in water stress induced seasonal loss in hydraulic conductivity? 3) Do xylem safety margins differ substantially between

tree species differing leaf phenology and drought tolerance ability? 4) Are there significant differences in water potential thresholds triggering leaf shedding and flushing for miombo tree species differing in leaf phenology and drought-tolerance ability? The main objectives of this study were, therefore, to:

- Investigate the relationship between seasonal changes in stem water status and patterns of leaf phenology for miombo woodlands canopy tree species.
- Examine the extent to which tree species differing in drought tolerance capability and leaf phenology differ in seasonal loss in hydraulic conductivity.
- Quantify the water potential thresholds triggering leaf phenophases and evaluate the extent to which it varies with species drought tolerance ability and habitat preference.

5.2 MATERIALS AND METHODS

5.2.1 Study site

The study was conducted in Mwekera national forest number 6 (12˚ 51′ S, 28˚ 22′ E, 1295m above sea level) in Kitwe, Zambia. The main vegetation type is closed miombo forest dominated by genus *Julbernardia, Marquesia, Brachystegia,* and *Isoberlinia*. The forest type is best described as wet miombo (Chidumayo 1987; White 1983). The average diameter at breast height is around 20 cm with a canopy height of 21 m. The long-term mean annual rainfall is 1200 mm and monthly maximum temperature range between 25˚C and 34˚C (averages based on the years 1960-2004). Climate data are from Ndola Airport (approximately 35 km from Mwekera national forest number 6).

We sampled nine sympatric miombo woodland canopy tree species differing in habitat specificity, representing six genera and two families. All the individuals sampled

in this study came from a uniform woodland (700 ha) where they shared a common environment. The nine tree species were selected on the basis that they differed substantially in habitat preference (Chidumayo 1987; Smith & Allen 2004; Trapnell & Smith 2001) and leaf phenology (Storrs 1979). Co-occurring individual trees were randomly sampled, tagged, and their GPS coordinates recorded to enable repeat measurements. To avoid confounding effects of soil characteristics and water availability we avoided sampling species on hill slopes (Trapnell et al. 1976) and riparian zones, respectively. The average diameter at breast height for the sample trees ranged from 30 to 39 cm on the wet site and from 18 to 25 cm on the dry site (Appendix 5.1).

5.2.2 Monitoring of Leaf phenology

Leaf phenology for nine co-occurring miombo woodlands tree species was closely monitored on a wet miombo woodlands site from April to December 2008. A total of 225 trees were tagged and monitored for a period of 9 months from leaf shedding to the time of leaf flush. Monitoring for each sample tree involved weekly monitoring of leaf fall and flushing. Two dedicated field assistants carried out the observations throughout the study period. Leaf shedding was taken to be the time when the leaf displayed signs of water stress and about to fall off the branch. Leaf emergence included the whole process from a bud being active, expanding and finally leaf emergence stage.

5.2.3 Measurement of stem water status

A measure of stem water status used in this study was pre-dawn water potential (Ψpd). Unlike other measures of plant water status (osmotic potential and water content), it is of direct relevance to the soil-plant-atmosphere continuum (SPAC) (Kramer & Boyer 1995).

Furthermore, water potential expresses the amount of free energy status of water in plant tissue (Taiz & Zeiger 1998). Given that plants have a tendency to equilibrate overnight in relation to the bulk wet soil zones (Schmidhalter 1997); predawn water potential Ψ_{PD} stands out to be a better candidate representing an estimation of soil water potential (Andrade et al. 1998; Borchert 1994b; Williams & Araujo 2002). On every field visit, two to five twigs per tree were harvested at random. All sample collections were carried out in the early mornings (between 05:30 and 08:00hrs). Immediately after excising the twig from the tree, they were covered in wet towels and placed in dark sample bags. The samples were then transported to the nearby laboratory at Zambia Forest College (less than 2 km). At the laboratory, small non-transpiring leaf-bearing distal twig portions were excised and water potential measured using pressure chamber method (SKPM 1405, Skye Instruments, Llandrindod Wells, UK). In order to minimize errors, all segments were always kept under moist-dark conditions prior to water potential determination. Furthermore, the time difference between harvesting and actual determination of Ψ_{PD} was kept to less than an hour.

5.2.4 Determination of native embolism

Measurement of seasonal progression of native embolism followed the methods of Sperry et al. (1988). At the laboratory, we trimmed the twigs to their maximum vessel lengths plus 10%. We measured maximum vessel lengths under different but closely related study (Vinya et al. unpublished). Vessel length determination involved forcing air at a pressure of less than 100 kPa through the basal end of the twig while at the same time keeping the distal end dipped into a bucket of water (Choat et al. 2005; Ewers & Fisher

1989; Zimmermann & Jeje 1981). The distal end of a twig was continuously cut off in sections of 1 cm until bubbles formed at the cut distal end.

Trimmed segments were always kept wholly immersed under water until flow rate determination. Trimming was always done under water using a sharp razor blade. The segments ranged in underbark diameter from 4 to 10 mm. Hydraulic conductivity (K_H) was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. A low delivery pressure head was ideal for this experiment because a high pressure would have easily dislodged the cavitation bubbles and hence generate bias in results. Laboratory rubber corks provided a water-tight connection between the segment and the water reservoir. The reservoir was constantly refilled in order to maintain the same delivery pressure. The segments were perfused with degassed, filtered (to 0.2 µm) and acidified (with HCl, pH = 2) distilled water. The perfusing solution was acidified to prevent microbial growth that would eventually plug xylem vessels (Kolb et al. 1994; Sperry et al. 1988). Each segment was allowed to equilibrate before initial flow rate was measured. Sap flow was measured by attaching a pre-weighed cotton wool ball covered in a plastic onto the free distal end of the segment. Hydraulic conductivity (K_H, kg s^{-1} MPa^{-1} m) was calculated as:

$$K_H = \frac{J_V}{(\Delta P / l)} \qquad \text{[Eqn 1]}$$

where, J_V is the flow rate (kg s^{-1}) through the segment; ΔP is the delivery pressure (MPa) and; l is segment length (m).

Maximum hydraulic conductivity (K_H max) was derived after flushing the segments at a pressure of 150 kPa for periods ranging from 20 to 30 minutes depending

on species and degree of xylem air blockage. Loss in hydraulic conductivity ($PLC_{Seasonal}$) was calculated as:

$$PLC_{Seasonal}\ (\%) = (K_H\ \max - K_H)/\ K_H\ \max \times 100 \qquad \text{[Eqn 2]}$$

5.2.5 Determination of xylem vulnerability to cavitation

Species vulnerability to cavitation for the selected nine miombo canopy tree species was determined in a parallel study (Vinya et al unpublished). The method involved inducing cavitation by dehydrating twigs using the traditional laboratory bench air-drying technique following the methods of Cochard et al. (1992). Segments were progressively dehydrated to various water potentials over a period of 6 to 48 hrs depending on species. At the end of each dehydration period, small distal segments were excised from the main twig for determination of Ψ using a pressure chamber (SKPM 1405, Skye Instruments, Llandrindod Wells, UK). The segments for Ψ determination were placed in air-tight plastic bags for 30 minutes following excision from the main stem in order to allow for water potential equilibration. Hydraulic measurements were determined as above. Percent loss in hydraulic conductivity was calculated in a similar manner to the mathematical function used for native embolism above. Vulnerability curves were fitted with the following sigmoid function:

$$PLC = 100 / (1 + \exp (a\ (\Psi - \Psi_{50}))) \qquad \text{[Eqn 3]}$$

where Ψ_{50} is the water potential associated with 50% loss in hydraulic conductance, and *a* represents the slope of the vulnerability curve. The two parameters (Ψ_{50} and *a*) in this function have direct physiological relevance in relation to Zimmermann's (1983) air-seeding theory (Pammenter & Van Der Willigen 1998).

Xylem safety margins were calculated using the fitted vulnerability curves (see supporting information) and minimum predawn stem water potential Ψ_{PD} coinciding with leaf shedding. Xylem safety margins were calculated as the difference between Ψ_{PD} triggering leaf shedding and the water potential threshold associated with xylem air-entry (Ψ_e) leading to rapid loss in hydraulic conductivity calculated from the vulnerability curves. We used Ψ_e because of its relevance in the context of stomatal regulation of transpirational losses. Although a number of plant water potential points have been employed in calculating xylem safety margin (Meinzer et al. 2009), we chose to use the water potential related to leaf shedding because it has direct physiological relevance to the process responsible for preventing runaway embolism in plants. If we agree with the hydraulic segmentation (Zimmerman, 1983) and vulnerability segmentation (Tyree & Ewers 2001) theories then the water potential related to leaf shedding should be the ideal candidate for calculating the safety margins of the xylem.

5.2.6 Statistics

In order to answer the question whether, seasonal changes in stem water status influence patterns of leaf display among miombo woodlands canopy tree species we used binomial logistic regression analysis. The dependent variable, leaf phenophase could only be classified into shedding or flushing, binary logistic regression was the best tool available to conduct such an analysis (Zar 2010). Pre-dawn water potential (Ψpd) was the predictor variable and leaf phenophase (flushing and shedding) was the dependent variable. We tested the unique relationship between seasonal changes in stem water status and progression of native embolism using linear regression analysis. Given that time-dependant data have a tendency of displaying auto-correlation, we tested data for serial-

correlation using the Durbin-Watson test prior to performing any regression analysis. We employed the Cochrane-Orcutt procedure to eliminate serial correlation (Chatfield 1997; Ostrom 1990; Schabenberger & Gotway 2005). We used a mixed-effects ANOVA model to answer the questions whether most of the variations in seasonal changes in hydraulic conductivity, Ψ triggering leaf phenophases and xylem safety margins occur at group or species or the individual nested within species. We used a paired *t*-test to test whether stem water potential threshold triggering leaf shedding differed significantly from water potential triggering leaf flushing. All statistical analyses were carried out in Minitab (version 15, Minitab Inc., Pennsylvania, USA).

5.3 RESULTS

5.3.1 Seasonal variation in stem water potential

Seasonal changes in pre-dawn stem water potential (Ψpd) for the nine co-occurring miombo tree species studied are presented in Figure 5.1.

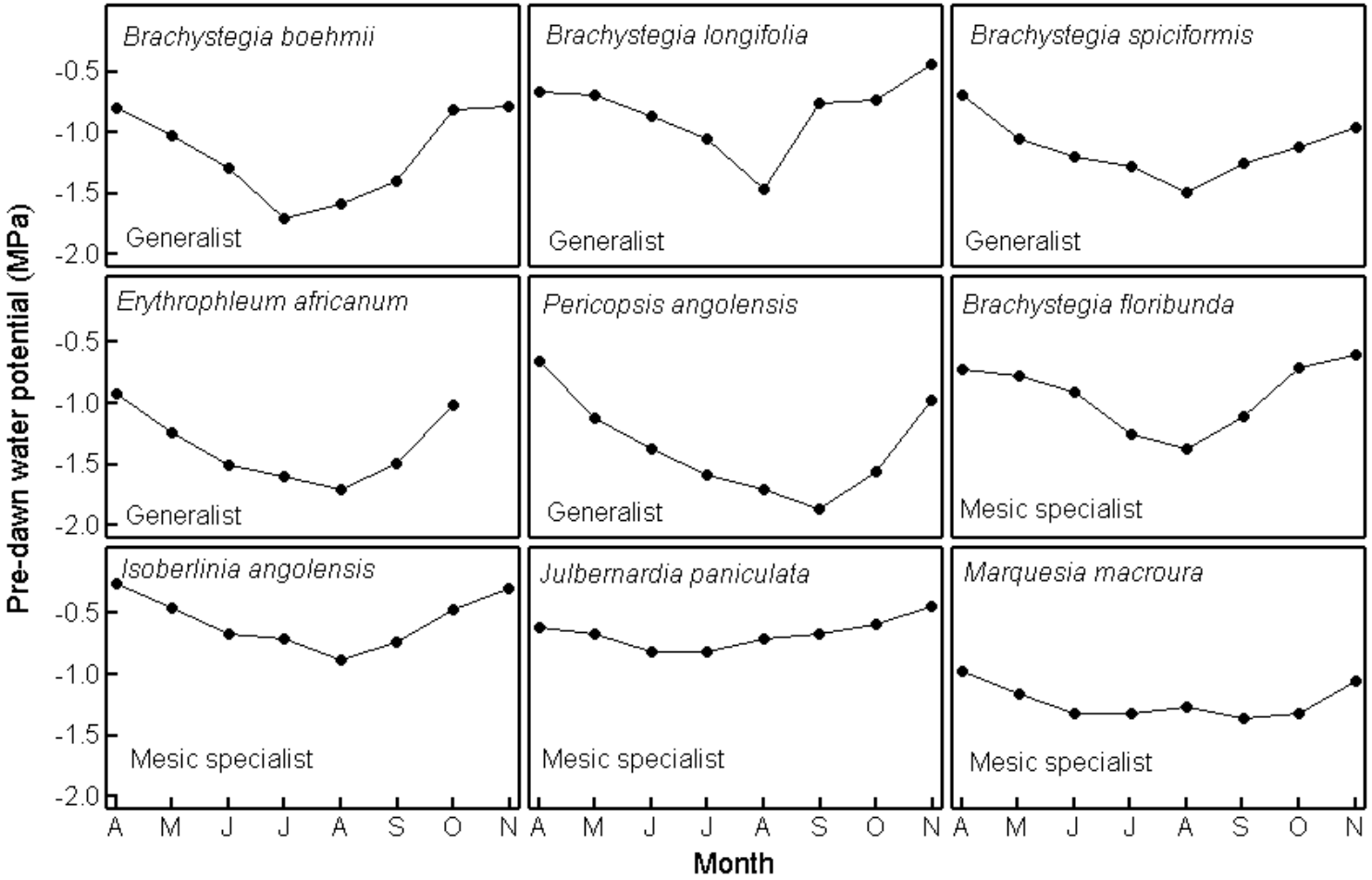


Figure 5.1: Seasonal variation in stem water potential for the nine miombo woodlands canopy tree species. Points are monthly averages.

Overall predawn stem water potential (Ψpd) for generalists dropped more than two folds from -0.7 MPa in April to -1.9 MPa midway though the dry season for the months of July and August before rising again to -0.8 MPa by November. For mesic specialists Ψpd dropped from -0.6 MPa in April to -1.1 in July-August period. By the end of November, average stem water potentials rose to -0.6 MPa. Mesic specialists exhibited the lowest seasonal variation in minimum Ψpd. Notable among mesic specialists, were *Isoberlinia angolensis* and *Brachystegia floribunda*, displayed the least amount of variation in minimum Ψpd. Generalists attained lower, (more negative) average minimum Ψpd, than co-occurring mesic specialists. Minimum Ψpd ranged from -1.4 to -1.8 MPa among wide ranging habitat generalists. For mesic specialists, the range was from -0.8 to -1.4 MPa. Changes in stem water potential significantly (regression; $P < 0.05$) influenced seasonal changes in leaf display (shedding and flushing) among miombo woodlands tree species (Table 5.1).

Table 5.1: Results of logistic regression analysis on leaf phenology and stem water status for each species. Leaf phenophase is the dependent variable and pre-dawn stem water potential is the predictor variable. Where β is the logistic regression coefficient.

Species	β	Std error of β	*P*-value
Brachystegia boehmii	-2.026	1.12	0.07
Brachystegia longifolia	-6.06	1.69	< 0.001
Brachystegia spiciformis	-7.88	2.41	0.001
Erythrophleum africanum	-4.67	1.56	0.003
Pericopsis angolensis	-7.64	2.16	< 0.001
Brachystegia floribunda	-5.60	1.78	0.002
Isoberlinia angolensis	-11.19	3.81	0.003
Julbernardia paniculata	-2.40	1.79	0.181
Marquesia macroura	-0.047	1.051	0.96
Generalists only	-1.13	0.47	0.016
Mesic specialists	-3.05	0.48	< 0.001
All species combined	-1.56	0.27	< 0.001

5.3.2 Seasonal changes in hydraulic conductivity

There were clear differences in seasonal losses in hydraulic conductivity among miombo woodlands canopy tree species differing in leaf phenology and habitat specialisation. Tree species with mesic specialisation experienced significantly (ANOVA, $P < 0.001$) lower seasonal losses in hydraulic conductivity than tree species with wide habitat specialisation (Fig 5.2).

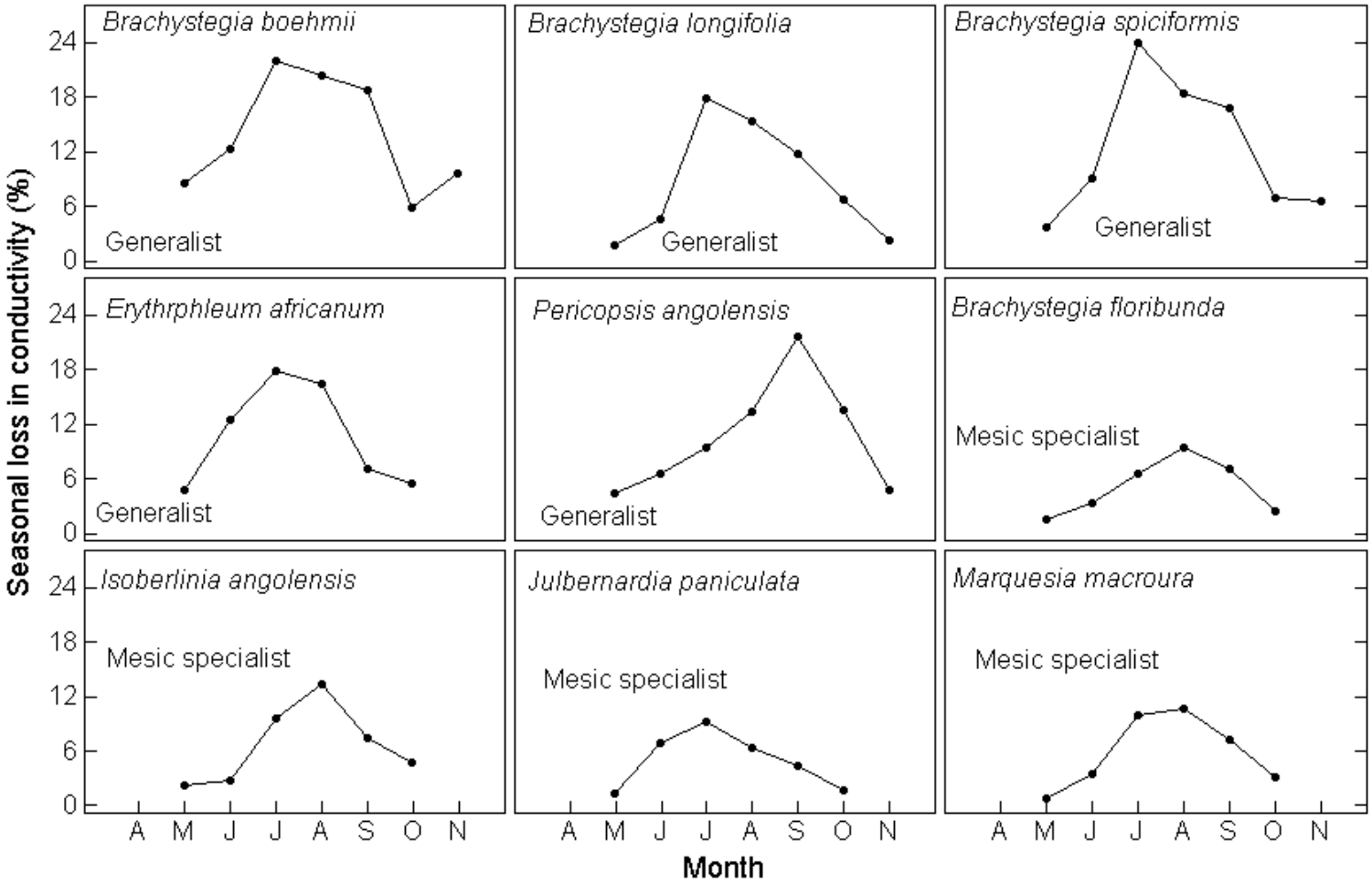


Figure 5.2: Seasonal losses in hydraulic conductivity for the nine miombo woodlands canopy tree species. Points are monthly averages.

More of the interspecific variance in native embolism was explained by differences between functional types (generalists versus specialists) than differences between species nested within-functional type. Functional type accounted for 24% of the variations, whereas only 3% of the variance was attributed to species nested within-functional type.

Cavitation vulnerability (Ψ_{50}) was negatively and significantly (P = 0.04) correlated with seasonal loss in hydraulic conductivity. A linear regression explained 73% of the variability in species native embolisms (Fig 5.3).

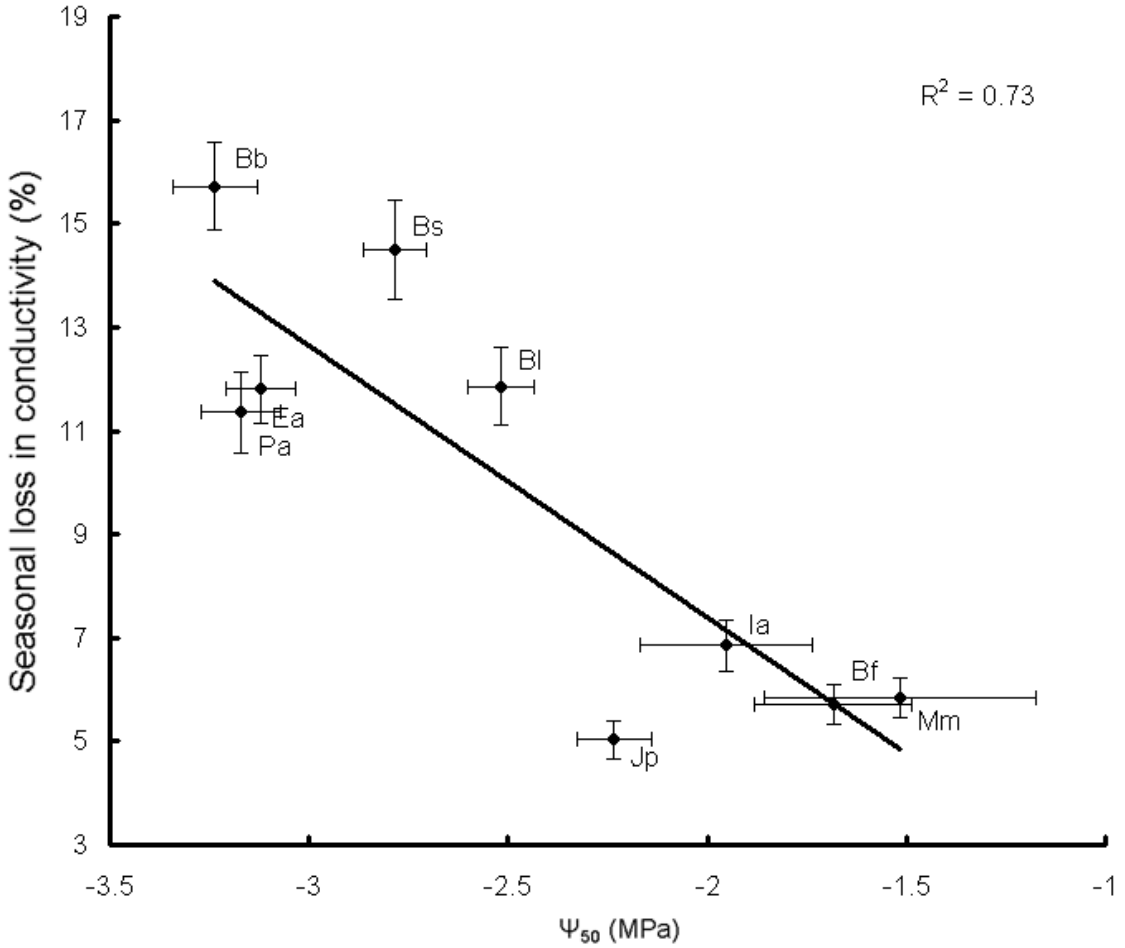


Figure 5.3: Relationship between seasonal loss in hydraulic conductance (%) and species drought tolerance ability (Ψ_{50}). Chart abbreviations are as follows: Bb, *Brachystegia boehmii*; Bf, *Brachystegia floribunda*; Bl, *Brachystegia longifolia*; Bs, *Brachystegia spiciformis*; Ea, *Erythrophleum africanum*; Pa, *Pericopsis angolensis*; Ia, *Isoberlinia angolensis*; Jp, *Julbernardia paniculata*; Mm, *Marquesia macroura*. Regression line data points are tree species means ± SE (n = 25 trees per species). Regression model describing the relationship is: y = -5.25 x - 3.12; P = 0.004.

Overall seasonal changes in hydraulic conductivity were significantly ($P < 0.05$) related to seasonal changes in stem water potential for seven out of the nine miombo tree species studied (Table 5.2).

Table 5.2: Results of linear regression analysis on seasonal loss in hydraulic conductance versus pre-dawn stem water potential for nine co-occurring miombo woodlands canopy tree species. The dependent variable is loss in conductivity (%) and the independent variable is water potential. Table abbreviations are: *Y* is percent loss in conductivity and *x* is stem water potential.

Species	**Equation**	***P***	$\mathbf{r^2}$
Brachystegia boehmii	$y = -5.87 - 16.4x$	< 0.001	60
Brachystegia longifolia	$y = 1.76 - 4.05x$	0.03	19.8
Brachystegia spiciformis	$y = -7.039 - 21.26x$	< 0.001	50
Erythrophleum africanum	$y = -0.94 - 3.84x$	0.015	27.3
Pericopsis angolensis	$y = -16.1 - 16.7x$	< 0.001	66.4
Brachystegia floribunda	$y = -0.074 - 4.79x$	< 0.001	52.5
Isoberlinia angolensis	$y = -0.84 - 13.7x$	0.045	18.7
Julbernardia paniculata	$y = 0.82 + 3.64x$	0.58	1.6
Marquesia macroura	$y = -1.06 - 6.44x$	0.022	21.7

An insignificant ($P > 0.05$) relationship was observed for *Isoberlinia angolensis* and *Julbernardia paniculata*.

5.3.3 Hydraulic safety margins

Xylem safety margins differed significantly (ANOVA; $P < 0.001$) among co-occurring miombo species. More of the variation in xylem safety margins was explained by differences between groups (generalists versus specialists) than differences between species. Group accounted for about 57% of the overall variance in comparison to 13% attributed to species nested within group. On average, generalists had wider xylem safety margins than mesic specialists. Generalists had average xylem safety margins ranging between 0.6 ± 0.06 to 1.4 ± 0.03 MPa. Xylem safety margins among mesic specialists

ranged between 0.09 ± 0.03 to 0.5 ± 0.05 MPa. *Marquesia macroura* an evergreen mesic specialist had the lowest safety margin suggesting that it operates at its theoretical cavitation threshold. Xylem hydraulic safety margin was positively and significantly correlated (r^2 = 0.79; P = 0.011) with species loss in hydraulic conductivity (Fig 5.4).

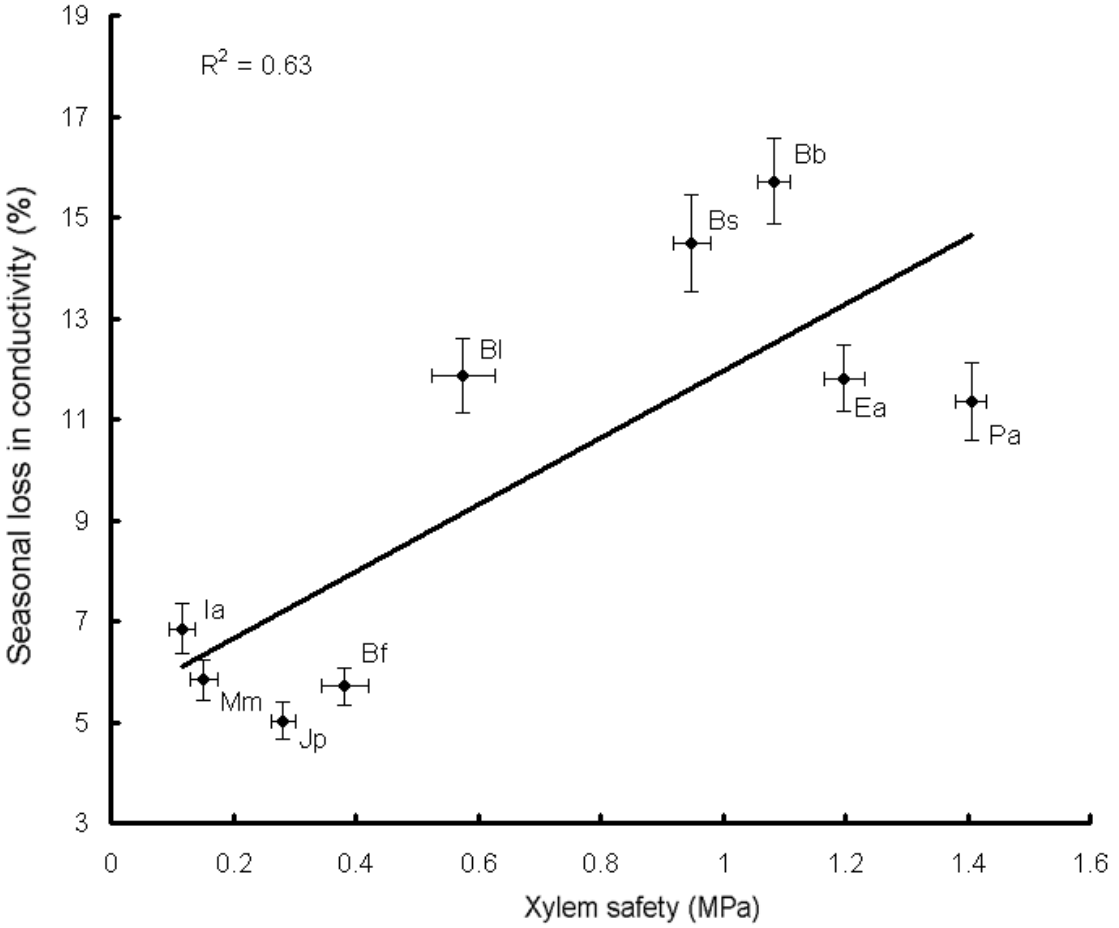


Figure 5.4: Relationship between xylem safety margin and seasonal loss in hydraulic conductivity. Chart abbreviations are as before. Regression line data points are tree species means ± SE (n = 25 trees per species). Regression model describing the relationship is: $y = 6.62x + 5.33$; P = 0.011 where y is seasonal loss in conductivity and x is xylem safety margin.

A linear regression explained 63% of the variability in seasonal native embolism.

5.3.4 Water potential threshold triggering leaf shedding and flushing

The water potential threshold triggering leaf shedding and flushing, varied significantly (ANOVA; $P < 0.001$) both between species and groups. On average generalists shed and flushed leaves at significantly lower water potential threshold than co-occurring mesic specialists (Fig 5.5).

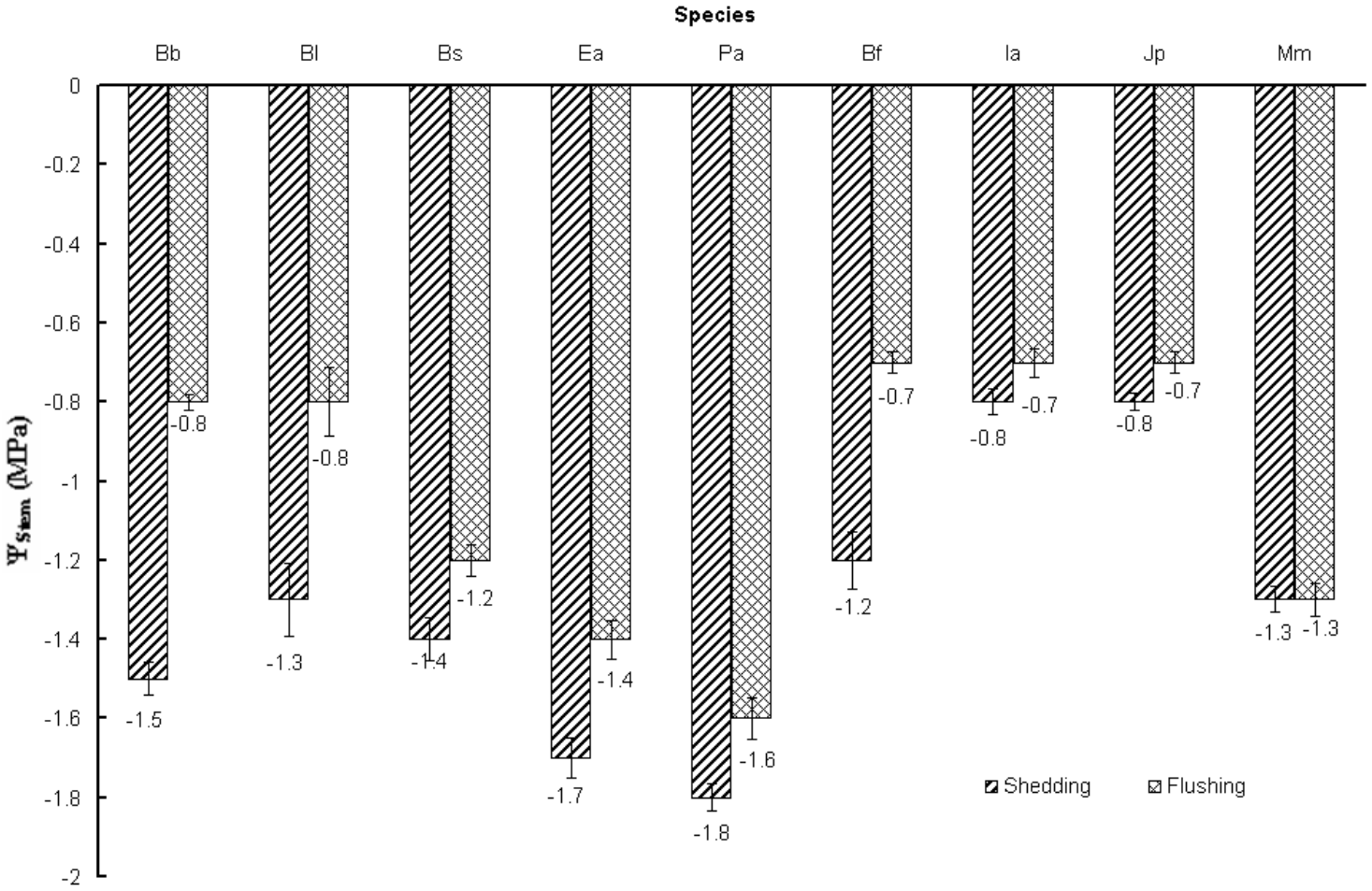


Figure 5.5: Water potential threshold triggering leaf shedding, and flushing for the nine miombo canopy tree species. Bars are species means ± SE (*n* = 25 trees per species). Error bars are at 95% confidence level. Chart abbreviations are as before.

For leaf shedding, more of the interspecific variance was explained by differences in habitat specialisation than tree species differences. Differences in habitat specialisation explained 37% of the variations in stem water potential triggering leaf shedding. In contrast, only 17% of the variance in stem water potential triggering leaf shedding was explained by tree species differences. Average Ψpd triggering leaf shedding varied between -1.8 ± 0.033 and -1.3 ± 0.063 MPa among generalists and between -1.4 ± 0.027 and -0.8 ± 0.026 MPa for mesic specialists.

Average stem water potential triggering leaf flush varied between -1.31 ± 0.042 and -0.7 ± 0.027 MPa for mesic specialists; between -1.7 ± 0.04 and -0.8 ± 0.07 MPa for habitat generalists. All generalists flushed leaves at significantly (Paired *t*-test; $P < 0.001$) higher stem water potential than that triggering leaf shedding. Of the four mesic specialists, *Isoberlinia angolensis* and *Marquesia macroura* displayed no significant (Paired *t*-test; $P > 0.05$) difference between stem water potential triggering leaf shedding and that triggering leaf flush.

5.4 DISCUSSION

5.4.1 Seasonal changes in stem water status and patterns of leaf display

In spite of growing under relatively homogenous climatic conditions, co-occurring miombo tree species display significant differences, in seasonal changes in stem water status, and patterns of leaf phenology (Fig 5.1; p 125). Mesic specialists display high seasonal stability in stem water status and are best described as being isohydric. On the contrary, generalists display significant instability in xylem water status. Generalists are best described as being anisohydric. Overall seasonal changes in stem water status are

strongly related to patterns of leaf display (Table 5.1; p 127). These results are consistent with findings from other seasonally dry tropical forests (Borchert 1994a; Fanjul & Barradas 1987; Williams et al. 1997). Our findings suggest seasonal changes in plant-water relations could be one of the main factors dictating patterns of leaf shedding and flushing in miombo ecosystems.

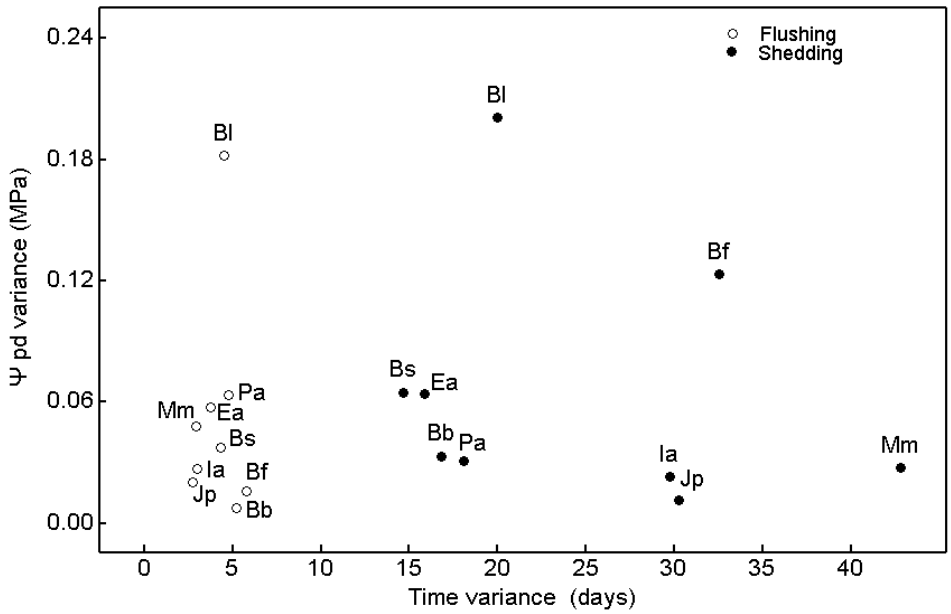


Figure 5.6: Variance plot for pre-dawn plant water potential versus time taken to complete the two leaf phenophases (shedding and flushing).

Chidumayo (2001) proposed the interaction between minimum and maximum temperatures to be one of the primary factors dictating patterns of leaf display in southern African savannas. We believe that this could be the case for leaf flush and not leaf shedding because leaf flush appears to be more constrained in time and stem water status suggesting other factors in addition to stem water potential exert some control on this leaf phenophase (Fig 5.6).

It has been proposed that plants shed leaves in order to reduce transpiration losses and maintain a positive plant water balance for the remaining organs (Rood et al. 2000; Tyree & Sperry 1988). Results of this study render further support to this hypothesis. In general, our findings support the functional dependence hypothesis of leaf phenology on stem water status (Borchert 1994b; Chapotin et al. 2006; Sayer & Newbery 2003).

5.4.2 Seasonal loss in hydraulic conductivity

Affected by similar climatic conditions, sympatric miombo woodlands canopy tree species display remarkable differences in hydraulic losses (Fig 5.2; p 128). Stem hydraulic efficiency has traditionally been linked to plant vulnerability to water stressed-induced cavitation (Martinez-Vilalta et al. 2002; Tyree & Zimmermann 2002). In this traditional view, a trade-off between xylem efficiency and safety has been proposed, such that tree species with high hydraulic efficiency tend to be more vulnerable to xylem cavitation than ones with low hydraulic efficiency (Sperry & Tyree, 1988). On the contrary, our findings show that tree species which are more resistant to xylem cavitation experience higher seasonal losses in hydraulic conductivity than co-occurring more vulnerable tree species. These findings suggest that under natural conditions drought-deciduous trees are more vulnerable to native embolism than mesic specialists (evergreen) (Fig 5.3; p 130). As expected the more drought-tolerant tree species have significantly wider safety margins than co-occurring drought intolerant species, suggesting that mesic specialists operate remarkably close to their cavitation thresholds (Fig 5.4; p 132).

Taken together, our results suggest that mesic specialists maintain high hydraulic efficiency throughout the dry season to cushion the potential impacts of xylem

dysfunction. We believe that the hydraulically efficient mesic specialists compensate for seasonal increase in evaporative demand by maintaining a high hydraulic supply. This prevents the development of potentially damaging low xylem tensions during the dry season. On the other hand, generalists mitigate the potential impacts of low-xylem pressures by annually shedding off the entire crown. This is consistent with Zimmermann's (1983) segmentation hypothesis and the proposed dynamic water balance theory (Tyree & Sperry 1988).

5.4.3 Stem water potential triggering leaf shedding and flushing

The water potential threshold triggering leaf shedding and flushing vary considerably both between species and groups (generalists versus specialists) (Fig 5.5; p 133). The less hydraulically efficient drought-deciduous wide ranging miombo tree species, shed leaves at significantly lower (more negative) stem water potential thresholds than co-occurring hydraulically efficient mesic specialists. Consistently the evergreen to semi-evergreen mesic specialists' exhibit significantly higher stem water potential thresholds that trigger leaf flushing than co-occurring habitat generalists. In Australian savannah woodland, Williams et al. (1997) reported stem water potential thresholds triggering leaf shedding ranging between -1.5 and -2.0 MPa for evergreen and semi-evergreen species, compared to an average of -0.5 to -1.0 MPa for the deciduous trees. These results contrast our findings. In the case of Australian trees, deciduous species are reportedly more hydraulically efficient and vulnerable to cavitation than the evergreen (Choat et al. 2005); whereas for miombo trees, the opposite is the case.

Predictions of leaf phenological modifications in response to ecosystem drying are slightly complicated due to many other confounding factors at play. However, these

results provides the basis for speculating that predicted reduction in ecosystem water availability under climate change may alter patterns of leaf phenology in miombo woodlands and different tree species will respond according to their hydraulic architectures.

5.4.4 Conclusion

Seasonal changes in plant-water relations influence patterns of leaf shedding and flushing among miombo woodlands canopy tree species. Patterns of leaf phenology are closely influenced by changes in stem water status. Response to changes in ecosystem water stress depends on species hydraulic design. The hydraulically efficient mesic specialists experience exceptionally low hydraulic losses. On the other hand, generalists have low hydraulic efficiency and mitigate water stress by annually shedding leaves. Generalists and specialists exhibit significant differences in the water potential thresholds that trigger leaf shedding and flushing. Mesic specialists shed and flush leaves at higher stem water potentials than co-occurring generalists. Differences in species response to water stress highlight the need to integrate species-specific plant-water relations in prediction models for ecosystem response to future climate trends.

Acknowledgements

This research was supported by funding from the Association of Commonwealth Universities. Fieldwork was supported by the Copperbelt University and Zambia Forestry College research grants. The two dedicated research assistants Metson Kasowe and Milimo Miyoba are greatly acknowledged for their dedication during the tedious data collection period.

5.5 REFERENCES

Andrade, J. L., Meinzer, F. C., Goldstein, G., Holbrook, N. M., Cavelier, J., Jackson, P., & Silvera, K.1998. Regulation of water flux through trunks, branches, and leaves in trees of a lowland tropical forest. *Oecologia* **115**: 463-471.

Borchert, R. .1994a. Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees* **8**: 198-204.

Borchert, R. .1994b. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* **75**: 1437-1449.

Brodribb, J. T. & Holbrook, N. M. .2003. Changes in Leaf Hydraulic Conductance during leaf shedding in seasonally dry tropical forest. *New Phytologist* **158**: 295-303.

Brodribb, J. T., Holbrook, N. M., Edwards, E. J., & Gutiérrez, M. V. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment* **26**: 443-450.

Bucci, S. J., Scholz, F. G., Goldstein, G., Meinzer, F.C. & Sternberg, L. DA S. L. 2003. Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant, Cell & Environment* **23**: 1633-1645

Chapotin, M. S., Razanameharizaka, J. H., & Holbrook, M. N. 2006. Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytologist* **169**: 549-559.

Chatfield, C. 1997. *The Analysis of Time Series: An Introduction*. Chapman and Hall, London.

Chidumayo, E. N. & Frost, P. 1996. Population biology of miombo trees. In: Campbell, B. (eds) *The Miombo in Transition: Woodlands and Welfare*, pp. 59-71. CIFOR, Bogor, Indonesia.

Chidumayo, E. N. 1987 Species structure in Zambian miombo woodland. *Journal of Applied Ecology* **3**: 109-118.

Chidumayo, E. N. 1994 Phenology and nutrition of miombo woodland trees in Zambia. *Trees* **9**: 67-72.

Chidumayo, E. N. 2001. Climate and phenology of savanna vegetation in southern Africa. *Journal of Vegetation Science* **12**: 347-354.

Choat, B., Ball, M. C., Luly, J. G., & Holtum, J. A. M. 2005. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from North-Eastern Australia. *Trees* **19**: 305-311.

Cochard, H., Cruiziat, P., & Tyree, M. T. 1992. Use of positive pressure to establish vulnerability curves. *Plant Physiology* **100**: 205-209.

Domec, J. & Gartner, B. L. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees* **15**: 204-214

Ewers, W. F. & Fisher, J. B. 1989. Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany* **76**: 645-656.

Fanjul, L. & Barradas, V. L. 1987. Diurnal and seasonal variation in the water relations of some deciduous and evergreen trees of a deciduous dry forest of the western coast of Mexico. *Journal of Applied Ecology* **24**: 289-303.

Filho, L. J. P. & Filho, C. V. M. .2000. Seasonal changes in the water status of three woody legumes from the Atlantic forest, Caratinga, Brazil. *Journal of Tropical Ecology* **16**: 21-32.

Frost, P. 1996. The Ecology of Miombo Woodlands. In *The Miombo in Transition: Woodlands and Welfare in Africa:* Ed B. Campbell. CIFOR, Bogor, pp. 11-57.

Fuller, D. O. & Prince, S. D. 1996. Rainfall and foliar dynamics in tropical southern Africa: Potential impacts of global climatic change on savanna vegetation. *Climate Change* **33**: 69-96.

Fuller, O. D. 1999. Canopy phenology of some mopane and miombo woodlands in Eastern Zambia. *Biogeography* **8**: 199-209.

IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Kolb, K. J. & Davis, D. S. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* **75**: 648-659.

Kramer, P. J. & Boyer, J. S. 1995. *Water Relations of Plants and Soils*. Academic Press, Inc., New York, USA.

Lopez, O. R., Kursar, T. A., Cochard, H., & Tyree, M. T. 2005. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology* **25**: 1553-1562.

Malaisse, F. 1978. The Miombo Ecosystem. In: UNESCO (eds) *Tropical Forest Ecosystems: A State-of-Knowledge Report Prepared by UNESCO/ UNEP/ FAO*. pp. 589-606. UNESCO, Paris, France

Martinez-Vilalta, J., Prat, E., Oliveras, I. & Piñol, J. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* **133**: 19-29.

Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., & Woodruffet, D. R. 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* **23**: 922-930.

Ostrom, C. W. 1990. *Time Series Analysis: Regression Techniques*. SAGE, London

Pammenter, N. W. & Van Der Willigen, C. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability ot xylem to cavitation. *Tree Physiology* **18**: 589-593.

Philips, O. L., Aragao, C. O. L., Lewis, L. S., Fisher, J., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., van der Heijden, G. et al. 2009. Drought Sensitivty of the Amazon Rainforest. *Science,* **323**: 1344-1347.

Reich, P. B. & Borchert, R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* **72**: 61-74.

Rood, S. B., Patiño, S., Coombs, K., & Tyree, M. T. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* **14**: 248–257.

Salleo, S. S., Nardini, A., Lo Gullo, M. A., Ghirardelli, L. A. 2002. Changes in stem and leaf hydraulics preceding leaf shedding in *Castanea sativa* L. *Biologia Plantarum* **45**: 227-234.

Sayer, E. J. & Newbery, D. M. 2003. The role of tree size in the leafing phenology of a seasonally dry tropical forest in Belize, Central America. *Journal of Tropical Ecology* **19**: 539-548.

Schabenberger, O. & Gotway, A. C. 2005. *Statistical Methods for Spatial Data Analysis*. Chapman and Hall, London, UK.

Schmidhalter, U. 1997. The gradient between pre-dawn rhizoplane and bulk soil matric potentials, and its relation to the pre-dawn root and leaf water potentials of four species. *Plant, Cell Environment* **20**: 953-960.

Sithole, A. & Murewi, F. J. C. 2009. Climate variability and change over Southern Africa: Impacts and challenges. *African Journal of Ecology* **47**: 17-20.

Smith, P. & Allen, Q. 2004. *Field Guide to The Trees and Shrubs of the Miombo Woodlands*. Royal Botanical Gardens Kew, London, UK.

Sperry, J. S., Donnelly, J. R., & Tyree, M. T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* **11**: 35-40.

Sperry, J. S. & Tyree, T. M. 1988. Mechanism of water stress induced xylem embolism. *Plant Physiolology* **88**: 581-587.

Storrs, A. E. G. 1979. *Know your Trees: Some Common Trees of Zambia*. Forest Department, Ndola, Zambia.

Taiz, L. & Zeiger, E. 1998. *Plant Physiology*. Sinauer Associates, Inc., Massachusetts, USA.

Trapnell, C. G., Friend, M. T., Chamberlain, G. T., Birch, F. H. 1976. The effects of fire and termites on a Zambian woodland soil. *Journal of Ecology* **64**: 577-588.

Trapnell, C. G. & Smith, P. 2001. *Ecological Survey of Zambia : the Traverse Records of C.G. Trapnell, 1932-43*. Royal Botanic Gardens Kew, London, UK.

Tyree, M. T., Cochard, H., Cruiziati, P., Sinclair, B., & Ameglio, T. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell & Environment* **16:** 87-882.

Tyree, M. T. & Sperry, J. S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction Caused by dynamic water stress? *Plant Physiology* **88**: 0574-0580.

Tyree, M. T. & Ewers, F. W. 2001. The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**: 345-360

Tyree, M. T. & Zimmermann, M. H. 2002. *Xylem Structure and the Ascent of Sap*. Springer, Berlin, Germany.

Wang, J., Ives, E. N., & Lechowicz, J. M. 1992. The relation of foliar phenology to xylem embolism in trees. *Functional Ecology* **6**: 469-475.

Wheeler, J. K., Sperry, J. S., Hacke, U. G., & Hoang, N. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* **28**: 800-812.

White, F. 1983. *The Vegetation of Africa : a Descriptive Memoir to Accompany the Unesco/AETFAT/UNSO Vegetation Map of Africa*. Unesco, Paris, France.

Williams, L. E. & Araujo, F. J. 2002. Correlations among predawn leaf, midday leaf, and midday stem water potential and their correlations with other measures of soil and plant water status in *Vitis vinifera*. *Journal of the American Society for Horticultural Science* **127**: 448-454.

Williams, R. J., Myers, B. A., Muller, W. J., Duff, G. A., & Eammus, D. 1997. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology* **78**: 2542-2558.

Zar, J. H. 2010. *Biostatistical Analysis*. 5th ed. Pearson Education International, London, UK.

Zimmermann, M. H. 1983. *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin, Germany.

Zimmermann, M. H. & Jeje, A. A. 1981. Vessel length in stems of some American woodyspecies. *Canadian Journal of Botany* **59**: 1882–1892.

CHAPTER 6

Functional coordination between hydraulic and leaf functional traits in miombo woodlands: Implications for water stress management and species habitat preference

OVERVIEW

Interactions between hydraulic properties and leaf functional traits associated with plant drought tolerance ability remain poorly understood. In the case of miombo woodlands, even the base line data on leaf functional traits (specific leaf area, leaf dry matter content, and leaf thickness) associated with drought tolerance ability are completely absent. What are the ranges of hydraulic and leaf functional traits related to water stress management in miombo woodlands? To what extent, do these hydraulic properties and leaf functional traits, vary between tree species differing in niche specialisation? How do stem hydraulic properties and leaf functional traits vary between wet and dry miombo woodlands sites? How much of this variation is caused by plasticity in wide-ranging species and how much is caused by community turnover? Are branch hydraulic properties coordinated with leaf functional traits? These are interesting but yet remain answered questions. This chapter addresses these questions by quantifying the range of leaf functional traits associated with drought tolerance for nine miombo woodlands tree species differing in habitat preference (objective 4; p 12). The relationship between hydraulic properties and leaf functional traits is presented in this chapter.

The paper was written by Royd Vinya. Nick Brown, Yadvinder Malhi and Joshua Fisher made comments. This chapter has been submitted as a journal paper to Acta Physiologiae Plantarum.

Functional coordination between hydraulic and leaf functional traits in miombo woodlands: Implications for water stress management and species habitat preference

Authors: Royd Vinya[1], Yadvinder Malhi[1], Nick Brown[2], Joshua B. Fisher[1],

1 Environmental Change Institute, School of Geography and the Environment
2 Plant Sciences Department, University of Oxford,

ABSTRACT

We investigated functional coordination between branch hydraulics and leaf functional traits among nine miombo woodland canopy tree species differing in habitat preference and phenology. Specifically we were seeking to answer the question: Are branch hydraulics coordinated with leaf functional traits linked to plant drought tolerance ability in seasonally dry tropical forests and what are the implications for species habitat preference? Results show that drought-tolerant tree species are significantly ($P < 0.05$) more resistant to xylem cavitation (Ψ_{50}), have low specific hydraulic conductivity (K_S), leaf specific conductivity (K_L), mean leaf area (*MLA*), dry matter content (*DMC*), but high specific leaf area (*SLA*). On the other hand, drought-intolerant (mesic specialists) tree species display high K_L, *MLA*, and *DMC*, but low *SLA* and Ψ_{50}. Generalists display plasticity only in K_S and K_L while leaf functional traits and Ψ_{50} remain constant from wet to dry miombo woodlands. K_L is negatively correlated with *SLA* but positively correlated with both *DMC* and *MLA*. Our results suggest that the interaction between branch

hydraulics and leaf functional traits linked with plant drought tolerance ability influence species habitat preference in miombo woodlands.

Key words: Dry matter content; Leaf specific conductivity; Miombo woodlands; Specific hydraulic conductivity; Specific leaf area

6.1 INTRODUCTION

Plant response to water stress can be at both physiological and morphological scales. At a physiological level, plants vary hydraulic properties in response to changing water availability (Engelbrecht et al. 2000; Pockman and Sperry 2000). Morphologically, plants respond to water stress by modulating patterns of foliar carbon allocation (Berry and Downton 1982; Fonseca et al 2000; Niinemets 2001; Reich et al 1997; Ryser 1996; Wright et al. 2002). Given that plant response to water stress occurs at both morphological and physiological levels (Mencuccini 2003), one could infer some functional coordination between hydraulic and leaf functional traits directly linked to plant drought tolerance ability. However, very little is known about this integrated plant drought response in seasonally dry tropical forests. Many studies have been undertaken to study separately physiological and morphological responses to water stress. These approaches, however, give very little insight into integrated plant drought response. Studying the interaction between hydraulic properties and leaf functional traits related to plant drought response may give the much needed insight into how plants in seasonally dry tropical forests will respond to a reduction in ecosystem water availability under global climate change (IPCC 2007).

As regards stem hydraulic architecture, it has been proposed that an evolutionary trade-off exists between hydraulic efficiency and xylem safety (Sperry et al. 2008; Tyree

and Zimmermann 2002). Ideally this relationship reflects species habitat preference by limiting hydraulically efficient individuals to the mesic habitats and those less efficient but with high resistance to xylem cavitation to the arid habitats (Brodribb and Hill 1999; Lopez et al. 2005; Pockman and Sperry 2000). Based on this observed relationship it has been proposed that pressure for selection under arid ecosystems favours individuals with low hydraulic efficiency and high resistance to water-stress induced xylem dysfunction (Tyree and Zimmermann 2002).

It is also well established that plants respond to water stress by modulating leaf size relative to leaf mass (Fonseca et al. 2000; Lamont et al. 2002; Reich et al. 1997; Wright et al. 2002). Specific leaf area (ratio of leaf area to its dried mass) is an essential plant functional trait that relates to plant resource exploitation (water, CO2, and light) (Sefton et al. 2002; Wilson et al. 1999; Wright et al. 2002). It represents a significant trade-off between resource capture and the restrictions imposed by structural adjustments and the mitigation of plant water loss through transpiration. The importance of SLA in relation to plant hydraulics is demonstrated by its correlation with plant water use efficiency (Parkhurst and Loucks 1972; Sefton et al. 2002). Furthermore, SLA has been demonstrated to be correlated with both relative growth rate (Meerts and Garnier 1996) and photosynthetic rate (Mencuccini 2003; Poorter and Evans 1998).

Leaf size, on the other hand, reflects plants structural strategies aimed at minimizing water loss and regulating overall leaf temperature so as to optimize plant photosynthetic rate (Parkhurst and Loucks 1972). Available evidence shows a trend towards compact leaf areas in hot and arid environments (Ackerly et al. 2002). One theory proposes that small leaves present reduced surface areas and, thus enhanced

capabilities of maintaining low leaf temperatures in comparison to large leaves, which tend to suffer from overheating, when soil water becomes limiting (Berry and Downton 1982). It has also been proposed that towards hot and arid ecosystems plants tend to develop leaf morphologies that are thicker and denser than under mesic habitats (Wright et al. 2002). The importance of dry matter content has been demonstrated by its correlation with leaf lifespan and resource acquisition (Ryser 1996).

In this study we chose the miombo woodlands in Africa to study the relationship between branch hydraulic properties and leaf functional traits linked with drought tolerance ability. Among seasonally dry tropical forests, the miombo woodlands in Africa are one case in point where there is a noticeable lack of data for both plant hydraulic architecture and leaf functional traits (Niinemets 2001; Wright et al. 2004). Future climatic trends for the Zambezian phytoregion which harbours the miombo woodlands point in the direction of increased aridity by the end of this century (Sithole and Murewi 2009). Development of an evidence-based climate-change adaptation plan will be hampered by the lack of data on the physiology of miombo woodlands tree species. A robust understanding of the relationship between tree hydraulic architecture and leaf functional traits related to plant drought tolerance will add insights into the ecological significance of these traits. In this study, we ask the following questions: 1) What are the ranges of hydraulic and leaf functional traits related to water stress management in miombo woodlands? 2) To what extent, do these hydraulic properties and leaf functional traits, vary between tree species differing in niche specialisation? 3) How do stem hydraulic properties and leaf functional traits vary between wet and dry miombo woodlands sites? 4) How much of this variation is caused by plasticity in wide-ranging

species and how much is caused by community turnover? 5) Are branch hydraulic properties coordinated with leaf functional traits? Therefore, the objectives of this study were to:

- Quantify the range of hydraulic and leaf functional traits in miombo woodlands and evaluate the extent to which these functional traits vary between tree species differing in habitat preference.
- Examine plasticity in hydraulic and leaf functional traits between wet and dry miombo woodland habitats.
- Evaluate the extent to which species turnover influences these perceived shifts in leaf functional traits between the wet and dry habitats.
- Investigate the relationship, between branch hydraulic properties and leaf functional traits related to plant drought management strategy in miombo woodlands.

6.2 MATERIALS AND METHODS

6.2.1 Study site

In this study, we chose two gazetted forest reserves to represent the wet and dry miombo woodlands (White 1983). The two forest reserves had known forest management history, current (less than 10 years) soil-vegetation surveys and reasonably similar in geology, although minor local variations may have been present. The two forest reserves experienced identical weather patterns in which summer rains occur between November and April. An extensive seasonal drought lasting from May to October follows the rainy season. The wet site is Mwekera National Forest No. 6 located on the outskirts of Kitwe City (12^{o} 49′ S and 28^{o} 22′ E; elevation of 1295m above sea level). The vegetation of the

wet site is typically *Brachystegia-Julbernardia* woodlands with the genus *Brachystegia, Isoberlinia, Julbernardia* and *Marquesia* as common canopy co-dominants (Chidumayo 1987). The wet site received an average annual precipitation of 1,200 mm with average annual temperatures ranging from 14 to 28 ^{o}C. The dry site was located in Choma district at 16^{o} 50' S and 27^{o} 03' E with an average elevation of 1266 m above sea level.

The vegetation of the dry site has *Brachystegia boehmii*, *Brachystegia spiciformis* and *Julbernardia globiflora* as the common canopy co-dominants. The dry site received 800 mm of mean annual precipitation with mean annual temperatures ranging between 12 and 27 ^{o}C.

6.2.2 Sampling

In this study we examined nine co-dominant miombo woodlands tree species. Four of the nine species [*Brachystegia floribunda* Benth (fabaceae), *Isoberlinia angolensis* (Benth.)Hoyle & Brenan (fabaceae), *Julbernardia paniculata* (Benth.)Troupin (fabaceae), and *Marquesia macroura* Gilg (dipterocarpaceae)] display a narrow habitat range with distribution mainly confined to wet miombo site and are referred to as mesic specialists in this study. The other five species [*Brachystegia boehmii* Benth (fabaceae), *Brachystegia longifolia* Benth (fabaceae), *Brachystegia spiciformis* Benth (fabaceae), *Erythrophleum africanum* (Benth.) Harms (fabaceae), and *Pericopsis angolensis* (Baker) Meeuwen (fabaceae)] exhibit wide habitat range with distribution throughout the miombo eco-region and are referred throughout this study as generalists.

The nine tree species were selected on the basis that: (1) they differed substantially in habitat preference (Chidumayo 1987, Smith and Allen 2004), (2) they had contrasting leaf phenology, (3) there was substantial taxonomical difference between

them and, (4) they form much of the canopy throughout the miombo woodlands. Twenty five (25) trees per species (giving a total of 225 trees on the wet and 100 trees on the dry sites) were selected based on the criteria that they were healthy, actively growing, and at least 100 m apart. On the dry site 100 trees were sampled due to the absence of *Brachystegia longifolia*. On both the dry and wet sites we controlled for local environmental variability by sampling individuals that co-occurred. The average diameter at breast height for the sample trees ranged from 30 to 39 cm on the wet site and from 18 to 25 cm on the dry site (Appendix 5.1).

6.2.3 Leaf measurements

We carried out leaf measurements in June 2007 and from April to June 2008. Data collection coincided with the end of the rainy season, by which time the leaves had reached full maturity and the soils were still well hydrated. We sampled leaves from twenty five (25) GPS referenced trees per species (giving a total of 225 trees at the wet site and 100 trees at the dry site). We sampled three leaves per tree, giving a total of 75 leaves per species in both wet and dry miombo sites. Three leaf-bearing, light-exposed twigs were harvested per tree between 05:30 and 07:30 local time. The height of trees sampled in the study sites ranged from 16 to 21 m on the wet and 11 to 18 m on the dry site.

Twigs were collected by climbing the trees. Second-order branches were excised from the main branch and quickly wrapped in a wet towel. The twigs were then placed in opaque plastic bags. This ensured that leaves remained well hydrated and transpiration was halted (Garnier et al. 2001; Westoby 1998). The twigs were transported to the nearby laboratory (Zambia Forestry College – wet site, and temporary laboratory – dry site)

located within the study site. The procedure for measuring specific leaf area and dry matter content determination followed those of Westoby (1998) and Garnier et al. (2001). At the laboratory, one healthy and fully expanded leaf was harvested from each twig. The main criteria for selecting a leaf for measurement were that it had not suffered any leaf blade damage, mature (hardened leaf blade), and was actively photosynthesizing (green in colour). The selected sample leaves were weighed to get wet weight, and their thickness determined using a digital micro-caliper (accuracy 0.01 mm). Leaf thickness was estimated from the leaf blade (i.e. excluding the leaf veins). The same leaf was then scanned using a flatbed scanner for area analysis (Packard Bell Diamond 1200 Plus). The scanned leaves were immediately oven-dried at a constant temperature of 72^{o}C for 48 hours to a constant oven-dry weight (Ackerly 2002; Sellin and Kupper 2006; Westoby and Wright 2003).

Leaf areas for the scanned images were determined using the software Image J (freely available from http://rsb.info.nih.gov/ij/). Specific leaf area (cm^2/ g) was then calculated as the ratio of the leaf area to its oven dry mass. Dry matter content (g g^{-1}) was calculated as the ratio of the leaf oven dry weight to its wet weight.

6.2.4 Hydraulic measurements

We measured the hydraulic properties for nine miombo tree species from April to May 2008. Given that hydraulic properties may vary considerably with branch diameter (van der Willigen et al. 2000), it is advisable to take measurements from morphologically-identical branch diameters (Patino et al. 1995). We confined hydraulic property evaluation to second-order leaf bearing branches. Since plant hydraulic properties show strong vertical variations within an individual tree (Tyree and Zimmermann 2002), care

was also taken to minimize this effect by sampling from roughly the same crown height. We harvested three healthy second-order leaf-bearing twigs in the early hours of the morning (between 05:30 and 07:30hrs) from each of the replicate individuals for each species giving a total of 675 twigs on the wet site and 300 twigs on the dry site. The diameter underbark for the harvested twigs ranged from 4 to 10 mm. The harvested twigs were immediately covered in wet towels and sealed in plastic sample bags in order to minimize air entry through the exposed cut vessels. Samples were then transported to the nearby laboratory for conductivity determination.

We trimmed the twigs to approximately equal in length as the determined species maximum vessel length plus 10% allowance in order to avoid open vessels. Throughout the process, of sample preparation twigs were always kept wholly immersed in water. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Laboratory rubber corks provided a water-tight connection between the segment and reservoir. The water reservoir was constantly refilled in order to maintain the same delivery pressure. The segments were perfused with degassed, filtered (to 0.2 µm) and acidified (with HCl, pH = 2) distilled water. Previous studies established that, in the absence of acidifying the perfusion solution, microbes tend to grow in the water reservoir and consequently leading to decline in conductivity (Kolb et al. 1996; Sperry et al. 1988). We acidified the perfusing solution with HCl acid in order to prevent microbial growth in the water reservoir and eventually clogging the xylem vessels. Each segment was allowed to equilibrate before initial flow rate was measured. Sap flow was measured by attaching a pre-weighed cotton wool covered in a plastic onto the free distal end of the segment.

Evaporation loses were kept to a minimum by covering the wool with plastic. All segments were flushed at a constant pressure of 150 kPa for periods ranging from 20 to 30 minutes depending on species and extent of native xylem air blockage, prior to sap flow measurement. Therefore, the figures reported here are maximum conductivities. At the end of each flow determination, segment underbark diameter and length were accurately measured. Segments where pith was highly pronounced (exceeding 10% of sapwood diameter) the pith diameter was also measured and subtracted from the total diameter. Maximum hydraulic conductivity (K_H) was calculated as:

$$K_H = \left(\frac{J_V}{(\Delta P / l)}\right) \qquad (\text{kg s}^{-1}\ \text{MPa}^{-1}\ \text{m}) \qquad \textbf{[Eqn. 1]}$$

Where K_H is the maximum hydraulic conductivity, J_V is the flow rate (kg s^{-1}); ΔP is the delivery pressure (MPa) and; l is segment length (m).

Stem-area specific conductivity (K_S, kg s^{-1} m^{-1} MPa^{-1}) was derived by dividing hydraulic conductivity with the effective sapwood cross-sectional area (A_W, m^2).

Huber value (*HV*) was calculated as the ratio of the twig area to total leaf area supported by that twig:

$$HV = \frac{A_W}{A_L} \qquad \textbf{[Eqn. 2]}$$

where; A_L (m^2) is the total leaf area supported by the twig.

Leaf specific conductivity (K_L, kg s^{-1} MPa^{-1} m^{-1}) was calculated as:

$K_L = K_S$ x HV **[Eqn. 3]**

6.3.5 Determination of xylem vulnerability to cavitation

The water potential leading to 50% (Ψ_{50}) reduction in hydraulic conductivity estimated from the vulnerability curves has often been used as a measure for plant drought tolerance capability (Tyree and Zimmermann 2002; Tyree and Sperry 1988). In summary, the procedure involved inducing cavitation by dehydrating twigs using the standard laboratory bench air-drying technique following methods of (Cochard et al. 1992). Segments were progressively dehydrated to various water potentials over a period of 6 to 48 hrs depending on species. We excised small distal segments from the main twig for determination of water potential (Ψ) using a pressure chamber (Skye Instruments Ltd, UK, SKPM 1405). The segments for Ψ determination were placed in air-tight plastic bags for 30 minutes following excision from the main stem in order to allow for water potential equilibration. We measured hydraulic properties as already explained in the previous section. We fitted the vulnerability curves with the following sigmoid function:

$$PLC = 100 / (1 + \exp (a (\Psi - \Psi_{50}))) \quad \textbf{[Eqn. 3]}$$

Where Ψ_{50} is the water potential causing 50% reduction in hydraulic conductance, and a represents the slope of the vulnerability curve. The two parameters (Ψ_{50} and a) in this function have direct physiological relevance in relation to Zimmermann's (1983) air-seeding theory (Pammenter and Van der Willigen 1998).

6.3.6 Statistics and data analysis

All values of specific leaf area and mean leaf area were log transformed prior to performing any statistical analyses to meet the preconditions for ANOVA and regression. Leaf dry matter content, Huber value and leaf specific conductivity values were initially angular transformed, followed by log transformation because they were proportions. The

question whether most of the differences were pronounced at the level of functional type (generalist versus mesic specialist) or between species nested within functional type or within-species was addressed by performing a mixed effects ANOVA model (Sokal 1995; Underwood 1997). We used a general linear model ANOVA to answer the question whether most of the variations in hydraulic properties and leaf functional traits occur from site to site or species to species (Zar, 2010). Since the overall interest was to derive general conclusions about the difference between wet and dry miombo woodlands sites, species was treated as a random factor and site as a fixed factor. The dependent variables were the hydraulic properties and leaf functional traits. The question whether changes in leaf functional traits were as a result of species turnover or mere plasticity was answered by weighting each trait by species contribution to basal area. Weighting the leaf functional traits by species contribution to basal area helped to reflect species community relative dominance. We used linear regression analysis to analyze the relationship between hydraulic properties and leaf functional traits. We used correlation coefficient to test for the strength of the relationships among hydraulic properties and leaf functional traits. Statistical analyses were carried out in Minitab (Version 15, Minitab Inc., Pennsylvania, USA).

6.4 RESULTS

6.4.1 Variations in hydraulic and leaf functional traits

There were significant variations in both hydraulic and leaf functional traits among tree species differing in habitat preference. Although specific leaf area varied significantly between species differing in habitat preference, individual tree nested within-species explained most of the variations (Table 6.1).

Table 6.1: Results of linear mixed effects analysis of variance for nine miombo woodlands tree species studied. SLA = specific leaf area; DMC = dry matter content; MLA = mean leaf area; K_S = stem-area-specific hydraulic conductivity; *HV* = Huber value; K_L = leaf specific conductivity; Ψ_{50} = water potential causing 50% loss in conductivity; *MS* = mean square; *VC* = variance component.

Variable	Source	*DF*	*MS*	*F-ratio*	*P-value*	*VC*
SLA (g cm^{-2})	Functional Type	1	1.0602	12.68	0.009	7.53
	Species (Functional Type)	7	0.0836	2.96	0.006	4.16
	Individual (Functional Type Species)	216	0.0282	2.01	< 0.001	43.35
DMC (g g^{-1})	Functional Type	1	1.9077	48.08	< 0.001	28.67
	Species (Functional Type)	7	0.0396	3.65	0.001	4.17
	Individual (Functional Type Species)	216	0.0108	2.31	< 0.001	35.30
MLA (cm^2)	Functional Type	1	43.3102	14.32	0.007	54.55
	Species (Functional Type)	7	3.0239	65.68	< 0.001	26.66
	Individual (Functional Type Species)	216	0.0460	4.17	< 0.001	12.53
K_S (kg s^{-1} MPa^{-1} m^{-1})	Functional Type	1	25.4633	661.33	< 0.001	49.72
	Species (Functional Type)	7	1.1288	29.32	< 0.001	15.43
	Individual (Functional Type Species)	216	0.0385	1.82	< 0.001	16.24
HV	Functional Type	1	0.0125	0.66	0.417	0.14
	Species (Functional Type)	7	0.0678	3.58	0.001	5.40
	Individual (Functional Type Species)	216	0.0189	2.02	< 0.001	46.52
K_L (kg s^{-1} MPa^{-1} m^{-1})	Functional Type	1	6.9027	234.3	< 0.001	32.07
	Species (Functional Type)	7	0.2375	8.06	< 0.001	7.72
	Individual (Functional Type Species)	216	0.0294	2.01	< 0.001	29.57
Ψ_{50} (MPa)	Functional Type	1	65.3256	12.18	0.01	7.63
	Species (Functional Type)	7	5.3625	3.10	0.004	4.18
	Individual (Functional Type Species)	216	1.7298	1.84	< 0.001	41.58

For dry matter content (*DMC*), functional type and individual nested within-species variances were more than variances explained between species nested within-functional type (Table 6.1). Huber value (*HV*) did not vary significantly between functional types but varied significantly between species and within-species, though the variability within-species were more than those between species (Table 6.1). For vulnerability to cavitation (Ψ_{50}), within-species variations were more pronounced than differences between functional types and species. Functional type explained most of the variances for specific hydraulic conductivity and leaf specific conductivity.

Mean hydraulic properties and leaf functional traits for miombo woodlands mesic specialists and habitat generalists are presented in Table 6.2. Average specific hydraulic conductivity (K_S) varied between 5.17 ± 0.37 and 9.97 ± 0.41 kg s^{-1} MPa^{-1} m^{-1} for generalists and from 13.73 ± 0.74 to 24.19 ± 1.82 kg s^{-1} MPa^{-1} m^{-1} for mesic specialists.

Table 6.2: Summary of species leaf and stem hydraulic traits. Table abbreviations are: *SLA* = specific leaf area; *MLA* = mean leaf area; *DMC* = Dry matter content; Ψ_{50} = cavitation resistance at 50% loss in conductivity; K_S = specific leaf conductivity; *HV* = Huber value; K_L = Leaf specific conductivity. Standard errors of the mean are at 95% confidence interval.

Site	Species	*SLA* (cm^2/ g)	*MLA* (cm^2)	*DMC* ($g\ g^{-1}$) x 10^{-2}	Ψ_{50} (MPa)	K_S ($kg\ s^{-1}\ MPa^{-1}\ m^{-1}$)	*HV*	K_L ($kg\ s^{-1}\ MPa^{-1}\ m^{-1}$) x 10^{-4}
Wet	*B.boehmii*	433 ± 14	30 ± 1	8.1 ± 0.4	-3.2 ± 0.11	5.74 ± 0.3	2.9 ± 0.02	1.66 ± 0.12
	B.longifolia	470 ± 13	27 ± 2	8.6 ± 0.3	-2.5 ± 0.08	5.17 ± 0.3	2.8 ± 0.02	1.41 ± 0.12
	B.spiciformis	522 ± 15	89 ± 4	7.8 ± 0.3	-2.8 ± 0.08	7.47 ± 0.5	2.3 ± 0.02	1.71 ± 0.15
	E.africanum	562 ±34	33 ± 1	6.6 ± 0.6	-3.1 ± 0.09	9.97 ± 0.4	2.0 ± 0.01	1.98 ± 0.15
	P.angolensis	504 ± 18	73 ± 3	6.3 ± 0.3	-3.2 ± 0.10	9.43 ± 0.4	2.4 ± 0.02	2.27 ± 0.22
	B.floribunda	488 ± 43	112 ± 4	11.3 ± 1	-1.7 ± 0.20	13.73 ± 0.6	2.4 ± 0.01	3.32 ± 0.27
	I.angolensis	383 ± 13	202 ± 8	12.1 ± 0.5	-2.0 ± 0.22	24.19 ± 1.3	2.8 ± 0.01	6.86 ± 0.05
	J.paniculata	403 ± 12	157 ± 6	13.6 ± 0.6	-2.2 ± 0.10	15.58 ± 0.9	2.1 ± 0.01	3.33 ± 0.24
	M.macroura	418 ± 13	122 ± 4	11.3 ± 0.4	-1.5 ± 0.34	21.07 ± 0.8	2.5 ± 0.02	5.32 ± 0.44
Dry	*B.boehmii*	629 ± 42	24 ± 0.8	7.2 ± 0.5	-3.6 ± 0.14	2.77 ±0.07	2.2 ± 0.1	0.59 ± 0.03
	B.spiciformis	620 ± 14	44 ± 1	7.0 ± 0.3	-3.6 ± 0.12	5.33 ± 0.18	1.4 ± 0.1	0.7 ± 0.04
	E.africanum	474 ± 8	32 ± 0.7	7.4 ± 0.5	-3.0 ±0.10	8.19 ± 0.28	2.1 ± 0.2	1.59 ± 0.09
	P.angolensis	562 ± 18	57 ± 2	7.0 ± 0.5	-2.8 ± 0.13	10.53 ± 0.35	2.2 ± 0.1	2.21 ± 0.1

Huber values (*HV*) ranged from 2.1 ± 0.01 to 2.8 ± 0.01 x 10^{-5} for mesic specialists and 2.0 ± 0.01 to 2.9 ± 0.02 x 10^{-5} for generalists. Leaf specific conductivity (K_L) among mesic specialists varied from 3.32 ± 0.27 to 6.86 ± 0.05 x 10^{-4} kg s^{-1} MPa^{-1} m^{-1} whereas, among generalists, it ranged from 1.41 ± 0.12 to 2.27 ± 0.22 x 10^{-4} kg s^{-1} MPa^{-1} m^{-1}. Average specific leaf area (*SLA*) ranged from 383 ± 13 to 488 ± 43 cm^2 g^{-1}, and for habitat generalist species mean *SLA* ranged from 433 ± 14 to 562 ± 33 cm^2 g^{-1}. Leaf dry matter content among mesic specialist species ranged from 0.11 ± 0.0098 to 0.13 ± 0.0056 g g^{-1}. Within habitat generalist species, leaf *DMC* varied significantly (ANOVA, $P < 0.001$), ranging from 0.063 ± 0.003 to 0.081 ± 0.004 g g^{-1}. Mean leaf area among generalists ranged between 28 ± 2 and 92 ± 6 cm^2, whereas among mesic specialists it ranged from 110 ± 7 to 208 ± 12 cm^2.

6.4.2 Shift in hydraulic and leaf functional traits between wet and dry miombo woodlands

Apart from mean leaf area, intra-species variations in leaf functional traits between wet and dry miombo woodlands site were highly insignificant (ANOVA, $P > 0.05$) (Table 6.3).

Table 6.3: Generalized linear model analysis of variance for hydraulic and leaf functional traits for miombo woodlands canopy tree species with wide habitat distribution. Table abbreviations and units are as above.

Variable	**Scale**	***df***	***ms***	***F*-ratio**	***P*-value**
SLA	site	1	0.57361	2.39	0.220
	species	3	0.09760	0.41	0.760
	site x species	3	0.24009	18.68	< 0.000
DMC	site	1	0.019574	0.63	0.487
	species	3	0.035735	1.14	0.458
	site x species	3	0.031283	4.94	0.002
MLA	site	1	2.2893	3.82	0.146
	species	3	5.8135	9.71	0.047
	site x species	3	0.5990	35.97	< 0.000
HV	site	1	0.23144	11.23	0.001
	species	3	0.16530	8.02	< 0.001
	site x species	3	0.11823	5.74	0.001
K_S	site	1	1.89255	84.78	< 0.001
	species	3	4.84983	217.27	< 0.001
	site x species	3	0.78715	35.26	< 0.001
K_L	site	1	1.36652	62.06	< 0.001
	species	3	1.07042	48.61	< 0.001
	site x species	3	0.49055	22.28	< 0.001
Ψ_{50}	site	1	3.8416	0.34	0.602
	species	3	6.1033	0.53	0.690
	site x species	3	11.4120	13.02	< 0.000

Apart from vulnerability to cavitation, both site and species differences in hydraulic properties between the wet and dry miombo woodlands sites were highly significant ($P < 0.05$) (Table 6.3).

Overall, response to ecosystem water variability for both hydraulic and leaf functional traits were diverse (Fig 6.1). While average specific leaf area (*SLA*) and dry matter content (*DMC*) increased from the wet to the dry sites, specific hydraulic conductivity (*KS*) showed the opposite response.

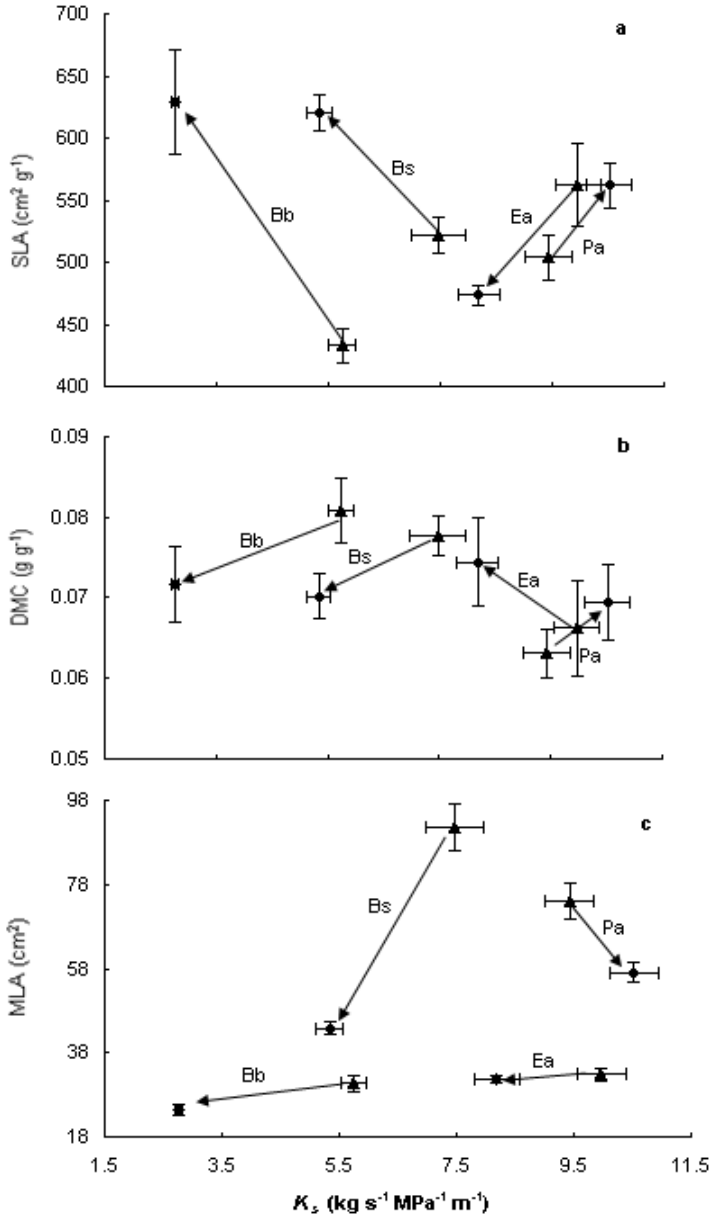


Figure 6.1: Shifts in specific hydraulic conductivity and leaf functional traits related to water stress management between wet and dry miombo woodlands habitats; (a) specific leaf area (*SLA*); (b) dry matter content (*DMC*); (c) Mean leaf area. Each point is species mean ± SE (n = 25 trees per species). Chart abbreviations are: Bb = *Brachystegia boehmii*, Bs = *Brachystegia spiciformis*, Ea = *Erythrophleum africanum*, Pa = *Pericopsis angolensis*. Chart symbols: Δ is wet site generalist and • is dry site generalist. Arrow is from wet to dry site.

Xylem cavitation vulnerability marginally increased from wet to dry miombo woodlands site and at the same time, specific leaf area, and dry matter content displayed a similar response. The opposite was true for mean leaf area (Fig 6.2).

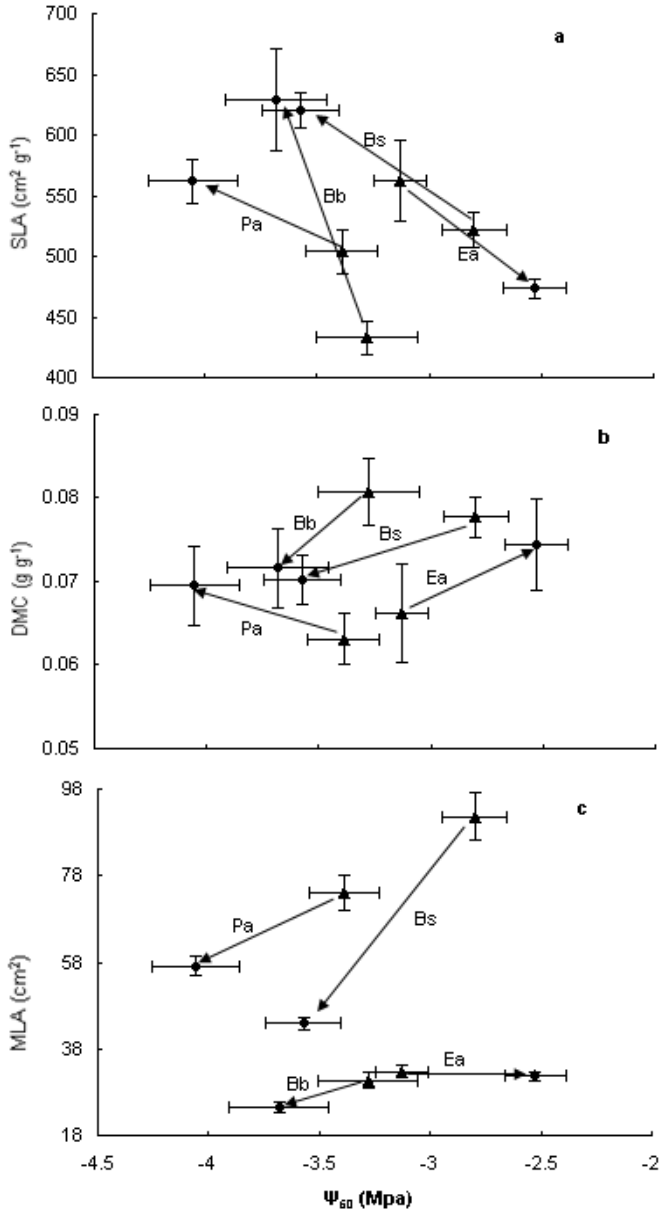


Figure 6.2: Shifts in xylem vulnerability to cavitation and leaf functional traits between wet and dry miombo woodlands habitats (a) specific leaf area (*SLA*); (b) dry matter content (*DMC*); (c) Mean leaf area. Each point is species mean ± SE (n = 25 trees per species). Chart symbols and abbreviations are as above. Arrow is from wet to dry site.

On average *SLA* increased from wet to dry miombo woodland sites by 31%, 16%, and 10% in *Brachystegia boehmii, Brachystegia spiciformis*, and *Pericopsis angolensis* respectively, a 16% reduction was observed in *Erythrophleum africanum*. DMC marginally increased by 9%, 11% and 11% in *Pericopsis angolensis, Brachystegia boehmii* and *Brachystegia spiciformis* respectively. Within-species mean leaf area declined from wet to dry miombo woodlands sites by 20%, 51%, and 22% in *Brachystegia boehmii*, *Brachystegia spiciformis*, and *Pericopsis angolensis* respectively.

At community level values of mean leaf area (*MLA*) and dry matter content (*DMC*) declined in the wet-dry miombo woodland direction. Specific leaf area showed an increase from wet to dry miombo woodlands sites. When average leaf functional trait data were weighted by relative basal area (Appendix 6.2) the influence of mesic specialists became amplified (Fig 6.3).

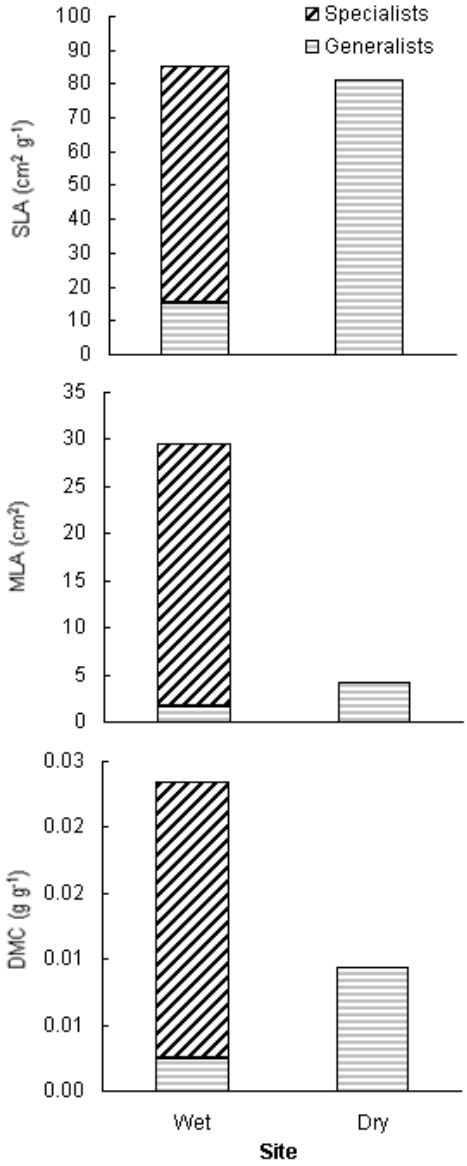


Figure 6.3: Leaf functional traits normalised by tree species contribution to basal area to reflect species dominance on trait shift between wet and dry miombo woodlands habitats

6.4.3 Relationships between branch hydraulics and leaf functional traits

Across the entire data set (n = 225), specific hydraulic conductivity was significantly (r = 0.39, P < 0.001) and negatively correlated to specific leaf area, but positively correlated to both dry matter content (r = 0.41, P < 0.001) and mean leaf area (r = 0.71, n = 225, P = 0.001).

At inter-species level (n = 9), the relationship between K_S and leaf functional traits remained significant ($P < 0.05$). A linear regression explained 58%, 54% and 82% of the variability in specific leaf area (*SLA*), dry matter content (*DMC*), and mean leaf area (*MLA*) respectively (Fig 6.4).

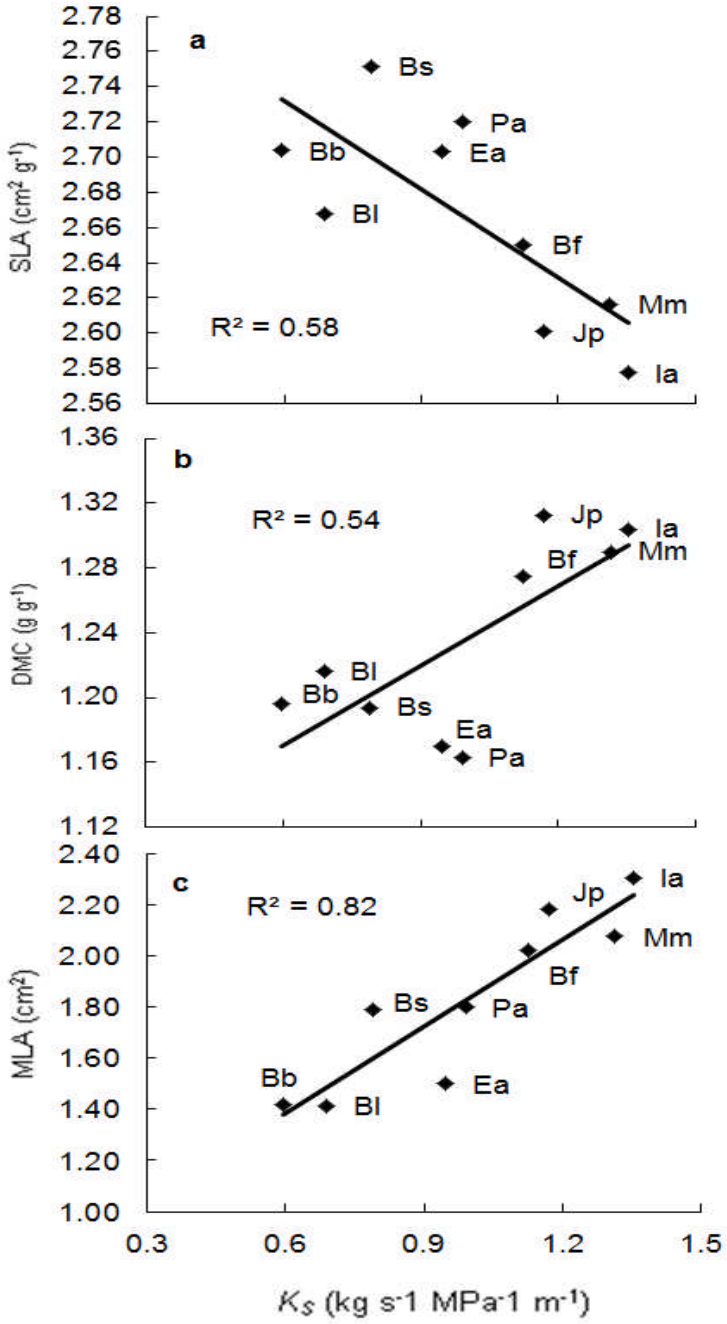


Figure 6.4: Relationship between stem area specific hydraulic conductivity (K_S) and leaf functional traits a) specific leaf area (*SLA*); b) dry matter content (*DMC*); c) mean leaf area (*MLA*). All data are log transformed (Note that *DMC* was arcsine transformed before log transformation). Regression line data points are tree species means ± SE (n = 25 trees per species). The fitted lines for graphs a, b and c, respectively, have the equations: $y = 2.83 - 0.17x$ ($F = 9.69$, $P = 0.017$); $y = 1.07 + 0.16\ x$ ($F = 8.37$, $P = 0.023$) and; $y = 0.71 + 1.13\ x$ ($F = 31.36$, $P = 0.001$). Chart abbreviations are: Bb = *Brachystegia boehmii*, Bl = *Brachystegia longifolia*, Bs = *Brachystegia spiciformis*, Ea = *Erythrophleum africanum*, Pa = *Pericopsis angolensis*, Bf = *Brachystegia floribunda*, Ia = *Isoberlinia angolensis*, Jp = *Julbernardia paniculata*, Mm = *Marquesia macroura*.

When all data points were pooled together (n = 225), Huber value was significantly positively correlated (r = 0.21, n = 225, P < 0.001) with *DMC* and negatively correlated with SLA (r = 0.38, P < 0.001). However, *MLA* was weakly correlated (r = 0.034, P = 0.54) with Huber value.

At species level, Huber value was insignificant (P > 0.05) related to leaf functional traits. A linear regression explained 43%, 19% and 2% of the variances in *SLA*, *DMC*, and *MLA* respectively (Fig 6.5).

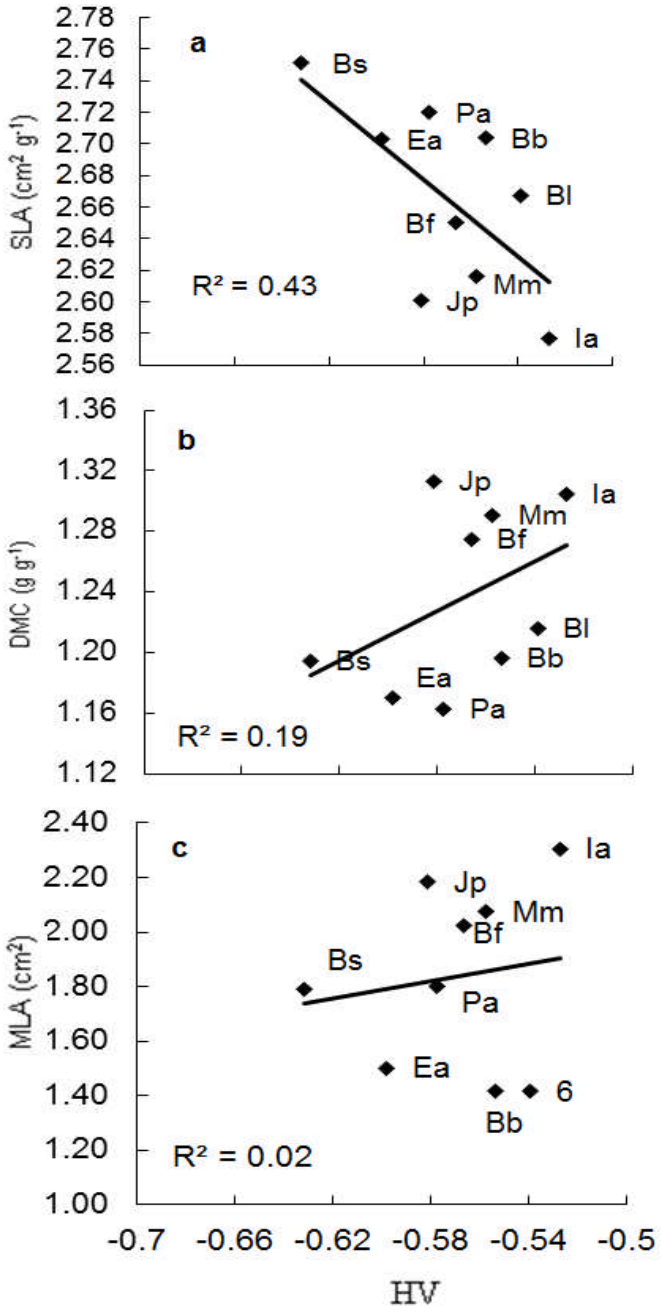


Figure 6.5: Relationship between sapwood area to leaf area ration (Huber value, HV) and leaf functional traits **a**) Specific leaf area, **b**) Dry matter content, **c**) Mean leaf area. All data is log transformed (Note that *DMC* and HV were arcsine transformed before log transformation). Regression line data points are tree species means (n = 25 trees per species). The fitted lines for graphs a, b and c, respectively, have the equations: $y = 2.05 – 1.11x$ ($F = 5.26$, $P = 0.056$); $y = 1.58 + 1.85\ x$ ($F = 1.65$, $P = 0.24$) and; $y = 2.83 + 1.85\ x$ ($F = 0.15$, $P = 0.71$). Chart abbreviations are as before.

When all data points were pooled together (n = 225), there was a positive correlation (r = 0.18, n = 225, P = 0.001) between xylem vulnerability to cavitation (Ψ_{50}) and specific leaf area. Vulnerability to cavitation was, however, uniquely negatively correlated to both dry matter content (r = 0.25, P < 0.001) and mean leaf area (r = 0.27, P < 0.001).

An inter-species trait level (n = 9) linear regression analysis revealed a significant relationship between Ψ_{50} and SLA as well as DMC. There was an insignificant relationship between Ψ_{50} and MLA. A linear regression explained 56%, 63% and 31% of the variability in *SLA*, *DMC*, and *MLA* respectively (Fig 6.6).

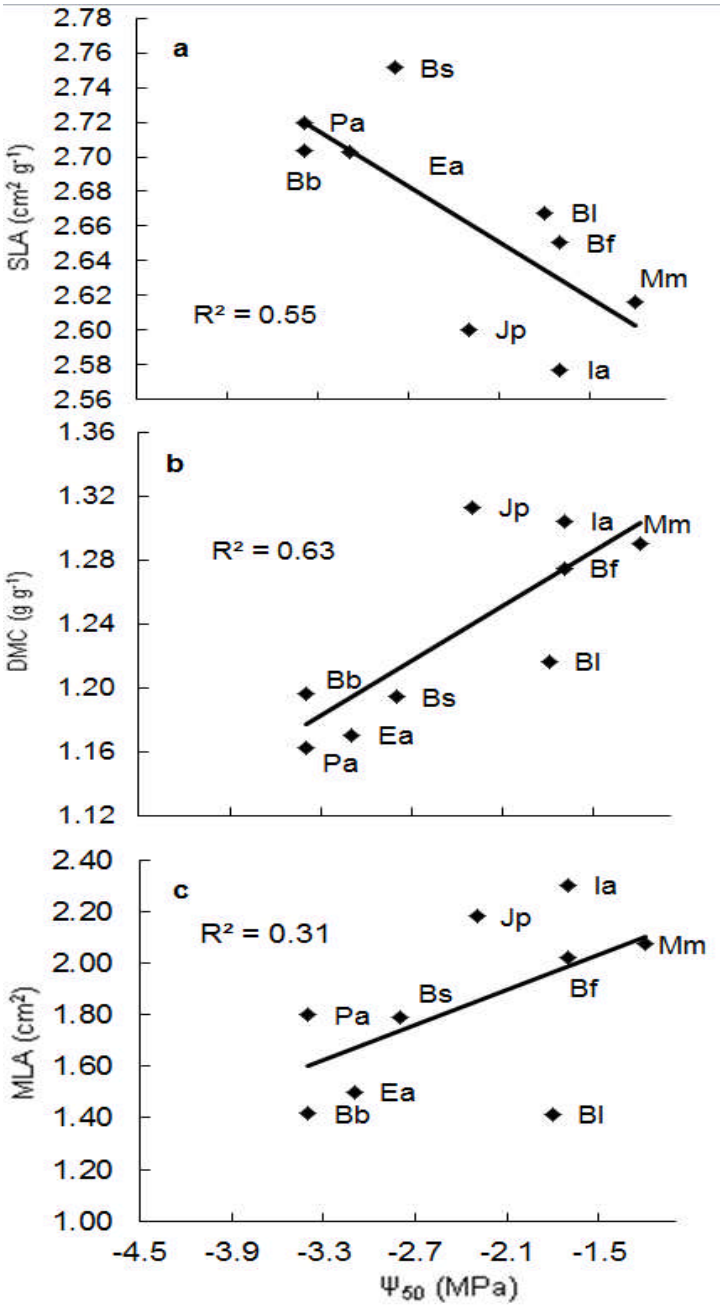


Figure 6.6: Species level, relationship between xylem vulnerability to cavitation and leaf functional traits **a**) specific leaf area (*SLA*), **b**) Dry matter content (*DMC*), **c**) mean leaf area (*MLA*). All data is log transformed. Regression line data points are tree species means ± SE (n = 25 trees per species). Regression models describing the relationships were: $y = 2.54 - 0.053x$ ($F = 8.72$, $P = 0.021$); $y = 1.37 + 0.057x$ ($F = 11.87$, $P = 0.011$) and; $y = 2.38 + 0.23x$ ($F = 3.18$, $P = 0.118$). Chart abbreviations are as before.

6.5 DISCUSSION

6.5.1 Variations in leaf functional traits and hydraulic architecture

There were clear differences in both hydraulic and leaf functional traits between mesic specialists and generalists despite sharing a relatively uniform environment. Low hydraulic efficiency coupled with high resistance to cavitation reflects the long-term adaptation to water stressed environments for generalists. Many studies have demonstrated that arid ecosystems favour plants with low specific leaf areas (Cornwell et al. 2007; Fonseca et al. 2000; Lamont et al. 2002). Furthermore, experimental evidence has demonstrated that plants from different environments, when grown under laboratory conditions, show little variation in relative ranking of their leaf functional traits when compared to their field rankings (Poorter and De Jong 1999; Wright and Westoby 1999).

Miombo woodland generalists display high specific leaf area and low dry matter contents. The plausible explanation to this is that the fully deciduous generalists tend to be conservative in leaf carbon investment because of their leaf phenology. Leaf construction costs are often expressed in terms of weight of carbohydrates per unit dry mass (Williams et al. 1989). Several pieces of evidence point in the direction of construction cost and leaf life span being negatively correlated with specific leaf area (Eamus et al. 1999; Kikuzawa 1995; Reich et al. 1992; Sobrado 1991; Villar and Merino 2001). On the basis of our findings, we can conclude that low specific leaf area coupled with high leaf dry matter content among mesic specialists reflects an adaptation towards investment in leaf longevity and water stress resistance.

6.5.2 Leaf functional trait and hydraulic adjustment in response to increasing aridity

Several pieces of literature have demonstrated that water-limited ecosystems tend to favour tree species with reduced leaf size (Fonseca et al. 2000), hydraulic efficiency (Engelbrecht et al. 2000) and increased leaf mass per leaf area (Reich et al. 1997; Wright et al. 2002). Our findings show diverse trait response patterns among the broad-ranging tree species. There are inconsistencies in the manner in which broad-ranging species respond to increasing ecosystem water stress. However, there are significant shifts in specific hydraulic conductivity and leaf specific conductivity (Fig 6.1; p 165). In contrast, resistance to cavitation and leaf functional traits remained unresponsive to changes in ecosystem water stress (Fig 6.2; p 166). In environments where water is limiting, a reduction in hydraulic efficiency coupled with high resistance to cavitation enables plants to exploit low moisture supply from soils (Engelbrecht et al. 2000). From the ecophysiological point of view, reductions in hydraulic efficiency towards dry ecosystems confer greater competitive ability among miombo woodlands generalist populations. However, inflexibilities in cavitation resistance in miombo generalists reinforce the hypothesis that specific hydraulic and leaf specific conductivities respond to environmental heterogeneity whereas cavitation resistance is genetically determined (Cornwell et al. 2007; van der Willigen et al. 2000; Tyree and Zimmermann, 2002). In general, generalists improve fitness in water-limited dry miombo sites by shifting to low hydraulic conductivities. Potentially, this adjustment in xylem long distance water transport capacity enables generalists to compensate for low soil water supply under dry miombo woodlands habitat.

One of the emerging controversies in leaf trait analyses is the use of community level averages to characterise an ecosystem, as opposed to using species level averages (Ackerly et al. 2002). This characterisation masks out the finer detail at the species level. It also makes it difficulty to infer whether the observed trait plasticity is as a result of species turnover or genuine individual trait shift. Results of this study cast further doubt on the validity of community level trait analyses. A considerable portion of the observed plasticity was mainly driven by species turnover rather than species level trait shifts (Fig 6.3; p 168). A mixed-model analysis of variance confirmed that, among broad ranging tree species, site and species differences were insignificant.

6.5.3 Relationship between hydraulic properties and leaf functional traits

Specific hydraulic conductivity and cavitation resistance varied proportionally with leaf functional traits associated with water stress management (Fig 6.4; p 170). In contrast, Huber value is uncorrelated with leaf functional traits (Fig 6.5; p 172). The lack of correlation between Huber value and leaf functional traits related to plant drought tolerance suggest that HV may have very little ecological significance for miombo specie. However, the positive and negative relationships between stem hydraulic properties and leaf functional traits reflect a balance between plant water transport capacity and plant water loss management. From a functional point of view, any physiological process that interferes with plant water status has the potential to limit overall plant growth (Boyer 1970). As expected, the earliest evidence of water stress in plants is a reduction in leaf size (Taiz, 1995). This is mainly because leaf expansion is a turgor driven process. Therefore, any reduction in water supply may negatively affect this process. Consistent with this line of reasoning, we believe that xylem long distance transport design, limits

the amount of carbon a given plant can invest in a leaf in order to enhance long-term plant water balance and fitness under water-limited habitats. This conclusion is strengthened by the finding, which shows that for a given increase in cavitation resistance, there is a corresponding reduction in both leaf dry matter content and leaf size (Fig 6.6; p 174). Overall our results add further insight into the eco-physiological compromise between stem hydraulic supply and leaf carbon investment in plants. Although we found a significant relationship between *SLA* and hydraulic properties, Taylor and Eamus (2008) found no significant correlation between hydraulic properties and *SLA*. Differences in sample size and general methodological approach may account for some the disparities in the results. In general, results suggest that stem hydraulic supply constrains leaf carbon investment among miombo woodland canopy tree species.

6.5.4 Conclusions

Leaf functional traits and hydraulic architecture differ significantly between miombo woodlands canopy tree species with contrasting habitat preferences. Tree species, which are obligate mesic, have significantly larger leaf sizes, lower specific leaf area, higher dry matter content, and an efficient xylem long distance water transport system but are extremely vulnerable to cavitation. In contrast, generalists have leaves which are lower in dry matter content, hydraulic efficiency, smaller leaves, but have higher specific leaf area. Generalists extend into dry habitats by significantly reducing specific hydraulic and leaf specific conductivities while displaying inflexibility in cavitation resistance and leaf functional traits. There is a strong correlation between stem hydraulic supply and leaf functional traits. Results from this study suggest that plants respond to water stress in an

integrated approach (morphological and physiological). Integrated response defines the range of habitats that any given species can competitively colonize in miombo ecosystem.

Acknowledgements

The lead author was funded by a scholarship from the Association of Commonwealth Universities and the Copperbelt University provided. We wish to thank the late Principal for Zambia Forestry College, Saxon Nyela Siame, who provided laboratory work space at the wet miombo site. The District Forestry Officer for Choma district Jones Mulomba is greatly appreciated for his logistical support during our stay on the dry site. Lab assistants in Zambia, Milimo Miyoba and Metson Kasowe are also acknowledged.

6.6 REFERENCES

Ackerly DD, knight CA, Weiss SB, Barton K, Starmer KP (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* **130**:449-457

Berry JA, Downton WJS (1982) Environmental Regulation of Photosynthesis. In: Govindjee (ed). *Photosynthesis. Vol. II: Development, Carbon metabolism, and plant productivity*. Academic Press, New York, pp. 263-343.

Boyer JS (1970) Leaf enlargement and metabolic rates in corn, soybean,and sunflower at various leaf 'water potentials. *Plant Physiology* **46**: 233-235.

Brodribb T, Hill RS (1999) The importance of xylem constraints in the distribution of conifer species. *New Phytologist* **143**:365-372.

Chidumayo EN (1987) Species structure in Zambian miombo woodland. *Journal of Applied Ecology* **3**:109-118.

Cochard H, Cruiziat P, Tyree MT (1992) Use of positive pressure to establish vulnerability curves. *Plant Physiology* **100**:205-209.

Cornwell WK, Bhaskar R, Slack L, Cordell S, Lunch CK (2007) Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs low precipitation. *Functional Ecology* **21**:1063-1071

Eamus D, Myers B, Duff G, Williams R (1999) A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. *Photosynthetica* **36**:575-586

Engelbrecht BMJ, Velez V, Tyree MT (2000) Hydraulic conductance of two co-occuring neotropical understorey shrubs with different habitat preferences. *Annals of Forest Science* **57**:201-208

Fonseca CR, Overton JM, Collins B, Westoby, M (2000) Shifts in trait-combination along rainfall and phosphorus gradients. *Journal of Applied Ecology* **88**:964-977

Garnier E, Shipley B, Roumet C, Laurent G (2001) A standardized protocol for the determination of specific leaf area and dry matter content. *Functional Ecology* **15**:688-695

Kikuzawa K (1995) The basis for variation in leaf longevity of plants. *Vegetatio* **121**:89-100.

Kolb KJ, Sperry JS, Lamont BB (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. *Journal of Experimental Botany* **47**:1805-1810.

Lamont BB, Groom PK, Cowling RM (2002) High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concetrations. *Functional Ecology* **16**:403-412.

Lopez O, Kursar TA, Cochard H, Tyree MT (2005) Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology* **25**: 1553-1562.

Meerts P, Garnier E (1996) Variation in relative growth rate and its components in the annual *Polygonum aviculare* in relation to habitat disturbance and seed size. *Oecologia* **108**:438-445.

Mencuccini M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell and Environment* **26**:163-182.

Niinemets U (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**:453-469.

Pammenter NW, Van der Willigen C (1998) A mathematical and statistical analysis of the curves illustrating vulnerability ot xylem to cavitation. *Tree Physiology* **18**: 589-593.

Parkhurst FD, Loucks OL (1972) Optimal leaf size in relation to environment. *Journal of Ecology* **60**:505-537.

Patino S, Tyree MT, Herre EA (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic Ficus species from Panama. *New Phytologist* **129**:125-134.

Pockman WT, Sperry JS (2000) Vulnerability to xylem cavitation and the distribution of sonoran desert vegetation. *American Journal of Botany* **87**:1287-1299.

Poorter H, De Jong R, (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of plants from 15 habitats differing in productivity. *New Phytologist* **143**:163-176.

Poorter H, Evans RJ (1998) Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* **116**:26-37

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA* **94**:13730-13734.

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characterics among diverse ecosystems. *Ecological Monographs* **62**:365-392.

Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**:717-723

Sobrado MA (1991) Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. *Functional Ecology* **5**:608-616.

Sefton AC, Montagu KD, Atwell BJ, Conroy JP (2002) Anatomical variation in juvenile eucalyptus leaves account for differences in specific leaf area and CO_2 assimilation rates. *Australian Journal of Botany* **50**:301-310.

Sithole A, Murewi FJC (2009) Climate variability and change over southern Africa: Impacts and challenges. *African Journal of Ecology 47*:17-20.

Smith P, Allen Q (2004) *Field Guide to The Trees and Shrubs of the Miombo Woodlands*. Royal Botanic Gardens Kew, London.

Sokal RR, Rohlf JF (1995) *Biometry.* 3rd edn. Freeman & Co., New York.

Sperry JS, Meinzer FC, McCulloh KA (2008) Safety and efficiency conflicts in hydraulic architecture: Scaling from tissues to trees. *Plant, Cell and Environment* **31**:632-645

Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment 11*:35-40.

Taiz, L. and Zeiger, E. 1998. *Plant Physiology*. Massachusetts: Sinauer Associates, Inc.

Taylor D, Eamus D (2008) Coordinating leaf functional traits with branch hydraulics conductivity: resource substitution and implications for carbon gain. *Tree Physiology* **28**:1169-1177.

Tyree MT, Zimmermann MH (2002) *Xylem Structure and the Ascent of Sap*. 2nd edn. Springer, Berlin.

Tyree TM, Sperry JS (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology* **88**: 574-580

Underwood AJ (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance.* Cambridge University Press, Cambridge.

Van der Willigen C, Sherwin HW, Pammenter NW (2000) Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. *New Phytologist* **145**:51-59.

Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist* **151**:213-226.

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant soil* **199**:213-227

Westoby M, Wright IJ (2003) The Leaf size - twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia* **135**:621-628.

White F (1983) *The vegetation of Africa : a Descriptive Memoir to Accompany the Unesco/AETFAT/UNSO Vegetation Map of Africa*. Unesco, Paris.

Williams K, Field CB, Mooney HA (1989) Relationships among leaf construction cost, leaf longevity, and light environment in rain forest plants of the genus *Piper*. *American Naturalist* **133**:198-211.

Wilson PJ Thompson K, Hodgson JG (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**:155-162

Wright IJ (2004) The worldwide leaf economics spectrum. *Nature* **428**:821-827

Wright IJ, Westoby M (1999) Differences in seedling growth behaviour among species: traits correlation across species and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87**:85-97.

Wright IJ, Westoby M, Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology* **90**:534-543.

Zar, J. H. (2010) *Biostatistical Analysis*. 5th Edn. Pearson Education International, London.

Zimmermann M. H. (1983) *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin.

CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS

7.1 FINAL CONCLUSIONS

7.1.1 Summary of the thesis objectives

This study was undertaken with a view to broaden our understanding on the role of plant-water relations in structuring miombo woodlands. The study pursued multiple but closely related goals which included the following:

- Quantifying and evaluating the hydraulic properties of miombo woodlands canopy tree species differing in habitat preference.
- Examining xylem cavitation vulnerability for miombo woodlands canopy tree species differing in drought tolerance capability and habitat preference.
- Investigating the extent to which seasonal changes in plant water relations influence seasonal changes in leaf phenology.
- Evaluating the relationship between hydraulic properties and leaf functional traits related to plant drought tolerance capability.

The study has yielded mixed but interesting results. In Chapter III, an evaluation of the hydraulic properties for nine miombo tree species differing in habitat preference, revealed significant variations in these properties. It has been demonstrated that under relatively similar environmental conditions broad and narrow habitat ranging miombo woodlands tree species display significant differences in hydraulic properties. Drought-avoiding (narrow ranging) tree species display remarkably efficient (in terms of conductance) hydraulic architectures in comparison with drought-tolerant (broad ranging) miombo

woodland tree species. Intra-species variations in hydraulic parameters for miombo woodland populations growing in the wet and dry miombo woodlands sites are significant. These results suggest hydraulic properties are very responsive to changes in ecosystem water availability. However, xylem anatomy does not show significant flexibility from wet to dry miombo woodlands. On the basis of these results alone, there is sufficient evidence to conclude that tree hydraulic architecture might be an essential trait that determines a species' habitat preference and overall distribution in miombo ecosystem (objective 1).

In Chapter IV an analysis of xylem vulnerability to water-stress-induced cavitation demonstrated broad-ranging species to have higher resistance to cavitation than narrow-ranging species. Resistance to cavitation measured as the water potential at which 50% in hydraulic conductivity is lost ranged from -1.1 to -2.3 MPa for narrow-ranging species and -1.7 to -3.4 MPa for broad ranging species. There is a strong trade-off between xylem efficiency and cavitation risk avoidance among miombo tree species. The results suggest that when water becomes more limiting, the hydraulic architecture of generalists is better adapted to exploit low soil moisture in comparison to mesic specialists. Thus, the adaptive significance of increased cavitation resistance as a drought tolerance mechanism might be of paramount importance in structuring the miombo woodlands. Overall the results suggest xylem vulnerability to cavitation might constrain species habitat preference in miombo ecosystem by confining the distribution of the more vulnerable but hydraulically efficient mesic specialists to wet miombo woodlands (objective 2). However, the observed intra-species inflexibilities in cavitation resistance and xylem anatomic structure between wet and dry miombo woodlands reinforce the idea

that cavitation vulnerability is genetically determined whereas hydraulic properties are environmentally driven. Overall, in terms of species distribution and vulnerability, I feel confident to conclude that vulnerability is the decisive factor determining when a plant will die under drought caused by climate change.

In Chapter V, an analysis of the role of stem water status in influencing seasonal leaf display in miombo woodland generated mixed patterns. While generalists displayed strong shifts in stem water status, mesic specialists showed exceptional stability in stem water status throughout the year. Results in Chapter VI suggest mesic specialists' possess a xylem hydraulic system that relies on high hydraulic efficiency to buffer the potential impacts of xylem dysfunction. Generalists possess inefficient hydraulic systems that fail to match up with atmospheric demand, and consequently shed leaves to prevent permanent xylem damage. While leaf emergence is constrained by both time and stem water status, leaf shedding is only constrained by stem water status and less constrained by time. This suggests that leaf shedding responds to water stress, whereas leaf emergence may be responding to other environmental cues. Generally, results of this study support the functional dependence theory of leaf phenology on tree water relations (objective 3).

In Chapter VI, when the relationship between stem hydraulic supply and leaf functional traits associated with plant drought tolerance is examined (objective 4), there is a remarkably consistent pattern in which mesic specialists display significantly higher hydraulic supply. They also possess leaves with low specific leaf area, large leaf areas and high leaf dry matter content in comparison to co-occurring generalists. These differences are more pronounced at the inter-species level than within species, suggesting

that these combinations of traits might have some adaptive significance on the ecological success of these species under a given suite of climatic factors.

The general conclusions from this study are that hydraulic architecture constrains tree species distribution by limiting the more vulnerable species to mesic habitats, while the more resistant miombo species attain wide distribution. Leaf shedding among miombo tree species responds to water stress whereas leaf emergence responds both to stem water status and other environmental variables. Hydraulic properties and leaf functional traits combine in diverse ways to enhance species drought tolerance capability in miombo woodlands. Results of this study have provided some valuable insights into the importance of plant-water relations in structuring miombo woodlands.

7.1.2 Implications of results in relation to future management and conservation of miombo woodlands in relation to adaptation plans for climate change

Although many factors will interact to determine tree species extinction rates under climate change, results from this study suggest that plant water relations may play a crucial role in influencing species population decline. Empirical data from this study show that miombo woodland tree species respond to water stress according to their hydraulic architecture. This suggests that miombo tree species are likely to show a strong individualistic response to climate change. Therefore, the implications of these findings in relation to future management, conservation and adaptation plans for miombo woodlands under climate change are that:

- Forest conservation goals for proactive climate change planning must include varying management intensities. These must take into account the obvious differences in drought stress response between generalists and mesic specialists.

For example, drought-intolerant mesic specialists may require a dynamic forest management prescription that promotes sound soil water conservation. In this regard, the resilience of mesic specialists to future drying can effectively be enhanced by promoting forest management practices that reduce forest fragmentation. Promoting forest utilisation practices that minimize forest cover degradation in miombo woodland habitats dominated by mesic specialists would provide a reasonable protection for species reproduction under the future dry miombo.

- Restoration of degraded miombo forests under climate change adaptation plans will depend on selecting tree species that are resilient to water stress. Success of the restoration programme may be assured by planting tree species whose hydraulic architecture matches the prevailing biophysical environment. For example, in regions which are projected to experience severe drought under climate change, replanting of generalist tree species may assure ecosystem resilience to future unfavourable plant growth environment.

7.1.3 Scientific contribution of thesis

This study has attempted to understand stem hydraulic architecture, xylem vulnerability to cavitation, hydraulic limitations on leaf phenology and the interaction between branch hydraulics and leaf functional traits related to drought tolerance for nine principal miombo woodlands tree species. The scientific contributions of this research are:

- Hydraulic architecture of the principal miombo tree species has been quantified for the first time and evaluated in relation to species habitat preference, thus

providing a physiological basis on how the miombo ecosystem is structured by precipitation.

- Xylem cavitation vulnerability has also been quantified and analyzed in relation to species drought tolerance capability, and this sets a sound scientific basis for explaining how water stress imposes considerable hydraulic restrictions on the distribution of principal miombo species.
- Functional dependence of seasonal leaf display on stem water status has generated some useful basis for understanding how future climate trends may affect ecosystem productivity in the miombo biome.

Overall this study has contributed to the ever-growing literature on plant-water relations in seasonally dry tropical forests.

7.2 RECOMMENDATIONS

Although this research has provided some of the most fascinating insights into the physiology of the miombo tree species, as always the case with most research studies, it has also opened up more questions that need answers. Specifically, the following themes need further research in order to broaden and deepen our understanding of the ecophysiology of miombo woodlands:

- Although the original intentions of this work were to study both root and stem hydraulic architecture, available time and resources could not permit such a mammoth study to be undertaken. It is recommended that future studies should focus on the root hydraulic properties for miombo woodlands tree species.

- Arriving at major conclusions on the relationship between plant-water relations and habitat preference for principal miombo woodlands tree species based on two sites was not easy. I believe that adding a couple of ground plots into the wet-dry miombo woodlands transitional zone would give more insights into the physiology of miombo trees as it relates to habitat preference. Whatever, the case this study has generated a good foundation on which other studies can build.
- This study only focused on one life-form (trees) and left out the shrub layer. In order to gain full insight into how water limits this ecosystem at all levels, it would be interesting to compare the hydraulic architecture of both trees and shrubs
- In the given time and resources available for this DPhil study, it was not possible to look at all aspects that contribute to plant drought tolerance ability. For, example the role of mycorrhizae in increasing plant root surface area and mitigating problems of water stress is well known. The miombo tree species examined in this study grow in association of different mycorrhizae species. Therefore, future studies should focus on unravelling the relationship between mycorrhizal and tree hydraulic architecture for miombo woodlands trees. This would add much needed insights into the various water stress management strategies that exist among miombo tree species..
- Although this study has established some connections between seasonal dynamics in plant water relations and leaf phenology, the duration involved was quite short to allow for accurate prediction. Therefore, long-term studies on the dynamics of

leaf phenology and seasonal plant water relations would add more insights into how temporal changes in stem water status control leaf phenology.

APPENDICES

3.1 Hydraulic properties and xylem anatomic dimensions

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (μm)	D_H (μm)	D_{95} (μm)
Wet	*Brachystegia boehmii*	1	0.000307	5.381	0.000035	0.00019	0.256	21.027	25.749	28.322
	Brachystegia boehmii	2	0.000243	7.28	0.000039	0.000297	0.243	22.71	29.083	31.022
	Brachystegia boehmii	3	0.000198	7.03	0.000028	0.000203	0.245	19.994	29.728	38.807
	Brachystegia boehmii	4	0.000228	7.654	0.000013	0.000091	0.24733	27.534	33.434	35.791
	Brachystegia boehmii	5	0.000214	5.106	0.000024	0.000128	0.25033	21.562	29.586	33.554
	Brachystegia boehmii	6	0.000182	4.421	0.000039	0.000175	0.244	24.744	36.186	46.237
	Brachystegia boehmii	7	0.000203	3.94	0.000017	0.00006	0.249	27.915	37.242	42.772
	Brachystegia boehmii	8	0.000231	5.536	0.00002	0.000127	0.24567	25.358	31.316	34.528
	Brachystegia boehmii	9	0.000217	5.77	0.000052	0.000302	0.24933	25.283	33.936	38.058
	Brachystegia boehmii	10	0.000199	4.567	0.000018	0.000081	0.24867	28.856	35.418	39.67
	Brachystegia boehmii	11	0.000233	4.832	0.000037	0.000183	0.25	21.231	23.59	24.138
	Brachystegia boehmii	12	0.000203	4.455	0.000024	0.000106	0.24433	26.354	30.732	33.27
	Brachystegia boehmii	13	0.000206	6.2	0.000023	0.000142	0.244	27.77	38.648	43.058
	Brachystegia boehmii	14	0.000219	4.91	0.00003	0.000128	0.249	27.073	39.715	45.477
	Brachystegia boehmii	15	0.000234	5.834	0.000041	0.000228	0.24433	26.228	34.387	53.063
	Brachystegia boehmii	16	0.000174	3.64	0.000064	0.000234	0.25	23.115	31.682	37.02
	Brachystegia boehmii	17	0.000207	6.77	0.000028	0.000145	0.245	23.331	26.366	28.089
	Brachystegia boehmii	18	0.000186	4.836	0.000015	0.000076	0.24167	28.012	40.545	46.144
	Brachystegia boehmii	19	0.000205	6.93	0.000022	0.000159	0.243	31.678	38.522	43.694
	Brachystegia boehmii	20	0.000201	6.78	0.00002	0.000142	0.24333	31.136	36.406	40.272
	Brachystegia boehmii	21	0.000184	6.957	0.000032	0.000228	0.24267	25.045	33.171	38.298
	Brachystegia boehmii	22	0.000185	6.685	0.000032	0.000209	0.248	24.289	32.133	37.801
	Brachystegia boehmii	23	0.000183	5.22	0.000025	0.000116	0.25467	22.604	27.055	29.227
	Brachystegia boehmii	24	0.000159	5.96	0.000026	0.000167	0.24933	26.536	29.981	31.575
	Brachystegia boehmii	25	0.000162	6.87	0.000029	0.000229	0.24267	26.443	29.939	31.672
	Brachystegia longifolia	1	0.000221	2.888	0.00003	0.000092	0.30333	23.159	30.503	33.477
	Brachystegia longifolia	2	0.000198	2.844	0.000028	0.00008	0.31	27.332	33.874	28.94
	Brachystegia longifolia	3	0.000255	7.46	0.000028	0.000191	0.312	22.487	26.801	35.542

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Brachystegia longifolia	4	0.000244	5.671	0.000019	0.000101	0.30567	29.528	33.83	37.832
	Brachystegia longifolia	5	0.00027	10.65	0.000045	0.000484	0.305	21.808	25.229	29.041
	Brachystegia longifolia	6	0.000223	5.138	0.000012	0.000065	0.315	22.973	26.184	36.552
	Brachystegia longifolia	7	0.000252	5.081	0.000026	0.000128	0.302	29.415	37.852	27.396
	Brachystegia longifolia	8	0.000221	4.515	0.000017	0.000079	0.3	25.366	28.521	27.316
	Brachystegia longifolia	9	0.000247	6.693	0.000032	0.000216	0.31133	22.734	28.972	43.348
	Brachystegia longifolia	10	0.000204	6.409	0.00004	0.000265	0.31433	23.402	27.982	30.281
	Brachystegia longifolia	11	0.000224	6.358	0.000035	0.000212	0.31433	21.512	24.162	33.989
	Brachystegia longifolia	12	0.000196	5.633	0.000022	0.000125	0.307	34.743	41.56	31.21
	Brachystegia longifolia	13	0.000228	7.17	0.000016	0.000109	0.31267	25.934	31.285	25.24
	Brachystegia longifolia	14	0.000219	4.932	0.000022	0.000107	0.307	23.81	29.715	45.684
	Brachystegia longifolia	15	0.000181	4.971	0.000028	0.000141	0.316	25.781	30.847	33.045
	Brachystegia longifolia	16	0.000183	3.53	0.000038	0.000136	0.30533	23.757	32.311	32.331
	Brachystegia longifolia	17	0.000238	4.218	0.00001	0.000042	0.30233	26.866	30.892	33.27
	Brachystegia longifolia	18	0.000218	4.55	0.000018	0.000069	0.309	19.972	31.341	38.816
	Brachystegia longifolia	19	0.000231	3.465	0.000047	0.000153	0.31733	23.304	28.13	29.65
	Brachystegia longifolia	20	0.00021	5.415	0.00002	0.000108	0.30667	22.858	29.396	45.263
	Brachystegia longifolia	21	0.000215	3.337	0.000029	0.000097	0.314	21.788	37.612	29.471
	Brachystegia longifolia	22	0.000176	3.407	0.000023	0.000077	0.31367	28.921	39.842	32.914
	Brachystegia longifolia	23	0.00019	3.204	0.000061	0.000207	0.309	26.245	28.713	47.95
	Brachystegia longifolia	24	0.000243	4.151	0.000033	0.000134	0.29767	20.365	22.634	49.97
	Brachystegia longifolia	25	0.0002	7.648	0.000015	0.00012	0.31267	30.094	35.827	44.01
	Brachystegia spiciformis	1	0.000235	3.975	0.000015	0.000059	0.26233	27.92	31.621	34.38
	Brachystegia spiciformis	2	0.000254	17.17	0.000023	0.000397	0.25733	21.88	30.423	25.68
	Brachystegia spiciformis	3	0.000262	11.4	0.000024	0.000301	0.25933	25.327	29.931	29.82
	Brachystegia spiciformis	4	0.000223	7.364	0.000021	0.000153	0.258	26.578	30.748	34.56
	Brachystegia spiciformis	5	0.000194	5.308	0.000036	0.000205	0.25533	23.121	29.92	32.84
	Brachystegia spiciformis	6	0.000197	6.72	0.000014	0.000087	0.25733	24.28	29.06	31.36
	Brachystegia spiciformis	7	0.000192	6.824	0.000026	0.000177	0.26367	26.026	29.522	32.585
	Brachystegia spiciformis	8	0.000192	8.16	0.000011	0.000082	0.255	26.3	29.511	32.726
	Brachystegia spiciformis	9	0.000208	7.91	0.000023	0.000192	0.26333	32.386	36.947	31.531

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Brachystegia spiciformis	10	0.000229	7.45	0.000014	0.000105	0.25767	24.467	30.743	31.124
	Brachystegia spiciformis	11	0.00027	6.465	0.000019	0.000129	0.26333	21.775	24.399	36.76
	Brachystegia spiciformis	12	0.000213	6.1292	0.000033	0.000201	0.25767	23.003	26.414	35.75
	Brachystegia spiciformis	13	0.000221	6.1903	0.000038	0.000239	0.26167	23.65	26.613	28.57
	Brachystegia spiciformis	14	0.00021	6.85	0.000015	0.000113	0.256	20.382	26.467	26.773
	Brachystegia spiciformis	15	0.000175	6.9	0.000029	0.000201	0.26633	26.936	31.855	27.861
	Brachystegia spiciformis	16	0.000209	6.26	0.000037	0.00024	0.26467	33.078	40.616	24.14
	Brachystegia spiciformis	17	0.000208	6.94	0.000015	0.00011	0.27133	24.369	34.865	30.89
	Brachystegia spiciformis	18	0.000273	6.515	0.000013	0.000084	0.262	24.526	30.804	42.26
	Brachystegia spiciformis	19	0.000237	8.454	0.000008	0.000066	0.263	27.93	33.381	40.97
	Brachystegia spiciformis	20	0.000223	7.364	0.00002	0.000153	0.24633	32.644	36.933	35.35
	Brachystegia spiciformis	21	0.000205	5.612	0.00003	0.000171	0.25933	25.475	32.635	35.096
	Brachystegia spiciformis	22	0.000187	6.43	0.00004	0.000225	0.26167	26.827	36.548	34.849
	Brachystegia spiciformis	23	0.000225	8.06	0.000021	0.00017	0.25567	31.274	36.641	34.902
	Brachystegia spiciformis	24	0.000201	8.43	0.000028	0.000252	0.26133	27.356	31.317	39.78
	Brachystegia spiciformis	25	0.000209	7.96	0.000022	0.000175	0.253	24.694	28.435	40.444
	Erythrophleum africanum	1	0.000427	7.5	0.000027	0.000191	0.25267	32.644	36.933	39.366
	Erythrophleum africanum	2	0.000377	9.38	0.000037	0.000296	0.25	24.694	28.435	33.33
	Erythrophleum africanum	3	0.000381	9.49	0.000024	0.000224	0.25067	26.077	30.076	31.618
	Erythrophleum africanum	4	0.000384	12.74	0.000013	0.000163	0.25567	24.489	32.907	35.71
	Erythrophleum africanum	5	0.000447	8.84	0.000021	0.000183	0.25267	30.658	34.967	37.473
	Erythrophleum africanum	6	0.000371	9.51	0.000014	0.000138	0.25133	23.427	26.597	31.12
	Erythrophleum africanum	7	0.00043	8.386	0.000012	0.00011	0.247	27.676	30.759	31.39
	Erythrophleum africanum	8	0.000454	10.71	0.000032	0.000306	0.25467	27.245	31.102	33.208
	Erythrophleum africanum	9	0.000508	11.13	0.000029	0.000332	0.25133	29.363	34.972	36.68
	Erythrophleum africanum	10	0.000411	12.8	0.000016	0.000219	0.257	23.096	26.945	31.75
	Erythrophleum africanum	11	0.00042	12.85	0.000024	0.000249	0.25167	27.703	30.92	31.3
	Erythrophleum africanum	12	0.000396	13.89	0.000015	0.000202	0.25367	30.89	36.126	36.67
	Erythrophleum africanum	13	0.000398	11.45	0.000029	0.000341	0.25033	24.788	28.233	32.96
	Erythrophleum africanum	14	0.000366	9.047	0.00002	0.000183	0.25033	21.808	26.51	29.179
	Erythrophleum africanum	15	0.000356	9.491	0.000026	0.000247	0.24633	2.529	34.017	33.67

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Erythrophleum africanum	16	0.000376	8.801	0.000017	0.000144	0.25167	26.834	31.657	34.774
	Erythrophleum africanum	17	0.000413	7.17	0.000013	0.000102	0.25267	23.891	29.282	32.07
	Erythrophleum africanum	18	0.00042	11.99	0.000016	0.000184	0.24767	29.354	37.556	37.74
	Erythrophleum africanum	19	0.000455	8.942	0.000015	0.000131	0.24333	26.231	31.618	35.62
	Erythrophleum africanum	20	0.00031	5.992	0.000015	0.000088	0.25067	23.292	26.994	29.55
	Erythrophleum africanum	21	0.000433	7.49	0.000021	0.000148	0.25167	24.524	29.388	29.63
	Erythrophleum africanum	22	0.000371	11.42	0.000014	0.000178	0.255	20.893	35.008	39.35
	Erythrophleum africanum	23	0.000426	7.95	0.000012	0.000091	0.25733	23.555	27.27	33.88
	Erythrophleum africanum	24	0.000374	10.08	0.000029	0.00032	0.249	27.086	32.028	32.51
	Erythrophleum africanum	25	0.000421	12.08	0.000017	0.000185	0.254	37.859	44.414	42.3
	Pericopsis angolensis	1	0.000314	7.735	0.000036	0.000283	0.2167	25.668	31.278	39.35
	Pericopsis angolensis	2	0.000347	10.63	0.000027	0.000277	0.21633	21.002	24.261	34.646
	Pericopsis angolensis	3	0.00032	11.71	0.000026	0.000344	0.22467	25.232	29.526	28.05
	Pericopsis angolensis	4	0.000336	10.708	0.000032	0.000342	0.22867	34.047	41.055	30.94
	Pericopsis angolensis	5	0.000406	10.79	0.000023	0.000259	0.22	24.129	34.626	41.73
	Pericopsis angolensis	6	0.000326	6.347	0.000021	0.000133	0.231	21.913	26.783	44.498
	Pericopsis angolensis	7	0.000371	7.525	0.000012	0.00009	0.21333	23.142	27.259	33.22
	Pericopsis angolensis	8	0.000359	7.191	0.000012	0.000083	0.2263	20.048	22.401	28.449
	Pericopsis angolensis	9	0.000348	11.55	0.000021	0.000239	0.22167	25.233	29.948	24.83
	Pericopsis angolensis	10	0.000312	8.93	0.00002	0.000195	0.21767	23.619	28.956	29.8
	Pericopsis angolensis	11	0.000337	12.77	0.000018	0.000205	0.2113	21.837	25.857	32.318
	Pericopsis angolensis	12	0.000377	10.03	0.000024	0.000247	0.218	26.232	35.807	28.38
	Pericopsis angolensis	13	0.000384	12.79	0.000016	0.000194	0.21533	23.889	33.421	36.93
	Pericopsis angolensis	14	0.000353	8.87	0.000016	0.000141	0.2167	22.729	26.145	41.497
	Pericopsis angolensis	15	0.000329	7.759	0.000023	0.000187	0.21867	20.343	28.413	32.12
	Pericopsis angolensis	16	0.000377	8.86	0.000068	0.000571	0.217	25.263	32.218	29.94
	Pericopsis angolensis	17	0.000359	9.23	0.00002	0.000193	0.22167	23.633	28.134	35.35
	Pericopsis angolensis	18	0.000305	9.858	0.000008	0.000077	0.216	25.788	35.15	32.68
	Pericopsis angolensis	19	0.000308	6.994	0.000023	0.000159	0.22067	24.668	28.141	37.8
	Pericopsis angolensis	20	0.000326	7.16	0.000034	0.00021	0.2253	21.757	28.409	33.12
	Pericopsis angolensis	21	0.000353	13.91	0.000044	0.00063	0.221	22.368	25.472	31.16

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Pericopsis angolensis	22	0.00033	6.665	0.000012	0.000079	0.22533	21.048	24.214	28.89
	Pericopsis angolensis	23	0.000373	9.106	0.000011	0.000107	0.22467	24.929	32.103	25.956
	Pericopsis angolensis	24	0.000366	8.76	0.000026	0.00023	0.22267	18.11	20.394	41.7
	Pericopsis angolensis	25	0.000384	9.92	0.00002	0.000191	0.21733	22.04	30.986	45.19
	Brachystegia floribunda	1	0.000573	14.99	0.00003	0.000397	0.303	29.098	40.576	38.73
	Brachystegia floribunda	2	0.000607	10.15	0.000035	0.000411	0.29633	24.22	34.875	40.79
	Brachystegia floribunda	3	0.000545	11.17	0.000013	0.000141	0.30067	24.929	32.103	48.95
	Brachystegia floribunda	4	0.000586	10.28	0.000022	0.000231	0.299	31.104	38.653	31.3
	Brachystegia floribunda	5	0.000472	11.52	0.000025	0.000315	0.29833	29.328	43.381	32.25
	Brachystegia floribunda	6	0.000458	12.082	0.000016	0.000195	0.293	18.11	20.394	34.73
	Brachystegia floribunda	7	0.000417	9.824	0.000019	0.000188	0.289	31.392	35.905	37.1
	Brachystegia floribunda	8	0.000517	13.657	0.000013	0.000175	0.298	22.974	29.513	38.164
	Brachystegia floribunda	9	0.000493	12.31	0.000025	0.000308	0.304	25.298	33.942	34.25
	Brachystegia floribunda	10	0.000504	9.34	0.000014	0.00014	0.28833	22.04	30.986	35.3
	Brachystegia floribunda	11	0.00049	9.62	0.00003	0.000285	0.29833	22.943	28.672	30.66
	Brachystegia floribunda	12	0.000441	17.69	0.000017	0.000298	0.3	22.479	32.184	38.49
	Brachystegia floribunda	13	0.000475	11.149	0.000027	0.000309	0.28667	24.371	26.525	43.464
	Brachystegia floribunda	14	0.000534	14.69	0.000018	0.000251	0.291	35.815	41.114	44.9
	Brachystegia floribunda	15	0.000435	23.36	0.00003	0.000738	0.28367	25.648	35.708	50.33
	Brachystegia floribunda	16	0.000447	10.898	0.000035	0.000382	0.2697	22.724	34.885	47.7
	Brachystegia floribunda	17	0.000458	13.73	0.000028	0.000382	0.3187	29.549	41.947	43.22
	Brachystegia floribunda	18	0.000499	15.29	0.000029	0.000421	0.283	25.034	37.418	26.57
	Brachystegia floribunda	19	0.000511	17.38	0.000015	0.000292	0.3197	27.87	33.442	34.95
	Brachystegia floribunda	20	0.000504	19.65	0.000039	0.000816	0.3	21.653	31.522	29.53
	Brachystegia floribunda	21	0.000592	18.95	0.000023	0.000439	0.29667	24.604	28.785	35.61
	Brachystegia floribunda	22	0.000487	10.845	0.000025	0.00027	0.29667	30.702	38.272	36.92
	Brachystegia floribunda	23	0.000447	11.188	0.000017	0.000196	0.28567	21.952	33.045	39.46
	Brachystegia floribunda	24	0.000472	15.53	0.000025	0.000393	0.28933	25.466	31.398	35.72
	Brachystegia floribunda	25	0.000466	18.02	0.000019	0.000338	0.28867	27.258	35.823	37.61
	Isoberlinia angolensis	1	0.00069	31.37	0.00003	0.00089	0.25567	26.121	31.023	39.252
	Isoberlinia angolensis	2	0.000784	22.98	0.000029	0.000696	0.25467	30.777	36.085	45.49

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Isoberlinia angolensis	3	0.00061	15.66	0.000022	0.000347	0.25033	28.5	36.11	37.82
	Isoberlinia angolensis	4	0.000641	13.86	0.000033	0.000442	0.25167	32.242	37.152	34.06
	Isoberlinia angolensis	5	0.00061	13.4	0.000013	0.00018	0.253	25.706	30.062	32.2
	Isoberlinia angolensis	6	0.00066	16.45	0.000031	0.000528	0.25633	29.548	33.407	34.96
	Isoberlinia angolensis	7	0.000597	12.75	0.000029	0.000362	0.254	25.906	29.218	38.96
	Isoberlinia angolensis	8	0.000672	46.1	0.000026	0.001123	0.25367	24.373	31.662	42.26
	Isoberlinia angolensis	9	0.000787	32.18	0.000044	0.001285	0.25533	30.447	36.891	38.59
	Isoberlinia angolensis	10	0.000645	13.96	0.000018	0.000264	0.25167	25.423	36.593	34.515
	Isoberlinia angolensis	11	0.000777	31.23	0.000016	0.000493	0.25133	27.149	32.643	34.008
	Isoberlinia angolensis	12	0.00062	11.41	0.000026	0.000286	0.256	27.735	31.334	35.717
	Isoberlinia angolensis	13	0.000585	14.02	0.000019	0.000269	0.25633	28.097	32.001	29.11
	Isoberlinia angolensis	14	0.000665	20.3	0.000051	0.001098	0.251	29.024	34.186	25.882
	Isoberlinia angolensis	15	0.000682	28.28	0.00004	0.001008	0.255	20.571	25.095	38.53
	Isoberlinia angolensis	16	0.000623	32.26	0.000031	0.000988	0.25233	22.331	25.951	44.362
	Isoberlinia angolensis	17	0.000621	26.5	0.000045	0.001174	0.24933	36.474	42.381	43.484
	Isoberlinia angolensis	18	0.000597	37.24	0.000032	0.001184	0.25667	28.277	38.514	38.41
	Isoberlinia angolensis	19	0.000721	33.6	0.000018	0.000643	0.26233	29.845	38.79	39.07
	Isoberlinia angolensis	20	0.000625	25.45	0.00003	0.000771	0.25867	28.262	33.43	33.23
	Isoberlinia angolensis	21	0.000608	25.076	0.000024	0.000595	0.24767	32.009	37.888	34.84
	Isoberlinia angolensis	22	0.00059	17.126	0.000028	0.000485	0.25567	24.353	29.27	36.288
	Isoberlinia angolensis	23	0.000573	23.83	0.00002	0.000465	0.252	27.571	33.307	24.31
	Isoberlinia angolensis	24	0.000578	29.29	0.000027	0.000776	0.25133	29.651	33.591	30.93
	Isoberlinia angolensis	25	0.000578	30.45	0.000026	0.000794	0.25133	16.545	18.095	38.95
	Julbernardia paniculata	1	0.000579	11.82	0.000015	0.000131	0.343	34.86	38.296	27.68
	Julbernardia paniculata	2	0.000615	14.91	0.00002	0.000279	0.34033	11.105	21.705	26.62
	Julbernardia paniculata	3	0.000619	10.262	0.000021	0.000212	0.339	24.981	28.061	29.063
	Julbernardia paniculata	4	0.000549	15.25	0.000023	0.000359	0.34567	25.892	28.092	26.16
	Julbernardia paniculata	5	0.000473	16.79	0.000027	0.000466	0.34067	21.683	23.72	30
	Julbernardia paniculata	6	0.0006	17.82	0.000024	0.000512	0.341	26.384	30.414	33.986
	Julbernardia paniculata	7	0.000539	13.595	0.000026	0.000346	0.342	30.155	33.343	29.93
	Julbernardia paniculata	8	0.000553	13.15	0.00002	0.00026	0.33733	23.268	26.064	33.56

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Julbernardia paniculata	9	0.000526	16.12	0.000015	0.000267	0.33667	32.936	35.243	31.12
	Julbernardia paniculata	10	0.000587	14.64	0.00002	0.000296	0.33833	25.116	27.803	27.947
	Julbernardia paniculata	11	0.000526	10.29	0.000021	0.00022	0.34233	24.272	26.506	23.27
	Julbernardia paniculata	12	0.000606	11.34	0.000021	0.000236	0.339	18.755	20.378	25
	Julbernardia paniculata	13	0.000555	23.7	0.000025	0.000611	0.3297	24.775	26.432	32.63
	Julbernardia paniculata	14	0.000555	22.23	0.000019	0.000437	0.34933	30.503	33.849	32.95
	Julbernardia paniculata	15	0.000521	15.45	0.000018	0.000315	0.3467	28.011	30.202	31.317
	Julbernardia paniculata	16	0.000605	27.9	0.000022	0.000528	0.35067	24.833	28.936	27.62
	Julbernardia paniculata	17	0.000542	25.72	0.000023	0.000529	0.33767	22.409	24.964	24.04
	Julbernardia paniculata	18	0.000536	12.784	0.000021	0.00027	0.34967	20.27	22.304	26.65
	Julbernardia paniculata	19	0.000536	14.09	0.000016	0.000225	0.353	23.459	26.666	25.85
	Julbernardia paniculata	20	0.000597	15.55	0.000021	0.000339	0.29567	21.947	23.631	32.41
	Julbernardia paniculata	21	0.000544	18.57	0.000026	0.000459	0.341	29.193	34.223	33.65
	Julbernardia paniculata	22	0.000597	14.644	0.000015	0.000225	0.34	27.239	31.053	29.45
	Julbernardia paniculata	23	0.000467	9.456	0.000022	0.000208	0.33833	24.812	27.399	28.129
	Julbernardia paniculata	24	0.000524	12.15	0.000021	0.000266	0.33967	23.954	26.844	27.935
	Julbernardia paniculata	25	0.000562	11.16	0.000031	0.000337	0.34	24.759	26.963	35.78
	Marquesia macroura	1	0.000933	20.06	0.000028	0.000555	0.5167	25.407	29.251	31.37
	Marquesia macroura	2	0.000879	24.57	0.000022	0.000449	0.5667	24.261	26.828	29.66
	Marquesia macroura	3	0.000907	21.24	0.000038	0.000829	0.49333	22.814	24.827	29.144
	Marquesia macroura	4	0.000977	28.95	0.000053	0.001312	0.5033	18.651	20.365	26.703
	Marquesia macroura	5	0.00076	14.29	0.000028	0.000434	0.5533	17.464	19.607	22.53
	Marquesia macroura	6	0.000819	18.5	0.000021	0.000397	0.54833	18.239	20.121	20.594
	Marquesia macroura	7	0.000891	24.65	0.000019	0.00048	0.49	20.155	22.656	20.405
	Marquesia macroura	8	0.000849	18.51	0.000035	0.000709	0.51	22.134	24.697	22.21
	Marquesia macroura	9	0.000905	18.18	0.000027	0.000487	0.49833	16.921	18.327	25.05
	Marquesia macroura	10	0.001071	17.924	0.000017	0.000303	0.55	19.74	23.993	21.17
	Marquesia macroura	11	0.000954	17.915	0.000024	0.000429	0.5333	23.564	26.139	23.07
	Marquesia macroura	12	0.000848	18.41	0.000015	0.000291	0.51	22.058	24.965	26.675
	Marquesia macroura	13	0.00085	11.51	0.000018	0.000183	0.495	19.08	21.048	26.339
	Marquesia macroura	14	0.000863	27.71	0.00002	0.000549	0.52	20.663	23.9	22.79

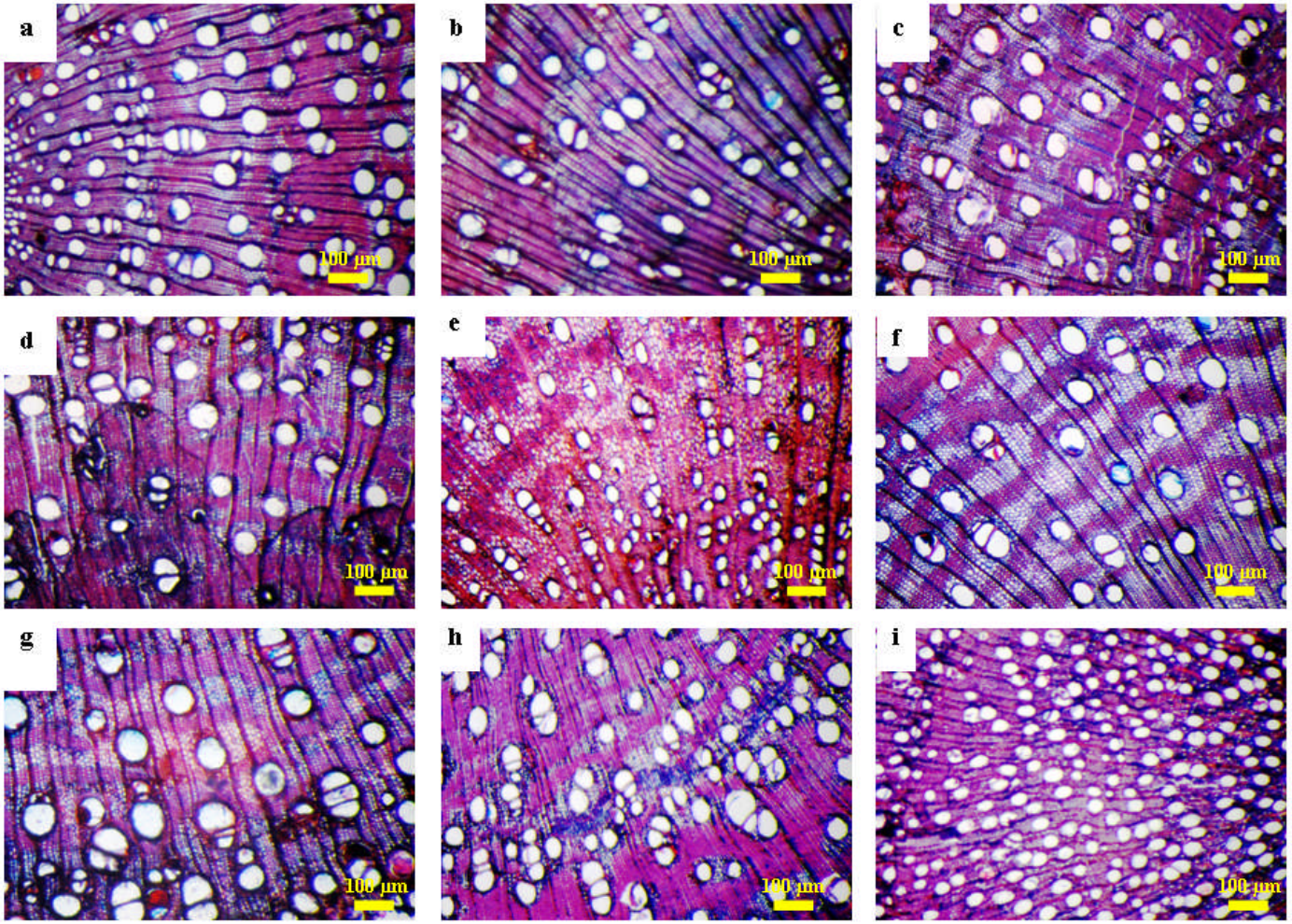
Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Marquesia macroura	15	0.000948	21.74	0.00003	0.000688	0.5517	19.427	21.734	23.63
	Marquesia macroura	16	0.000824	17.42	0.000046	0.000884	0.49333	22.289	28.409	23.168
	Marquesia macroura	17	0.000824	22.897	0.00002	0.000458	0.53333	19.473	21.051	27.07
	Marquesia macroura	18	0.000957	16.08	0.000012	0.000201	0.4867	20.841	23.681	24.36
	Marquesia macroura	19	0.000903	17.66	0.000029	0.000535	0.49167	22.089	26.597	23.48
	Marquesia macroura	20	0.000981	24.51	0.000035	0.000888	0.5383	15.872	17.093	26.51
	Marquesia macroura	21	0.001012	28.51	0.000019	0.000563	0.53467	25.275	27.814	20.62
	Marquesia macroura	22	0.000874	22.82	0.00001	0.000223	0.554	15.943	16.894	25.4
	Marquesia macroura	23	0.000917	21.39	0.00002	0.000478	0.537	19.368	21.294	21.09
	Marquesia macroura	24	0.000922	21.73	0.00002	0.0004	0.55167	18.268	19.972	20.41
	Marquesia macroura	25	0.001039	29.6	0.000022	0.000579	0.5473	21.346	25.493	20.948
Dry	*Brachystegia boehmii*	1	0.000133	2.583	0.000014	0.000035	0.24267	18.504	27.279	32.751
	Brachystegia boehmii	2	0.000131	3.6744	0.000015	0.000054	0.242	24.126	27.988	30.187
	Brachystegia boehmii	3	0.000131	3.02	0.00002	0.000058	0.245	26.472	39.618	51.186
	Brachystegia boehmii	4	0.000132	3.258	0.000024	0.000078	0.24367	26.991	36.09	42.614
	Brachystegia boehmii	5	0.00013	2.5479	0.000024	0.000061	0.24333	25.441	33.391	36.272
	Brachystegia boehmii	6	0.000128	2.917	0.00003	0.00008	0.249	21.145	31.811	39.208
	Brachystegia boehmii	7	0.000144	3.223	0.000022	0.00007	0.24633	24.778	36.161	43.076
	Brachystegia boehmii	8	0.000127	2.81	0.000024	0.000063	0.24433	23.008	27.742	30.341
	Brachystegia boehmii	9	0.000125	2.537	0.000026	0.00006	0.244	23.001	31.953	33.705
	Brachystegia boehmii	10	0.00013	2.856	0.000019	0.000054	0.245	26.147	37.658	42.232
	Brachystegia boehmii	11	0.000123	2.346	0.000025	0.000057	0.24633	23.419	30.406	34.886
	Brachystegia boehmii	12	0.000128	2.543	0.000018	0.000045	0.24533	18.604	27.526	31.201
	Brachystegia boehmii	13	0.000125	2.691	0.000025	0.000065	0.244	24.419	34.944	41.94
	Brachystegia boehmii	14	0.000125	2.467	0.000031	0.00008	0.241	26.043	30.904	32.899
	Brachystegia boehmii	15	0.000125	2.334	0.000014	0.000033	0.242	27.449	43.729	52.217
	Brachystegia boehmii	16	0.00013	2.853	0.000028	0.000075	0.242	23.844	34.378	41.569
	Brachystegia boehmii	17	0.000122	2.997	0.00002	0.000059	0.242	33.264	58.075	63.296
	Brachystegia boehmii	18	0.000124	2.437	0.00003	0.000071	0.246	27.269	34.274	37.263
	Brachystegia boehmii	19	0.000131	2.962	0.000009	0.000024	0.24533	34.998	37.136	37.364

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Brachystegia boehmii	20	0.000134	2.883	0.000021	0.000066	0.242	24.014	28.023	30.567
	Brachystegia boehmii	21	0.000123	2.3811	0.000046	0.000109	0.244	28.211	43.147	52.595
	Brachystegia boehmii	22	0.000125	2.546	0.00002	0.000047	0.24467	24.382	35.607	41.243
	Brachystegia boehmii	23	0.000122	2.818	0.000012	0.000032	0.25033	23.264	33.979	40.632
	Brachystegia boehmii	24	0.000125	2.482	0.000027	0.000063	0.24533	22.893	27.845	29.986
	Brachystegia boehmii	25	0.000124	3.013	0.00001	0.000031	0.24533	25.243	28.593	30.57
	Brachystegia spiciformis	1	0.000183	6.051	0.000025	0.000139	0.26133	26.201	29.229	31.153
	Brachystegia spiciformis	2	0.000198	8.89	0.000013	0.000108	0.26	29.903	35.418	38.238
	Brachystegia spiciformis	3	0.000203	4.413	0.000017	0.000074	0.26033	30.045	33.774	35.554
	Brachystegia spiciformis	4	0.000202	5.537	0.000011	0.000065	0.25967	18.156	20.613	21.493
	Brachystegia spiciformis	5	0.000221	5.745	0.000007	0.000039	0.261	17.994	21.919	23.367
	Brachystegia spiciformis	6	0.000215	5.526	0.000012	0.000067	0.259	20.278	22.789	23.496
	Brachystegia spiciformis	7	0.000207	5.45	0.000009	0.000044	0.25967	21.79	24.719	31.692
	Brachystegia spiciformis	8	0.000179	3.804	0.00001	0.000034	0.26067	24.94	29.01	26.63
	Brachystegia spiciformis	9	0.000207	4.508	0.000012	0.000056	0.26133	22.622	25.578	30.436
	Brachystegia spiciformis	10	0.000205	6.816	0.000007	0.000046	0.26067	25.141	28.729	35.282
	Brachystegia spiciformis	11	0.000204	4.382	0.000018	0.000077	0.26033	28.767	32.654	34.055
	Brachystegia spiciformis	12	0.000201	5.065	0.000012	0.000061	0.26	27.23	31.58	25.183
	Brachystegia spiciformis	13	0.000208	5.12	0.000018	0.000081	0.262	21.333	23.847	32.169
	Brachystegia spiciformis	14	0.000208	4.55	0.000011	0.000051	0.261	25.749	29.943	36.811
	Brachystegia spiciformis	15	0.000211	5.193	0.000021	0.000109	0.261	28.361	33.242	24.493
	Brachystegia spiciformis	16	0.000214	5.378	0.000021	0.000108	0.261	20.179	23.375	33.194
	Brachystegia spiciformis	17	0.000223	7.29	0.000011	0.000077	0.262	25.619	30.851	29.985
	Brachystegia spiciformis	18	0.00021	5.293	0.000013	0.000068	0.25967	25.606	28.876	24.246
	Brachystegia spiciformis	19	0.000217	5.251	0.000014	0.00007	0.26033	21.138	23.357	37.41
	Brachystegia spiciformis	20	0.000208	4.817	0.000017	0.00008	0.261	28.993	34.076	39.095
	Brachystegia spiciformis	21	0.000207	3.718	0.000015	0.000056	0.26	33.838	37.269	44.04
	Brachystegia spiciformis	22	0.000208	4.615	0.00001	0.000048	0.26133	22.805	33.34	31.232
	Brachystegia spiciformis	23	0.000192	6	0.000007	0.000039	0.25967	25.484	29.257	36.801
	Brachystegia spiciformis	24	0.000207	5.433	0.000015	0.000079	0.25567	24.287	31.799	30.208
	Brachystegia spiciformis	25	0.000217	4.53	0.000016	0.000066	0.26	25.895	28.699	18.07

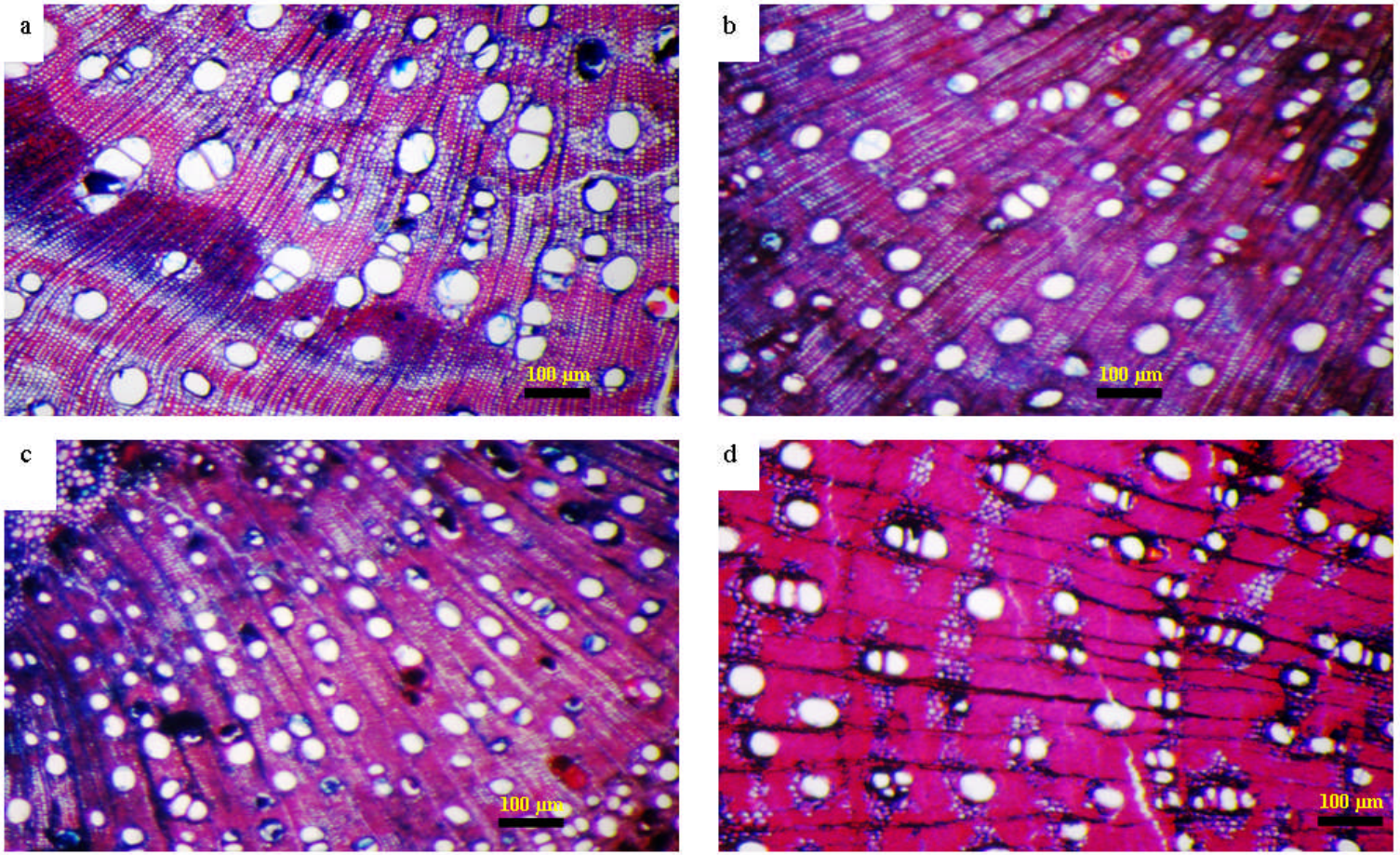
Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Erythrophleum africanum	1	0.000329	4.967	0.000041	0.000199	0.252	23.649	26.148	27.047
	Erythrophleum africanum	2	0.000322	9.178	0.000016	0.000147	0.253	23.66	26.271	27.33
	Erythrophleum africanum	3	0.000326	5.71	0.000034	0.000192	0.25167	21.085	24.372	25.553
	Erythrophleum africanum	4	0.0003	7.7	0.000011	0.000087	0.25	24.516	27.43	29.008
	Erythrophleum africanum	5	0.000308	7.333	0.000037	0.000246	0.25	25.694	29.251	29.925
	Erythrophleum africanum	6	0.000336	13.09	0.000014	0.000161	0.25267	17.18	21.096	22.351
	Erythrophleum africanum	7	0.000319	9.885	0.000015	0.000142	0.25167	19.741	22.097	22.696
	Erythrophleum africanum	8	0.000334	9.87	0.000017	0.000166	0.25233	22.093	24.943	26.024
	Erythrophleum africanum	9	0.000315	8.71	0.000012	0.000112	0.25333	22.672	24.656	25.026
	Erythrophleum africanum	10	0.000335	8.51	0.000011	0.000093	0.249	21.705	25.172	26.572
	Erythrophleum africanum	11	0.000322	6.221	0.000022	0.000131	0.25233	17.966	21.179	21.748
	Erythrophleum africanum	12	0.000318	9.748	0.000012	0.000118	0.25167	20.079	23.36	24.608
	Erythrophleum africanum	13	0.000318	7.92	0.000013	0.000106	0.25367	20.252	24.268	23.92
	Erythrophleum africanum	14	0.000337	9.28	0.000014	0.000119	0.25167	26.047	28.494	29.371
	Erythrophleum africanum	15	0.000322	11.31	0.000019	0.000206	0.24833	21.32	25.462	26.499
	Erythrophleum africanum	16	0.000326	8.35	0.000022	0.000172	0.24833	23.608	27.041	28.691
	Erythrophleum africanum	17	0.000322	7.67	0.000024	0.000164	0.24633	23.607	26.399	27.096
	Erythrophleum africanum	18	0.000325	6.423	0.000017	0.000108	0.24667	20.069	21.716	22.386
	Erythrophleum africanum	19	0.000325	8.96	0.000014	0.000116	0.251	19.72	22.635	22.934
	Erythrophleum africanum	20	0.000326	8.86	0.000021	0.000179	0.25067	21.221	23.67	24.25
	Erythrophleum africanum	21	0.00034	9.057	0.000021	0.000189	0.25033	2.2373	27.19	28.291
	Erythrophleum africanum	22	0.000318	5.961	0.000042	0.00026	0.253	21.666	25.315	26.036
	Erythrophleum africanum	23	0.000332	7.595	0.000031	0.00023	0.25033	21.74	23.571	24.409
	Erythrophleum africanum	24	0.000321	5.958	0.000021	0.000121	0.252	19.149	21.442	22.105
	Erythrophleum africanum	25	0.000316	6.505	0.000032	0.000202	0.25767	20.254	21.989	22.693
	Pericopsis angolensis	1	0.000352	13.338	0.000016	0.000206	0.21967	22.553	25.745	26.091
	Pericopsis angolensis	2	0.000367	15.65	0.000021	0.000309	0.215	17.999	19.718	20.072
	Pericopsis angolensis	3	0.000374	9.952	0.000025	0.000246	0.221	20.771	22.908	23.425
	Pericopsis angolensis	4	0.000361	13.34	0.000017	0.000238	0.21833	19.909	22.032	22.483
	Pericopsis angolensis	5	0.000368	8.143	0.000032	0.000257	0.21533	19.276	21.224	21.808
	Pericopsis angolensis	6	0.000382	9.69	0.000024	0.000225	0.223	16.165	17.819	17.928

Site	Species	Tree Number	K_H (kg s^{-1} MPa^{-1} m)	K_S (kg s^{-1} MPa^{-1} m^{-1})	*HV*	K_L (kg s^{-1} MPa^{-1} m^{-1})	V_L (m)	*D* (µm)	D_H (µm)	D_{95} (µm)
	Pericopsis angolensis	7	0.000377	10.56	0.000018	0.000184	0.21767	21.489	23.938	24.391
	Pericopsis angolensis	8	0.000391	9.84	0.000022	0.000199	0.21833	23.792	28.806	32.072
	Pericopsis angolensis	9	0.000352	10.291	0.000019	0.00019	0.215	20.771	23.663	24.712
	Pericopsis angolensis	10	0.000373	6.98	0.000022	0.000149	0.21667	18.274	20.044	20.123
	Pericopsis angolensis	11	0.000355	9.252	0.000013	0.000119	0.219	20.994	24.258	25.377
	Pericopsis angolensis	12	0.000372	11.67	0.000022	0.000243	0.22067	22.867	25.716	27.466
	Pericopsis angolensis	13	0.000332	9.76	0.00002	0.000201	0.21967	20.378	22.259	22.813
	Pericopsis angolensis	14	0.000363	10.46	0.000023	0.000216	0.21867	19.567	21.876	23.325
	Pericopsis angolensis	15	0.000367	9.949	0.000014	0.000142	0.21933	19.208	27.852	24.767
	Pericopsis angolensis	16	0.000372	10.52	0.000029	0.000292	0.22067	24.01	29.197	30.477
	Pericopsis angolensis	17	0.000338	11.256	0.000021	0.000235	0.21833	24.268	26.676	27.482
	Pericopsis angolensis	18	0.000372	8.34	0.000021	0.000166	0.21867	25.31	28.246	29.844
	Pericopsis angolensis	19	0.000338	13.52	0.000032	0.000359	0.222	19.719	21.901	22.507
	Pericopsis angolensis	20	0.000363	11.95	0.000015	0.000176	0.21867	16.849	19.667	19.011
	Pericopsis angolensis	21	0.000382	10.119	0.00003	0.000305	0.21933	19.55	21.946	22.77
	Pericopsis angolensis	22	0.000347	8.073	0.00003	0.000243	0.21767	17.936	19.331	19.706
	Pericopsis angolensis	23	0.00037	12.78	0.00002	0.000233	0.21833	18.766	21.395	21.692
	Pericopsis angolensis	24	0.000323	8.75	0.000016	0.000153	0.22033	20.069	22.314	22.943
	Pericopsis angolensis	25	0.000357	9.04	0.000027	0.000229	0.222	22.394	26.028	28.754

3.2 Wet site xylem micro-sections a) *Brachystegia boehmii* b) *B. longifolia* c) *B. spiciformis* d) *Erythrophleum africanum* e) *Pericopsis angolensis* f) *B. floribunda* g) *Isoberlinia angolensis* h) *Julbernardia paniculata* i) *Marquesia macroura* (Photos: R. Vinya, 2008)



3.3 Dry site xylem micro-sections a) *Brachystegia boehmii* b) *Brachystegia spiciformis* c) *Erythrophleum africanum* d) *Pericopsis angolensis* (Photos: R. Vinya, 2008)



4.1 Average vulnerability data

Site	Species	Tree No.	Ψ (MPa)	PLC (%)	Predicted
Wet	*Brachystegia boehmii*	1	-1.8	31.3	20.4
	Brachystegia boehmii	2	-1.9	26.2	22.3
	Brachystegia boehmii	3	-2.0	26.5	23.5
	Brachystegia boehmii	4	-3.0	38.3	38.0
	Brachystegia boehmii	5	-2.7	15.8	33.0
	Brachystegia boehmii	6	-2.7	29.3	33.8
	Brachystegia boehmii	7	-5.9	87.3	79.7
	Brachystegia boehmii	8	-2.1	26.5	24.9
	Brachystegia boehmii	9	-0.3	2.8	8.0
	Brachystegia boehmii	10	-5.4	68.6	75.4
	Brachystegia boehmii	11	-1.2	15.5	14.6
	Brachystegia boehmii	12	-5.5	75.9	75.9
	Brachystegia boehmii	13	-0.6	7.0	10.0
	Brachystegia boehmii	14	-0.2	4.1	7.4
	Brachystegia boehmii	15	-4.0	47.5	56.0
	Brachystegia boehmii	16	-7.0	86.4	86.7
	Brachystegia boehmii	17	-1.5	18.1	17.0
	Brachystegia boehmii	18	-1.5	20.1	17.5
	Brachystegia boehmii	19	-2.8	33.1	35.5
	Brachystegia boehmii	20	-4.3	59.1	60.1
	Brachystegia boehmii	21	-3.0	22.8	38.0
	Brachystegia boehmii	22	-5.0	62.7	70.2
	Brachystegia boehmii	23	-1.9	21.0	21.6
	Brachystegia boehmii	24	-3.2	68.8	42.2
	Brachystegia boehmii	25	-4.3	74.4	60.1
	Brachystegia longifolia	1	-1.8	45.3	40.0
	Brachystegia longifolia	2	-1.5	35.2	32.2
	Brachystegia longifolia	3	-2.6	56.2	56.5
	Brachystegia longifolia	4	-1.4	35.1	30.1
	Brachystegia longifolia	5	-3.7	74.6	70.3
	Brachystegia longifolia	6	-2.2	55.4	48.7
	Brachystegia longifolia	7	-3.4	68.5	67.6
	Brachystegia longifolia	8	-2.0	46.9	43.3
	Brachystegia longifolia	9	-3.1	65.9	63.5
	Brachystegia longifolia	10	-1.7	38.2	36.6
	Brachystegia longifolia	11	-3.0	65.1	62.1
	Brachystegia longifolia	12	-1.1	24.3	25.0
	Brachystegia longifolia	13	-0.5	11.9	14.9
	Brachystegia longifolia	14	-2.6	49.4	55.6
	Brachystegia longifolia	15	-1.7	29.6	36.6
	Brachystegia longifolia	16	-1.9	41.7	41.1
	Brachystegia longifolia	17	-2.5	53.6	54.7
	Brachystegia longifolia	18	-2.7	48.8	57.4
	Brachystegia longifolia	19	-3.3	65.7	66.5
	Brachystegia longifolia	20	-0.8	14.9	19.9
	Brachystegia longifolia	21	-2.0	43.0	44.4

Site	Species	Tree No.	Ψ (MPa)	PLC (%)	Predicted
	Brachystegia longifolia	22	-2.8	54.3	59.0
	Brachystegia longifolia	23	-2.0	46.1	44.4
	Brachystegia longifolia	24	-4.2	67.7	73.1
	Brachystegia longifolia	25	-4.3	78.3	73.8
	Brachystegia spiciformis	1	-4.8	68.6	73.9
	Brachystegia spiciformis	2	-0.6	18.1	14.8
	Brachystegia spiciformis	3	-4.1	57.6	65.4
	Brachystegia spiciformis	4	-3.8	64.7	61.8
	Brachystegia spiciformis	5	-1.4	19.0	22.8
	Brachystegia spiciformis	6	-1.3	24.2	21.5
	Brachystegia spiciformis	7	-3.8	61.8	61.8
	Brachystegia spiciformis	8	-5.4	85.5	79.4
	Brachystegia spiciformis	9	-3.1	48.3	50.5
	Brachystegia spiciformis	10	-4.5	72.5	70.6
	Brachystegia spiciformis	11	-4.2	58.5	67.4
	Brachystegia spiciformis	12	-1.0	16.2	18.0
	Brachystegia spiciformis	13	-2.1	36.1	33.7
	Brachystegia spiciformis	14	-2.5	55.9	39.4
	Brachystegia spiciformis	15	-1.2	21.7	20.9
	Brachystegia spiciformis	16	-1.6	23.7	26.1
	Brachystegia spiciformis	17	-1.0	21.5	18.6
	Brachystegia spiciformis	18	-2.5	41.3	39.4
	Brachystegia spiciformis	19	-0.6	7.0	14.1
	Brachystegia spiciformis	20	-2.8	32.5	44.5
	Brachystegia spiciformis	21	-1.6	26.9	26.1
	Brachystegia spiciformis	22	-0.9	14.9	17.5
	Brachystegia spiciformis	23	-4.1	73.9	65.4
	Brachystegia spiciformis	24	-1.6	24.6	26.1
	Brachystegia spiciformis	25	-3.5	59.8	57.1
	Erythrophleum africanum	1	-3.9	60.4	58.5
	Erythrophleum africanum	2	-0.7	5.9	10.6
	Erythrophleum africanum	3	-1.8	21.0	21.9
	Erythrophleum africanum	4	-0.4	3.9	8.7
	Erythrophleum africanum	5	-1.1	16.8	13.7
	Erythrophleum africanum	6	-1.1	13.4	14.2
	Erythrophleum africanum	7	-3.4	50.8	50.4
	Erythrophleum africanum	8	-0.8	16.3	11.4
	Erythrophleum africanum	9	-5.3	89.2	77.8
	Erythrophleum africanum	10	-2.6	30.0	35.5
	Erythrophleum africanum	11	-2.6	42.4	34.6
	Erythrophleum africanum	12	-3.3	49.7	47.6
	Erythrophleum africanum	13	-1.9	27.6	23.3
	Erythrophleum africanum	14	-1.1	20.2	14.0
	Erythrophleum africanum	15	-2.9	50.9	41.0
	Erythrophleum africanum	16	-1.1	13.2	14.2
	Erythrophleum africanum	17	-4.6	68.2	69.3
	Erythrophleum africanum	18	-2.3	23.9	29.9
	Erythrophleum africanum	19	-1.0	7.4	13.2
	Erythrophleum africanum	20	-1.1	12.9	14.2

Site	Species	Tree No.	Ψ (MPa)	PLC (%)	Predicted
	Erythrophleum africanum	21	-4.8	60.7	71.9
	Erythrophleum africanum	22	-4.7	67.2	71.3
	Erythrophleum africanum	23	-5.0	73.6	74.3
	Erythrophleum africanum	24	-0.9	11.2	11.8
	Erythrophleum africanum	25	-2.7	30.7	37.3
	Pericopsis angolensis	1	-3.1	50.3	44.8
	Pericopsis angolensis	2	-2.2	31.6	31.0
	Pericopsis angolensis	3	-1.7	30.1	24.2
	Pericopsis angolensis	4	-0.5	7.6	11.9
	Pericopsis angolensis	5	-4.3	62.4	65.1
	Pericopsis angolensis	6	-3.1	50.4	45.6
	Pericopsis angolensis	7	-3.1	43.6	44.8
	Pericopsis angolensis	8	-3.6	44.5	54.3
	Pericopsis angolensis	9	-4.3	57.5	65.1
	Pericopsis angolensis	10	-6.1	92.2	87.2
	Pericopsis angolensis	11	-4.4	79.2	67.5
	Pericopsis angolensis	12	-4.6	74.3	70.5
	Pericopsis angolensis	13	-2.6	30.3	36.4
	Pericopsis angolensis	14	-1.9	29.7	26.1
	Pericopsis angolensis	15	-1.4	18.6	20.1
	Pericopsis angolensis	16	-2.9	43.6	41.4
	Pericopsis angolensis	17	-3.5	51.5	51.7
	Pericopsis angolensis	18	-2.2	29.9	30.3
	Pericopsis angolensis	19	-1.8	25.7	25.5
	Pericopsis angolensis	20	-4.6	70.3	70.5
	Pericopsis angolensis	21	-1.1	13.8	16.9
	Pericopsis angolensis	22	-5.8	74.6	85.0
	Pericopsis angolensis	23	-6.5	93.0	90.5
	Pericopsis angolensis	24	-2.5	37.4	34.9
	Pericopsis angolensis	25	-2.6	33.6	36.4
	Brachystegia floribunda	1	-1.3	44.0	35.2
	Brachystegia floribunda	2	-2.5	77.7	66.6
	Brachystegia floribunda	3	-2.5	50.2	68.3
	Brachystegia floribunda	4	-2.2	48.9	61.0
	Brachystegia floribunda	5	-0.9	19.3	24.2
	Brachystegia floribunda	6	-1.2	28.8	31.3
	Brachystegia floribunda	7	-0.8	14.8	23.1
	Brachystegia floribunda	8	-1.4	42.3	37.9
	Brachystegia floribunda	9	-1.1	29.6	29.4
	Brachystegia floribunda	10	-1.2	34.7	31.3
	Brachystegia floribunda	11	-0.2	5.5	12.1
	Brachystegia floribunda	12	-1.3	25.0	35.4
	Brachystegia floribunda	13	-1.7	50.2	46.4
	Brachystegia floribunda	14	-1.4	27.4	36.5
	Brachystegia floribunda	15	-2.3	56.0	62.9
	Brachystegia floribunda	16	-2.4	71.4	64.2
	Brachystegia floribunda	17	-2.9	82.8	76.0
	Brachystegia floribunda	18	-1.3	49.2	35.2
	Brachystegia floribunda	19	-1.8	56.9	47.8

Site	Species	Tree No.	Ψ (MPa)	PLC (%)	Predicted
	Brachystegia floribunda	20	-1.6	48.6	42.1
	Brachystegia floribunda	21	-4.4	99.9	90.8
	Brachystegia floribunda	22	-2.8	70.7	73.2
	Brachystegia floribunda	23	-2.9	80.3	76.0
	Brachystegia floribunda	24	-3.3	81.0	82.1
	Brachystegia floribunda	25	-3.5	72.2	83.9
	Isoberlinia angolensis	1	-1.6	52.4	41.4
	Isoberlinia angolensis	2	-1.9	55.7	52.6
	Isoberlinia angolensis	3	-1.1	23.7	26.8
	Isoberlinia angolensis	4	-1.2	25.0	30.8
	Isoberlinia angolensis	5	-1.3	26.3	32.3
	Isoberlinia angolensis	6	-0.2	3.2	10.2
	Isoberlinia angolensis	7	-3.5	84.8	86.4
	Isoberlinia angolensis	8	-1.5	51.8	40.3
	Isoberlinia angolensis	9	-1.6	47.5	43.0
	Isoberlinia angolensis	10	-0.7	22.8	18.6
	Isoberlinia angolensis	11	-1.8	54.4	47.8
	Isoberlinia angolensis	12	-1.1	24.1	26.8
	Isoberlinia angolensis	13	-1.2	18.6	29.4
	Isoberlinia angolensis	14	-2.0	42.9	55.7
	Isoberlinia angolensis	15	-2.0	60.2	55.7
	Isoberlinia angolensis	16	-3.3	82.3	84.7
	Isoberlinia angolensis	17	-1.1	36.0	28.8
	Isoberlinia angolensis	18	-1.2	28.2	29.4
	Isoberlinia angolensis	19	-2.3	57.5	64.6
	Isoberlinia angolensis	20	-3.7	96.6	88.3
	Isoberlinia angolensis	21	-2.9	64.6	78.6
	Isoberlinia angolensis	22	-1.1	23.5	28.1
	Isoberlinia angolensis	23	-1.6	49.1	43.0
	Isoberlinia angolensis	24	-3.5	81.2	86.9
	Isoberlinia angolensis	25	-3.5	98.7	86.4
	Julbernardia paniculata	1	-2.6	51.7	53.4
	Julbernardia paniculata	2	-0.7	14.9	15.2
	Julbernardia paniculata	3	-2.1	43.7	42.6
	Julbernardia paniculata	4	-1.1	20.8	21.0
	Julbernardia paniculata	5	-3.3	77.1	68.9
	Julbernardia paniculata	6	-1.5	31.6	29.2
	Julbernardia paniculata	7	-2.1	31.5	41.4
	Julbernardia paniculata	8	-2.2	41.1	45.0
	Julbernardia paniculata	9	-2.4	51.6	49.8
	Julbernardia paniculata	10	-1.4	35.4	27.2
	Julbernardia paniculata	11	-2.1	49.7	42.6
	Julbernardia paniculata	12	-3.6	74.9	75.3
	Julbernardia paniculata	13	-3.3	67.7	69.9
	Julbernardia paniculata	14	-1.3	18.4	25.3
	Julbernardia paniculata	15	-1.3	26.2	25.3
	Julbernardia paniculata	16	-1.2	28.7	22.6
	Julbernardia paniculata	17	-2.3	54.2	46.2
	Julbernardia paniculata	18	-1.7	31.6	33.4

Site	Species	Tree No.	Ψ (MPa)	PLC (%)	Predicted
	Julbernardia paniculata	19	-1.0	22.8	20.2
	Julbernardia paniculata	20	-2.0	38.4	40.2
	Julbernardia paniculata	21	-2.9	60.9	61.5
	Julbernardia paniculata	22	-3.3	63.4	68.9
	Julbernardia paniculata	23	-1.3	22.0	24.6
	Julbernardia paniculata	24	-1.1	16.9	21.0
	Julbernardia paniculata	25	-1.7	28.9	33.2
	Marquesia macroura	1	-0.5	14.6	19.9
	Marquesia macroura	2	-1.1	45.2	39.2
	Marquesia macroura	3	-0.7	41.1	25.1
	Marquesia macroura	4	-0.2	3.9	11.5
	Marquesia macroura	5	-0.5	14.9	19.7
	Marquesia macroura	6	-0.6	27.7	23.5
	Marquesia macroura	7	-2.1	87.9	75.1
	Marquesia macroura	8	-0.6	18.0	21.2
	Marquesia macroura	9	-0.8	24.9	29.7
	Marquesia macroura	10	-0.4	25.6	17.7
	Marquesia macroura	11	-0.7	24.2	26.0
	Marquesia macroura	12	-2.1	65.0	74.0
	Marquesia macroura	13	-1.9	69.2	70.3
	Marquesia macroura	14	-1.6	32.7	61.8
	Marquesia macroura	15	-1.4	58.8	53.5
	Marquesia macroura	16	-2.0	62.9	72.9
	Marquesia macroura	17	-1.8	60.7	66.0
	Marquesia macroura	18	-1.8	64.5	67.5
	Marquesia macroura	19	-1.5	38.3	55.4
	Marquesia macroura	20	-0.6	14.2	21.2
	Marquesia macroura	21	-2.2	82.4	76.2
	Marquesia macroura	22	-1.6	77.5	61.8
	Marquesia macroura	23	-2.1	80.2	75.1
	Marquesia macroura	24	-1.5	83.5	57.3
	Marquesia macroura	25	-1.4	53.7	53.5

5.1 Average diameter at breast height (dbh), height (ht), and timing of leaf shedding and flushing for the nine miombo woodlands trees species.

Species	**dbh (cm)**	**ht (m)**	**Shedding**		**Leaflessness**	**Flushing**	
			Timing (months)	*****Duration (days)	*Duration (days)	Timing (months)	*****Duration (days)
Brachystegia boehmii	36	20	Aug – Sept	11 ± 1	24 ± 2	Sept - Oct	7 ± 0.5
Brachystegia longifolia	34	20	Jul – Aug	14 ± 1	19 ± 1	Aug – Sept	6 ± 0.4
Brachystegia spiciformis	39	21	Jul – Aug	12 ± 1	23 ± 1	Aug – Sept	8 ± 0.5
Erythrophleum africanum	25	16	Aug – Sept	12 ± 1	19 ± 1	Sept – Oct	8 ± 0.4
Pericopsis angolensis	33	19	Sept	12 ± 1	20 ± 1	Sept – Oct	7 ± 0.4
Brachystegia floribunda	31	19	Aug – Sept	24 ± 1	16 ± 1	Sept – Oct	8 ± 0.5
Isoberlinia angolensis	30	18	Jul – Aug	16 ± 1	22 ± 1	Aug – Sept	8 ± 0.4
Julbernardia paniculata	38	21	Jun – Aug	20 ± 1	25 ± 1	Aug – Sept	8 ± 0.3
Marquesia macroura	39	21	Jun - Sept	30 ± 1	19 ± 1	Jul - Oct	8 ± 0.3

* Average time taken by an individual tree to complete a given leaf phenological event.

6.1 Leaf functional traits associated with plant drought tolerance

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
Wet	*Brachystegia boehmii*	1	434.5115	0.100062	39.3699
	Brachystegia boehmii	2	406.199	0.095916	26.26828
	Brachystegia boehmii	3	372.3377	0.106016	29.00978
	Brachystegia boehmii	4	617.9634	0.053941	29.23257
	Brachystegia boehmii	5	343.4805	0.10156	18.42432
	Brachystegia boehmii	6	316.7222	0.121436	26.99277
	Brachystegia boehmii	7	416.3211	0.071346	47.71216
	Brachystegia boehmii	8	432.3002	0.078859	17.39158
	Brachystegia boehmii	9	443.9605	0.060334	13.79847
	Brachystegia boehmii	10	475.9953	0.068506	26.80272
	Brachystegia boehmii	11	322.4473	0.091214	19.08929
	Brachystegia boehmii	12	514.2009	0.081032	43.96003
	Brachystegia boehmii	13	402.0313	0.071751	30.96939
	Brachystegia boehmii	14	410.0306	0.079527	26.01701
	Brachystegia boehmii	15	291.8039	0.135275	34.94133
	Brachystegia boehmii	16	463.934	0.064024	42.51276
	Brachystegia boehmii	17	425.9471	0.083847	35.63053
	Brachystegia boehmii	18	455.7155	0.058777	31.90009
	Brachystegia boehmii	19	426.735	0.065702	31.40306
	Brachystegia boehmii	20	472.5274	0.072146	20.76318
	Brachystegia boehmii	21	486.4092	0.071717	48.0744
	Brachystegia boehmii	22	469.2627	0.075212	26.94303
	Brachystegia boehmii	23	450.9608	0.083156	22.46386
	Brachystegia boehmii	24	454.1854	0.069529	42.1318
	Brachystegia boehmii	25	514.158	0.058937	37.45408
	Brachystegia longifolia	1	381.2129	0.103548	24.32611
	Brachystegia longifolia	2	497.3416	0.077334	30.10544
	Brachystegia longifolia	3	451.9613	0.092191	32.63308
	Brachystegia longifolia	4	497.243	0.078354	23.67602
	Brachystegia longifolia	5	403.9834	0.07426	16.20536
	Brachystegia longifolia	6	462.9549	0.091269	21.45876
	Brachystegia longifolia	7	313.3354	0.106382	33.27764
	Brachystegia longifolia	8	406.2356	0.081152	21.40009
	Brachystegia longifolia	9	529.2449	0.076601	20.66922
	Brachystegia longifolia	10	529.3253	0.063681	20.40731
	Brachystegia longifolia	11	425.4783	0.111919	12.88393
	Brachystegia longifolia	12	498.8205	0.092526	27.82355
	Brachystegia longifolia	13	527.8018	0.065333	17.74915
	Brachystegia longifolia	14	487.1574	0.086735	19.16029
	Brachystegia longifolia	15	531.8372	0.071403	50.23682
	Brachystegia longifolia	16	442.5529	0.082669	40.85927
	Brachystegia longifolia	17	528.0187	0.056816	18.99277
	Brachystegia longifolia	18	484.7002	0.074571	17.81165
	Brachystegia longifolia	19	445.2024	0.077454	31.6875
	Brachystegia longifolia	20	484.3165	0.073742	18.81888

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Brachystegia longifolia	21	518.4881	0.083856	60.64243
	Brachystegia longifolia	22	649.8192	0.053682	42.52509
	Brachystegia longifolia	23	429.9138	0.091818	26.37245
	Brachystegia longifolia	24	404.8077	0.087187	32.30952
	Brachystegia longifolia	25	419.4059	0.079478	37.4426
	Brachystegia spiciformis	1	565.9492	0.082825	99.47704
	Brachystegia spiciformis	2	441.9821	0.091724	48.20833
	Brachystegia spiciformis	3	516.1412	0.084237	61.70833
	Brachystegia spiciformis	4	446.1485	0.084053	70.04634
	Brachystegia spiciformis	5	467.6909	0.081196	98.74022
	Brachystegia spiciformis	6	457.9891	0.06753	126.4388
	Brachystegia spiciformis	7	651.1757	0.074307	73.04039
	Brachystegia spiciformis	8	452.1542	0.083986	83.52679
	Brachystegia spiciformis	9	547.1399	0.073107	79.76105
	Brachystegia spiciformis	10	484.229	0.082606	152.3597
	Brachystegia spiciformis	11	494.54	0.061275	79.89838
	Brachystegia spiciformis	12	493.0963	0.079013	81.32866
	Brachystegia spiciformis	13	580.299	0.07833	110.2568
	Brachystegia spiciformis	14	657.1714	0.055671	141.8342
	Brachystegia spiciformis	15	451.9451	0.089702	137.8036
	Brachystegia spiciformis	16	488.7648	0.07307	67.2483
	Brachystegia spiciformis	17	654.8792	0.060276	102.1241
	Brachystegia spiciformis	18	514.3603	0.072006	71.03954
	Brachystegia spiciformis	19	589.2014	0.059205	114.6433
	Brachystegia spiciformis	20	581.0631	0.06977	100.6998
	Brachystegia spiciformis	21	485.1687	0.08709	74.44898
	Brachystegia spiciformis	22	477.9317	0.083694	55.81335
	Brachystegia spiciformis	23	624.9586	0.06957	110.0646
	Brachystegia spiciformis	24	377.5846	0.111905	77.00043
	Brachystegia spiciformis	25	543.8343	0.087562	72.27338
	Erythrophleum africanum	1	504.6913	0.095875	48.51446
	Erythrophleum africanum	2	551.7571	0.051294	28.01531
	Erythrophleum africanum	3	451.126	0.100758	27.78444
	Erythrophleum africanum	4	432.3585	0.070088	23.35799
	Erythrophleum africanum	5	631.8918	0.049455	45.98937
	Erythrophleum africanum	6	648.2109	0.049765	37.3142
	Erythrophleum africanum	7	603.9349	0.049182	45.98597
	Erythrophleum africanum	8	1034.316	0.029597	33.70748
	Erythrophleum africanum	9	285.9938	0.158935	21.83546
	Erythrophleum africanum	10	482.2364	0.072337	26.15731
	Erythrophleum africanum	11	649.1187	0.0424	29.1267
	Erythrophleum africanum	12	773.765	0.034617	29.08248
	Erythrophleum africanum	13	343.6786	0.089991	30.20408
	Erythrophleum africanum	14	548.6469	0.053608	34.39201
	Erythrophleum africanum	15	370.8139	0.097474	29.96386
	Erythrophleum africanum	16	553.6619	0.053648	30.34949
	Erythrophleum africanum	17	694.2705	0.041549	39.17304
	Erythrophleum africanum	18	801.2771	0.037818	36.38988
	Erythrophleum africanum	19	530.051	0.051925	29.23342

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Erythrophleum africanum	20	773.5301	0.03494	33.28741
	Erythrophleum africanum	21	450.7844	0.078295	32.09269
	Erythrophleum africanum	22	563.5555	0.056035	34.03954
	Erythrophleum africanum	23	580.4896	0.064601	33.1943
	Erythrophleum africanum	24	375.3871	0.092927	25.01956
	Erythrophleum africanum	25	417.2501	0.098492	34.72959
	Pericopsis angolensis	1	434.5787	0.067679	70.1199
	Pericopsis angolensis	2	431.5246	0.057934	71.8176
	Pericopsis angolensis	3	444.2083	0.065569	50.08844
	Pericopsis angolensis	4	497.7625	0.070906	38.63393
	Pericopsis angolensis	5	566.8547	0.052924	75.05017
	Pericopsis angolensis	6	480.7459	0.062403	100.4668
	Pericopsis angolensis	7	758.1206	0.055735	88.54762
	Pericopsis angolensis	8	486.5972	0.020214	37.75383
	Pericopsis angolensis	9	531.3567	0.073324	76.11139
	Pericopsis angolensis	10	436.7586	0.078054	102.3363
	Pericopsis angolensis	11	465.4442	0.067847	109.04
	Pericopsis angolensis	12	379.8883	0.096306	69.04082
	Pericopsis angolensis	13	468.4678	0.082101	87.46003
	Pericopsis angolensis	14	546.7414	0.058373	100.6305
	Pericopsis angolensis	15	475.821	0.076889	87.04719
	Pericopsis angolensis	16	445.9103	0.070819	61.79762
	Pericopsis angolensis	17	543.6446	0.048835	89.18707
	Pericopsis angolensis	18	579.6675	0.050246	66.43665
	Pericopsis angolensis	19	485.7058	0.053246	75.85374
	Pericopsis angolensis	20	384.6293	0.062901	53.47491
	Pericopsis angolensis	21	369.4854	0.076598	39.7585
	Pericopsis angolensis	22	612.7846	0.047997	82.07058
	Pericopsis angolensis	23	671.1419	0.055875	95.28827
	Pericopsis angolensis	24	595.8832	0.075142	47.8852
	Pericopsis angolensis	25	500.8872	0.050757	73.26531
	Brachystegia floribunda	1	418.221	0.125846	94.43155
	Brachystegia floribunda	2	496.2121	0.08762	81.81633
	Brachystegia floribunda	3	1067.569	0.046068	126.0315
	Brachystegia floribunda	4	372.7987	0.113341	109.1331
	Brachystegia floribunda	5	979.5822	0.051042	232.5123
	Brachystegia floribunda	6	437.8942	0.076977	111.0578
	Brachystegia floribunda	7	395.1346	0.124465	101.5719
	Brachystegia floribunda	8	662.5632	0.079436	95.76318
	Brachystegia floribunda	9	680.7797	0.068855	162.8125
	Brachystegia floribunda	10	609.5506	0.083418	108.1237
	Brachystegia floribunda	11	204.5192	0.232834	55.39498
	Brachystegia floribunda	12	322.1055	0.124183	103.5557
	Brachystegia floribunda	13	302.8926	0.183417	102.6161
	Brachystegia floribunda	14	708.6653	0.066145	134.1386
	Brachystegia floribunda	15	477.484	0.099729	130.4588
	Brachystegia floribunda	16	403.9656	0.128041	89.36012
	Brachystegia floribunda	17	325.502	0.13756	111.7368
	Brachystegia floribunda	18	555.7469	0.088494	119.3457

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Brachystegia floribunda	19	552.8779	0.082214	77.15221
	Brachystegia floribunda	20	567.1887	0.086709	124.5918
	Brachystegia floribunda	21	315.0799	0.156088	91.15774
	Brachystegia floribunda	22	290.7106	0.13402	93.3142
	Brachystegia floribunda	23	533.141	0.08275	96.62968
	Brachystegia floribunda	24	194.4385	0.233773	74.39583
	Brachystegia floribunda	25	321.9712	0.125914	112.2934
	Isoberlinia angolensis	1	380.6608	0.109459	179.8002
	Isoberlinia angolensis	2	425.6069	0.11369	140.6514
	Isoberlinia angolensis	3	412.2233	0.101078	354.5625
	Isoberlinia angolensis	4	360.2803	0.138781	366.4175
	Isoberlinia angolensis	5	396.5444	0.132726	231.0238
	Isoberlinia angolensis	6	410.5807	0.096141	190.9247
	Isoberlinia angolensis	7	341.3943	0.131157	221.0213
	Isoberlinia angolensis	8	377.5974	0.110347	179.4116
	Isoberlinia angolensis	9	563.2063	0.067426	196.4158
	Isoberlinia angolensis	10	367.2958	0.098407	237.4991
	Isoberlinia angolensis	11	369.2488	0.093386	200.9188
	Isoberlinia angolensis	12	472.1554	0.100855	151.9923
	Isoberlinia angolensis	13	363.8614	0.079278	186.4094
	Isoberlinia angolensis	14	330.7919	0.13337	157.9915
	Isoberlinia angolensis	15	246.7272	0.139761	220.9651
	Isoberlinia angolensis	16	405.2102	0.129887	165.6322
	Isoberlinia angolensis	17	370.8635	0.120735	191.0315
	Isoberlinia angolensis	18	397.2451	0.125867	134.5438
	Isoberlinia angolensis	19	410.1241	0.123981	233.6514
	Isoberlinia angolensis	20	311.1624	0.155504	161.7462
	Isoberlinia angolensis	21	368.9331	0.147846	260.548
	Isoberlinia angolensis	22	387.3802	0.129072	186.5383
	Isoberlinia angolensis	23	257.7964	0.190772	163.8627
	Isoberlinia angolensis	24	438.9158	0.124273	284.5421
	Isoberlinia angolensis	25	405.8139	0.13441	213.0523
	Julbernardia paniculata	1	397.5781	0.1237	206.0438
	Julbernardia paniculata	2	407.3895	0.131499	157.0357
	Julbernardia paniculata	3	409.6829	0.124114	160.0906
	Julbernardia paniculata	4	379.2266	0.113012	139.6645
	Julbernardia paniculata	5	378.8245	0.095412	134.7806
	Julbernardia paniculata	6	449.9643	0.125796	140.0578
	Julbernardia paniculata	7	308.087	0.216389	113.5514
	Julbernardia paniculata	8	364.1112	0.109857	98.67602
	Julbernardia paniculata	9	481.9035	0.080848	189.9332
	Julbernardia paniculata	10	409.2906	0.140957	123.3074
	Julbernardia paniculata	11	414.8108	0.113003	107.2853
	Julbernardia paniculata	12	404.3156	0.132499	197.0077
	Julbernardia paniculata	13	313.858	0.164801	152.5876
	Julbernardia paniculata	14	414.3719	0.141958	100.8308
	Julbernardia paniculata	15	610.0272	0.076841	244.0344
	Julbernardia paniculata	16	425.2989	0.117564	198.6288
	Julbernardia paniculata	17	324.5429	0.137967	129.8741

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Julbernardia paniculata	18	347.0544	0.137209	126.645
	Julbernardia paniculata	19	424.5479	0.103917	144.1042
	Julbernardia paniculata	20	363.6144	0.158663	176.7798
	Julbernardia paniculata	21	438.6969	0.112105	192.4239
	Julbernardia paniculata	22	441.3761	0.109628	197.4583
	Julbernardia paniculata	23	413.8601	0.115061	121.5935
	Julbernardia paniculata	24	387.8398	0.133365	169.9919
	Julbernardia paniculata	25	358.9154	0.130602	219.3924
	Marquesia macroura	1	309.8532	0.12574	137.395
	Marquesia macroura	2	476.3757	0.106738	100.8418
	Marquesia macroura	3	377.7654	0.091281	133.9911
	Marquesia macroura	4	411.633	0.105624	159.3635
	Marquesia macroura	5	447.3921	0.117641	138.3937
	Marquesia macroura	6	372.3937	0.127873	129.0859
	Marquesia macroura	7	353.847	0.126541	140.1331
	Marquesia macroura	8	403.7116	0.094064	151.6463
	Marquesia macroura	9	538.2653	0.081963	181.8197
	Marquesia macroura	10	561.6381	0.098917	113.5685
	Marquesia macroura	11	435.8279	0.107554	91.69005
	Marquesia macroura	12	402.7725	0.08369	107.031
	Marquesia macroura	13	476.7431	0.116531	161.0753
	Marquesia macroura	14	378.9748	0.131935	123.4902
	Marquesia macroura	15	476.7211	0.080679	90.01318
	Marquesia macroura	16	319.9324	0.156283	62.35034
	Marquesia macroura	17	524.4647	0.102145	117.8771
	Marquesia macroura	18	348.1191	0.132581	106.79
	Marquesia macroura	19	417.8956	0.119647	148.9116
	Marquesia macroura	20	398.2069	0.115904	95.39923
	Marquesia macroura	21	466.6323	0.103694	108.0719
	Marquesia macroura	22	381.3359	0.140484	105.7092
	Marquesia macroura	23	407.9918	0.082619	120.2798
	Marquesia macroura	24	394.1969	0.146354	107.0493
	Marquesia macroura	25	366.7979	0.136315	116.3805
Dry	*Brachystegia boehmii*	1	596.0317	0.089	29.24277
	Brachystegia boehmii	2	499.1929	0.0932	24.97491
	Brachystegia boehmii	3	821.7262	0.07367	20.1233
	Brachystegia boehmii	4	474.0322	0.0337	25.93963
	Brachystegia boehmii	5	491.2755	0.04931	26.23342
	Brachystegia boehmii	6	501.3216	0.1024	18.39796
	Brachystegia boehmii	7	508.4255	0.0674	27.08248
	Brachystegia boehmii	8	617.8472	0.08361	30.59226
	Brachystegia boehmii	9	558.9605	0.05782	25.86735
	Brachystegia boehmii	10	560.9396	0.062451	25.63393
	Brachystegia boehmii	11	756.7035	0.0447	18.97449
	Brachystegia boehmii	12	651.0686	0.08149	36.63605
	Brachystegia boehmii	13	579.9575	0.064217	28.90561
	Brachystegia boehmii	14	596.3669	0.075812	25.75
	Brachystegia boehmii	15	585.462	0.1412	34.69515
	Brachystegia boehmii	16	634.3892	0.0534	20.87755

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Brachystegia boehmii	17	607.9365	0.0457	17.85502
	Brachystegia boehmii	18	580.3359	0.0738	23.21344
	Brachystegia boehmii	19	847.6509	0.0786	24.07781
	Brachystegia boehmii	20	618.7287	0.04651	26.93027
	Brachystegia boehmii	21	238.3022	0.09354	10.54507
	Brachystegia boehmii	22	840.3132	0.08159	13.1773
	Brachystegia boehmii	23	1318.994	0.0927	31.89073
	Brachystegia boehmii	24	340.7398	0.0438	17.91114
	Brachystegia boehmii	25	891.6596	0.06218	22.62117
	Brachystegia spiciformis	1	708.5133	0.0759	37.48597
	Brachystegia spiciformis	2	578.3671	0.06931	44.38563
	Brachystegia spiciformis	3	656.6699	0.0683	38.78231
	Brachystegia spiciformis	4	617.6162	0.09427	41.04464
	Brachystegia spiciformis	5	659.4839	0.08231	43.48597
	Brachystegia spiciformis	6	574.702	0.07398	34.3227
	Brachystegia spiciformis	7	741.255	0.06952	61.02551
	Brachystegia spiciformis	8	756.0286	0.08479	54.35077
	Brachystegia spiciformis	9	550.1116	0.05287	39.93878
	Brachystegia spiciformis	10	539.7187	0.072901	53.70493
	Brachystegia spiciformis	11	670.9332	0.05371	53.76148
	Brachystegia spiciformis	12	547.5347	0.08341	41.72662
	Brachystegia spiciformis	13	639.9681	0.08195	31.24872
	Brachystegia spiciformis	14	726.5464	0.06532	45.64243
	Brachystegia spiciformis	15	587.495	0.047002	36.68282
	Brachystegia spiciformis	16	695.7217	0.0537	55.65774
	Brachystegia spiciformis	17	557.0585	0.07159	47.42772
	Brachystegia spiciformis	18	548.6827	0.078	41.92049
	Brachystegia spiciformis	19	620.4335	0.04851	43.16752
	Brachystegia spiciformis	20	575.4029	0.0719	38.36267
	Brachystegia spiciformis	21	707.8019	0.09317	39.42857
	Brachystegia spiciformis	22	622.695	0.08	45.48087
	Brachystegia spiciformis	23	552.0249	0.07583	44.16199
	Brachystegia spiciformis	24	522.5311	0.0371	49.20876
	Brachystegia spiciformis	25	545.4993	0.070249	34.35587
	Erythrophleum africanum	1	467.6585	0.08324	32.55187
	Erythrophleum africanum	2	373.0065	0.06005	33.62032
	Erythrophleum africanum	3	513.326	0.08567	35.93282
	Erythrophleum africanum	4	473.6908	0.0834	41.20366
	Erythrophleum africanum	5	541.6752	0.0659	23.38435
	Erythrophleum africanum	6	462.6296	0.057	35.22704
	Erythrophleum africanum	7	493.0588	0.0832	39.25128
	Erythrophleum africanum	8	460.0128	0.06034	27.60077
	Erythrophleum africanum	9	434.1146	0.07439	31.82568
	Erythrophleum africanum	10	527.6026	0.168	38.60119
	Erythrophleum africanum	11	521.4009	0.0715	22.45323
	Erythrophleum africanum	12	448.4534	0.0943	34.33929
	Erythrophleum africanum	13	479.6202	0.03002	27.1824
	Erythrophleum africanum	14	439.9435	0.0296	26.25425
	Erythrophleum africanum	15	478.5269	0.0574	31.85204

Site	Species	Tree no.	*SLA* ($cm^2 g^{-1}$)	*DMC* ($g g^{-1}$)	*MLA* (mm^2)
	Erythrophleum africanum	16	430.6295	0.0759	28.65476
	Erythrophleum africanum	17	515.2243	0.057	38.85799
	Erythrophleum africanum	18	416.695	0.06489	27.80825
	Erythrophleum africanum	19	482.3257	0.07456	25.27721
	Erythrophleum africanum	20	533.4781	0.0497	31.87798
	Erythrophleum africanum	21	448.0837	0.1167	31.30952
	Erythrophleum africanum	22	470.0832	0.0952	29.70876
	Erythrophleum africanum	23	497.7218	0.0852	32.94685
	Erythrophleum africanum	24	460.2459	0.06048	35.14456
	Erythrophleum africanum	25	473.0412	0.0759	29.96216
	Pericopsis angolensis	1	626.9567	0.0973	59.50978
	Pericopsis angolensis	2	635.1547	0.0715	48.7381
	Pericopsis angolensis	3	705.816	0.0329	51.5591
	Pericopsis angolensis	4	485.4397	0.0583	35.94983
	Pericopsis angolensis	5	458.0546	0.0251	41.22491
	Pericopsis angolensis	6	653.6017	0.049	61.02253
	Pericopsis angolensis	7	446.4262	0.0674	47.27976
	Pericopsis angolensis	8	602.4339	0.0591	65.81293
	Pericopsis angolensis	9	646.0808	0.0349	68.04337
	Pericopsis angolensis	10	700.1631	0.0937	70.21854
	Pericopsis angolensis	11	653.6688	0.11908	90.81845
	Pericopsis angolensis	12	677.3476	0.05724	72.37202
	Pericopsis angolensis	13	418.3149	0.0582	55.05102
	Pericopsis angolensis	14	543.073	0.0941	45.71301
	Pericopsis angolensis	15	599.8902	0.06137	49.88818
	Pericopsis angolensis	16	557.3774	0.09413	64.77721
	Pericopsis angolensis	17	496.4116	0.0718	52.96259
	Pericopsis angolensis	18	578.7481	0.0813	55.79804
	Pericopsis angolensis	19	538.2839	0.09157	62.39031
	Pericopsis angolensis	20	540.1498	0.07473	52.01913
	Pericopsis angolensis	21	515.0867	0.03294	65.09609
	Pericopsis angolensis	22	516.3695	0.0652	47.99787
	Pericopsis angolensis	23	582.9202	0.0742	57.66284
	Pericopsis angolensis	24	346.8045	0.0947	54.43112
	Pericopsis angolensis	25	524.3958	0.0785	52.21726

6.2 Wet and dry miombo woodlands sites stand structure

Site	Species	Dbh (cm)	Basal area (m^2/ ha)	Relative basal area	Contribution to basal area (%)	Tree density (stems per ha)
Wet	*Brachystegia boehmii*	29.7	2.4	0.062	6.2	30.7
	Brachystegia longifolia	29.3	1.3	0.034	3.4	17.2
	Brachystegia spiciformis	26.4	1.4	0.037	3.7	22.3
	Erythrophleum africanum	20.2	0.05	0.001	0.1	1.1
	Pericopsis angolensis	20.7	1.0	0.025	2.5	21.6
	Brachystegia floribunda	26.5	1.1	0.029	2.9	17.6
	Marquesia macroura	23.5	5.8	0.154	15.4	110.2
	Isoberlinia angolensis	28.6	7.0	0.184	18.4	145.6
	Julbernardia paniculata	22.2	12.3	0.324	32.4	176.2
	Other species	12.0	5.6	0.15	15	346.7
Dry	*Brachystegia boehmii*	19.7	4.6	0.327	32.7	119
	Brachystegia spiciformis	14.7	2.4	0.17	17.0	108
	Erythrophleum africanum	14.1	0.2	0.011	1.1	9
	Pericopsis angolensis	11.5	0.2	0.016	1.6	16
	Other species	12.6	8.9	0.48	48	414