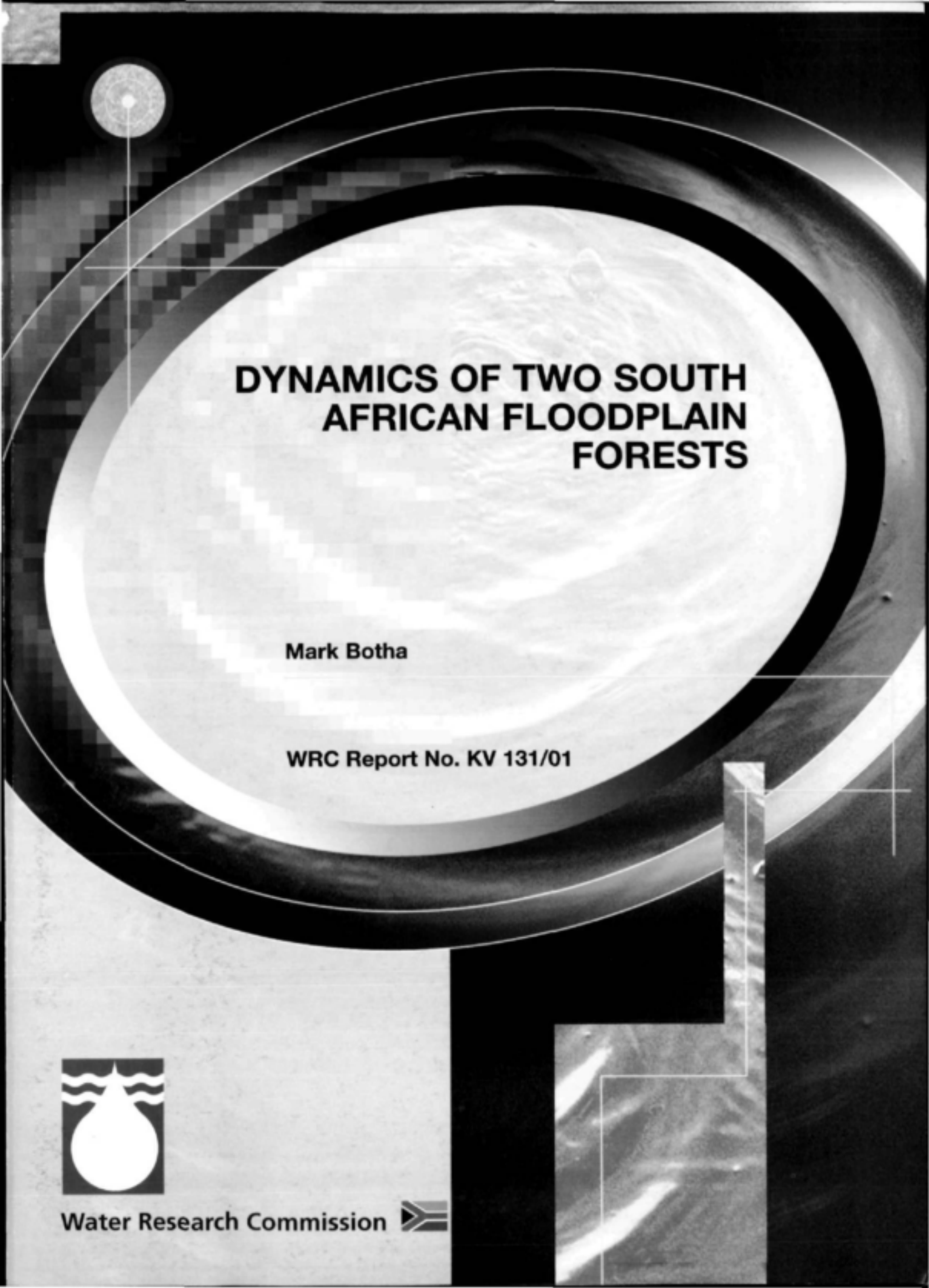

DYNAMICS OF TWO SOUTH AFRICAN FLOODPLAIN FORESTS

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Dynamics of Two South African Floodplain Forests

by

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Photo 1: The Luvhuvhu River at the height of the drought in 1992. Note *Faidherbia* saplings in leaf, and dying adult *Ficus* in middle background. Courtesy JM King.

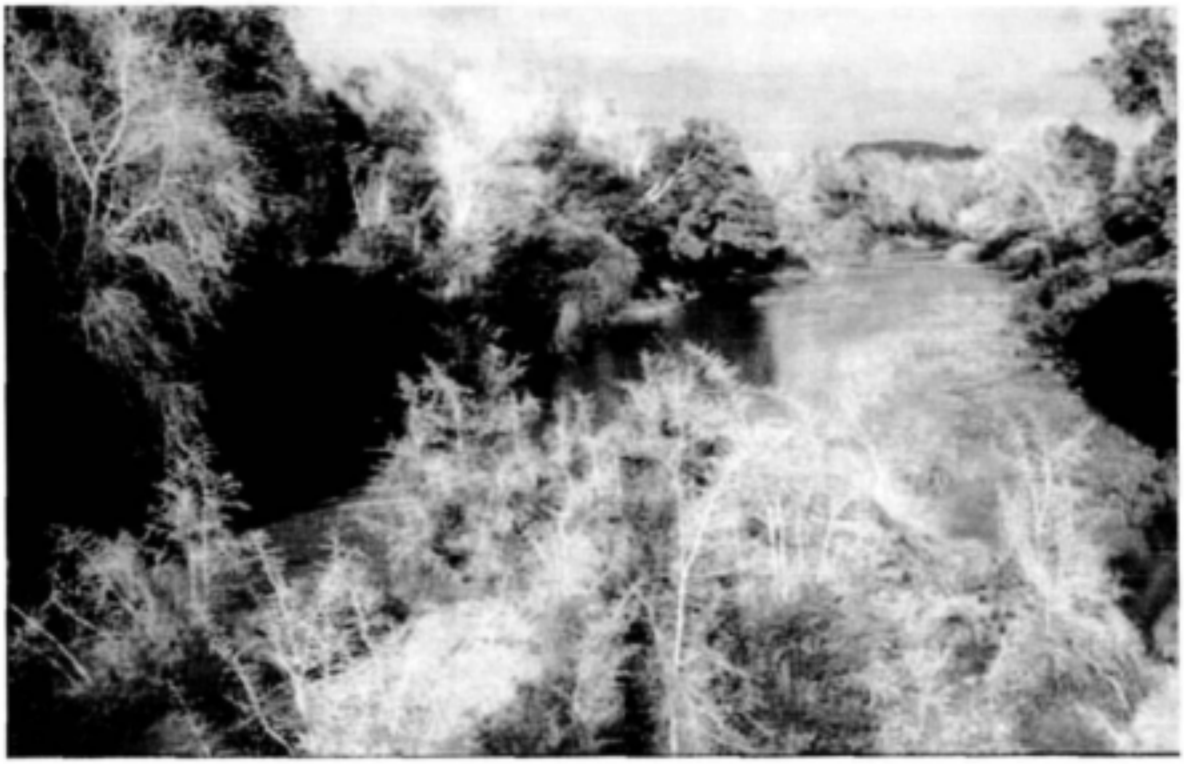

Photo 2: The Luvhuvhu in summer 1998 after good rains and year round flow. Adult *Faidherbia* on the banks have lost their leaves, but saplings (foreground) not.

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CHAPTER 1: INTRODUCTION

1. WHY STUDY FLOODPLAIN FORESTS?

Floodplain forests develop on low gradient rivers and are subject to the influence of river flow and ground water availability. They dominate many lowland rivers in the African tropics and are particularly important resources for animal and human communities.

Floodplain forests are some of the most enigmatic places in southern Africa. The characteristically tall, imposing trees cover significantly larger areas than the gallery woodland of other riparian systems and provide unique habitat for a host of other plant and animal species. They form the ecotone at the interface of two contrasting ecosystems, one driven by fluvial dynamics and river flow regimes, and the other by the harsh realities of semi-arid African savanna.

Riverine systems are an important component of landscape diversity because of the interaction of biodiversity patterns, disturbance regimes and environmental gradients therein (Ward 1998, Gregory *et al.* 1991). They stabilise migrating river channels and ameliorate hydrological extremes. Concern is growing over the degradation of riparian environments through upstream abstraction, impoundments, altered flood regimes and increased incidence of low flows (Louw 1994). These processes may lead to subtle or significant vegetation changes that will affect the understanding, management and conservation of these systems. This is particularly true in semi-arid environments where a functioning river is a vital source of water and nutrients for the maintenance of riparian biota, especially riverine forests (Louw 1995).

There remains, however, a lack of ecological understanding of riparian forests in Africa (Hughes 1988), especially tree regeneration requirements, community level patterns and water relations. The major determinants of tree distribution have yet to be fully elucidated for many riverine systems, particularly in tropical areas, and the potential consequences of changes in causal agents are unquantified.

More specifically, floodplain forests are interesting to study in that they display unique features, which may simplify investigation, compared to more heterogeneous bedrock affected river reaches (Birkhead *et al.* 1996). In particular, a gradient from waterlogged to xeric conditions allows direct analysis of environmental limitations on vegetation. The possibility of floods both facilitating tree establishment and drowning individuals raises interesting dilemmas for the life history strategies of riparian species. Floodplains are often highly dynamic systems raising questions about how river geomorphology interacts with individual species' biological attributes.

Floodplains are the more productive reaches of many river systems, and, thus, are globally threatened owing to their abundance of natural resources, good agricultural potential and water availability. This is no less so in Africa where significant population densities on most major floodplains (*e.g.* Nile, Niger, Zambezi) have completely altered prevailing vegetation patterns. Many forests enjoy no protection, and, even so, demands for access to natural resources in protected areas in southern Africa are increasing (Attwell and Cotterill 2000).

Background to this study

Recently, a significant number of unusual events have affected many rivers and associated riverine forests in southern Africa, such as large floods (1984, 1996) and the associated recruitment of Cluster Figs and Fever trees. Evidence of large-scale drought-induced tree mortality (Kuiseb River: Seely *et al.* 1981, Jobst 1996; Phongolo River: *pers obs.* and the Luvhuvhu River: van Coller - unpublished data) stimulated me to understand the nature of these floodplain forests, and the key factors governing their persistence. It may be easier to understand large demographic changes in floodplains, where they are often all too visible, than in other forests where these processes may be more cryptic. Whether these processes are caused or exacerbated by river management, dams and abstraction, is also a topic of great speculation. An investigation of the feasibility of damming the Luvhuvhu River in North East South Africa (Louw 1994) called for an easily replicable and rapid vegetation monitoring approach to determine the effects of managing river flow below the dam.

Furthermore, riparian systems are known to be important corridors for bird distribution (Wachtans *et al.* 1996). Floodplain forests, by virtue of their unique structure and diversity of niches and fruiting trees also provide a haven for a great variety of animals, especially birds (Hunter *et al.* 1987, Monadgem 1996). Many scarce species only make their way into South Africa along these river fringes. If the forests are somehow dependent on critical aspects of river flow, and if these are vulnerable to human or climatic disturbance, the tree communities may well change with time. This may have significant consequences for a multitude of sensitive or dependent animal species.

I chose to look at 3 floodplain sites (Pafuri on the Luvhuvhu River, the Fig Forest on the Mkuze River and Ndumu on the Phongolo River) that provide the best-conserved examples of floodplain forest in South Africa. They displayed very different forest communities, all were threatened by changes in hydrological regime due to dams or abstraction, had experienced significant stochastic events (either floods or droughts) but were sufficiently undisturbed by direct human intervention, being within protected areas. The site on the Phongolo River had to be abandoned halfway through the study due to unrest in neighbouring Mozambique and an aseasonal flood.

2. DETERMINANTS OF FLOODPLAIN ECOLOGY:

Gregory *et al.* (1991) and Carter and Rogers (1995) present hierarchical classifications of the determinants of riparian vegetation and the scale at which they operate (see **Table 1** for a modified classification).

In particular, two broadly related aspects appear to be primary determinants of floodplain vegetation: landform elevation and hydrology, and landform stability and sediment characteristics. At all sites I attempted to determine the impact of these on tree community structure and dynamics.

Landform elevation and hydrology

Many studies on floodplain forests have revealed that geomorphological factors and water availability are paramount in controlling plant and, particularly, tree distribution (Furness and Breen 1980, Hughes 1988, 1990, Rogers and van der

Zel 1989, Blom *et al.* 1990, Gregory *et al.* 1991, Bate and Walker 1993). Elevation above the river, as a surrogate for flood return frequency and inundation time, is widely viewed as the strongest determinant of vegetation (Hughes 1990). Floods may physically kill trees and seedlings, remove them through erosive forces.

Table 1. A hierarchical scheme of some key determinants and characteristics of floodplain vegetation (modified from Carter and Rogers 1995).

Scale domain	Determinants of riparian structure and dynamics	Vegetation characteristics or processes.
Biogeoclimatic region	Mountain system, geology, geomorphological history, climate	Biogeographic vegetation patterns Speciation and extinction
Catchment	Catchment area, shape, length, relief, longitudinal profile, geology, vegetation cover, landuse Hydrological regime, frequency, magnitude, duration, season of flow Sediment nature, yield, storage	Biome distribution Long distance dispersal
Reach/ section	Stream gradient, geomorphic history, channel width, shape. Sediment deposition, movement	Longitudinal variation in riparian vegetation pattern. Vegetation communities on different landforms Dispersal processes
Site	Bank slope, height, cross sectional elevation, dynamics of larger geomorphic features Local geomorphological processes, erosion and deposition Supra-annual hydrological regime	Vegetation patch formation, dynamics Succession Scour, undercutting and burial
Patch/ landform	Landform (*e.g.* channel bars, levees) altering geomorphic processes Annual flow patterns, variability and flood characteristics	Plant life history characteristics: dispersal, establishment, and local extinction. Patch interactions, replacement events, and evolution. Herbivory Habitat characteristics: cover, height, turnover
Cell/plot	Local hydrological conditions Sediment nature, infiltration	Individual growth, reproduction and mortality Succession and competition, modification of light, nutrient, flow, sediment, thermal regimes Sediment stabilisation and aggradation
Point	Sediment chemistry, hydraulics	Seed deposition, germination, establishment Physiological processes

bury them under sediment (Everitt 1968), drown them through submergence (Blom *et al.* 1990), or create new conditions for establishment (Walker *et al.* 1986) and replenish soil water and bank aquifers (Hughes 1990, Bate and Walker

1993). Elevation above the riverbed may also determine access to ground water (Hughes 1988), and sediment characteristics (Dunham 1989).

Landform stability and sediment

Geomorphic processes lead to the formation of different landforms under different conditions (Everitt 1968). Active channels have rapidly aggrading channel bars, terracing and meander cuts. Inactive channels show greater build-up of levees and sandbars, leaving more opportunities for tree establishment and community development (Hughes 1990). This would have a profound effect on the persistence of tree communities and the potential for any successional development within a stand.

The role of substrate (sediment) in determining tree distribution along floodplains is not fully understood, and the literature reveals conflicting reports of its importance (see for example Dunham 1990 and Furness and Breen 1980). Landforms formed from coarse sediment are less stable and will become waterlogged more rapidly at low elevations and desiccate more quickly higher up on the channel profile. This will have massive implications for seedling establishment and rooting characteristics. Finer sediments will be more stable and nutrient rich and may be more suitable for seedling establishment, thus leading to denser tree stands and increased competition for space and light. The interplay between fine and coarse sediments may therefore be a strong force structuring floodplain communities (Hughes 1990).

Other factors to be considered

However, other factors such as light availability, nutrients and desiccation may be more important on a local site or patch scale (Walker and Chapin 1986). The differential importance of selective forces on adults and saplings is unknown and only recently have attempts been made to clarify this (Hall and Harcombe 1998).

The sensitivity of floodplain systems to altered flow regimes is also largely unknown (Dunham 1990, Nilsson 1992), specifically those in stochastic environments with unpredictable rainfall and flooding frequencies (Hughes 1988). The consequences of a river becoming seasonal (from an originally perennial state) due to abstraction or damming are little investigated in Africa, although rivers are now drying up more frequently. Almost all suitably large rivers in South Africa have been dammed, and impoundments on other African rivers have severely impacted natural processes (Davies *et al.* 1993) and vegetation, although this remains to be fully documented.

Floodplain forests may be good indicators of river "health". By virtue of their very low relief and subsurface water regime, they should respond significantly to the full spectrum of changes in flow characteristics. Thus, they could be used to indicate subtle changes that may be less visible in higher reaches. Changes could be manifested in the altered composition (structure or species) of the forests that dominate the lower reaches. Moreover, if the effects of flow regime on vegetation are understood, it may be possible to manage river flow below impoundments to maintain ecosystem integrity or a desired river state (*e.g.* Rogers and Bestbier 1997). If stream fauna, such as fish, require flooding at a certain time of year for spawning (say mid-late Summer), then this could be simulated with dam releases. The Phongolo River in northern KwaZulu-Natal provides a sad example of managed river flow where the ecological requirements of the riparian system have been subverted to the short-term economic needs of politically powerful farmer lobbies. In this instance, unseasonal water releases to prepare land for planting may seriously disrupt floodplain ecology.

2.1 Research outside Africa

Schnitzler (1997) reviewed the concept of river dynamics as a forest structuring process, but its application has mostly been limited to Northern Hemisphere and temperate catchments. Other European workers have looked at the effects of regulation on riparian and bottomland vegetation (Nilsson *et al.* 1991) and concluded that although regulation had little effect on river form and mean annual runoff, species richness and canopy cover were significantly lower on regulated river-margins. This was correlated with water level regime, presence of pre-regulation margin vegetation, height of river margin and annual discharge (Nilsson *et al.* 1991).

North American work has concentrated on the floodplains of the Mississippi-Missouri drainage and associated bottomland hardwood forests, as well as Alaska (Walker *et al.* 1986) and East Texas (Streng *et al.* 1989). A well-developed understanding has emerged of the effects of flow regime on forest processes (see for example Bradley and Smith 1985, Hall and Harcombe 1998) and succession and community dynamics (Everitt 1968, Jones *et al.* 1994, Hughes and Cass 1997). Frangi and Lugo (1985) studied ecosystem processes in moist subtropical floodplain forest in Puerto Rico, and concluded that periodic flooding, poor soil aeration and mesic conditions were the driving forces of forest functioning.

Besides abiotic determinants, only a few authors have analyzed the contribution of biotic forces on community composition. Walker *et al.* (1986) investigated abiotic selective pressures on different tree ages, combining physical controls with a successional approach, and determined the role of life history processes in succession. Jones *et al.* (1994) found that seedling survival was unrelated to seed size or dispersal, but correlated with time of germination and flood regime in four South Carolina floodplain forests. Shade tolerance and other life history traits explained most of the variation found in seedling distribution. Hall and Harcombe (1998) showed that although seedling flood tolerance was a good indicator of their distribution on a Texan floodplain, this was not correlated with published seedling light requirements. This shows that seedling location in relation to light availability was modified by species-specific response to flood tolerance.

2.2 Review of African Research

Hughes (1988, 1990) reviewed our current understanding of floodplain forest functioning in Africa and outlined the main environmental variables responsible for tree distribution. She delineated forest distribution patterns along the Tana River in Kenya, relating them to an elevation gradient above mean river height from which inundation frequencies for each forest type were calculated. The distinction between *Acacia* type and broad-leafed evergreen forest was made, and the latter was further classified according to its position in the macro channel, *i.e.* active or inactive levee forest. However, little experimental research on recruitment, succession and temporal dynamics of these forests was carried out. Predictions of the effect of changed flood regimes, due to impoundments or abstraction, were necessarily largely descriptive. Flooding is often seen as the major driving variable in the dynamics of lowland rivers (Davies *et al.* 1993) in southern Africa.

Dunham (1989, 1990), working on the floodplains of the middle Zambezi, used a chronosequence approach to investigate woodland dynamics through aerial and fixed-point photograph analysis, and described vegetation communities with environmental correlates. These were primarily related to sediment type and flooding frequency, but no investigation into mechanisms of establishment, or causes of species patterns was carried out. A floristic analysis was used that incorporated trees, shrubs and annuals that respond to different habitat variables and temporal phenomena. Recognition of the influence of herbivores, termites and fire, and detailed tree mortality indices, were important contributions in understanding the demographic characteristics of some riverine species.

The vegetation of the Phongolo River was described by Furness and Breen (1980), who related the occurrence of different vegetation types to water levels in this storage floodplain. The influence of a high flood level, and maximum pan retention level as determinants of forest distribution was shown, but no mechanisms or consideration of establishment, regeneration or temporal dynamics were given. Forest pattern was discerned at a broad analytical scale and therefore no subtle floristic differences in forest types were observed. De Moor *et al.* (1977) and Pooley (1978) constructed a physiognomic classification of the vegetation of Ndumu Game Reserve, which included riparian communities along the Phongolo River.

As part of the Kruger National Park Rivers Research Programme (Breen 1989, Breen *et al.* 1995), Carter and Rogers (1995) used Markovian modelling to study landscape change in 5 rivers, looking at catchment scale variables that might explain landscape structure and transitions between different states. Although this ignored vegetation subtleties at the community level, and did not propose detailed biological mechanisms for the transitions, it was a useful step in identifying causal agents of riparian change. Some of the proposed successional pathways or state transitions are probably not valid for all rivers under study (*e.g.* the transition from reeds and/or bedrock to forest is not applicable on the floodplain reaches of the Luvhuvhu). Bredenkamp and van Rooyen (1993) compiled a phytosociological study of the Kruger National Park reaches of the

Luvhuvhu River for an Instream Flow Requirements study. Van Coller (1993) and McKenzie (in prep), studied vegetation-environment relations and the regeneration niche along the Sabie, a bedrock influenced, complex-channel type river in the southern Kruger Park. It is expected that this programme will provide valuable insights into the physical environmental determinants of riverine vegetation in Kruger National Park, and offer useful insights into options for water and conservation managers.

South African forests studied differ in several crucial respects from those of Europe and North America. The prevailing semi-arid environment places strict controls on tree growth rate and establishment, whereas in mesic systems the forests may be less dependent on river influence (Hughes 1988). Further, in mesic systems, the river serves to limit or facilitate establishment, but in arid regions, it may be crucial for adult persistence as well as seedling survival. Birkhead *et al.* (1996) were the first to attempt a water budget for an African riparian system, determining absolute tree requirements through transpiration analysis to further our understanding of instream flow requirements for trees. Roupsard *et al.* (1999) looked at environmental factors and water use of *Faidherbia albida* (Del.) A. Chev, although not in a floodplain context. Both studies highlighted tree dependence on the water table and the latter observed a facultative use of surface soil (rain) water when available. However, it is uncertain of what consequence these mean or equilibrium conditions are for juvenile establishment or long term adult persistence.

2.4 What's missing from the picture?

Despite a sizeable amount of research into African riparian systems, there still appear to be some fundamental gaps in our understanding, discussed below in the following themes:

Demographic analysis

Studies of floodplain vegetation have tended to be phytosociological (*e.g.* Pooley 1978, Bredenkamp and van Rooyen 1993, Smith 1998). No demographic studies have been published to date for South African floodplains. A better understanding of the life history stages limiting a population can be gained from an analysis of its age structure (Walker *et al.* 1986B). If a population is strongly cohorted, this may indicate that certain cues or events are required for seedling recruitment. This is relatively easy data to collect and can be useful for monitoring certain species, but its utility for long lived, persistent species is doubtful. Although there may be problems with naïve use of demographic data, I have attempted to keep sampling groups coarse and kept the technique as robust as possible (White 1980). If limiting life history stages are known, investigation can highlight whether this is due to seed numbers, viability, germination, seedling establishment, sapling survival or adult vulnerability. These factors may then be related to critical environmental factors that may have to be managed if specific conservation goals for forests are to be met.

Succession

Biotic processes may also determine vegetation patterns, in particular successional change due to facilitation. Succession involving long-lived species in stochastic environments is difficult to study, except through space-time substitution techniques (Terborgh *et al.* 1996), aerial photography or population structure analysis of pioneer species (Walker *et al.* 1986B, Shackleton 1993, van Wyk *et al.* 1996). This has seldom been attempted on rivers in Africa (except see Dunham 1990), although much work has been done elsewhere on colonising species (Everitt 1968, Walker and Chapin 1986). Some studies (Jones and Sharitz 1989) suggest that flooding inhibits recruitment of all but a few species, whereas this process may be crucial for establishment of others. If so, pioneer species would show strongly cohorted demographies, after responding to a particular flood event, which would be reflected in any demographic analysis.

By ignoring successional aspects of vegetation description, it is unknown whether the different communities are merely seral in nature, or if they reflect absolute differences in governing variables. Further, the nature of succession is important if tree community dynamics are to be understood and managed. If succession (vegetation dynamics) is geomorphologically driven or sediment controlled, this will be important over long time scales, or on actively incising (or meandering) rivers. However, in mesic or inactive systems it may be mediated by flood patterns or biological constraints such as light availability.

Plant water relations

Most studies in arid-zone Africa have ignored the seemingly fundamental hydrological controls of water availability, including movement in sediment, and depth to the phreatic zone, on tree distribution. Hughes (1988) mentions that distribution of vegetation is often determined by flooding, but total forest extent is related to depth to the water table. Plant/water interactions have mostly been conducted on species with agroforestry potential in Africa (Roupsard *et al.* 1999), and sometimes in areas where falling groundwater levels have threatened tree populations (Bate and Walker 1993, Jobst 1996).

Flow regimes and flooding effects

Floodplain forests occur on different river systems with an enormous range in flow regimes, making it unclear which hydrological aspects or factors may be crucial in determining forest structure. Other African systems studied have much longer flooding duration and higher base flow rates than the rivers investigated in this study. The Tana River (Kenya) has a mean annual discharge of 6000 million m^3 (Hughes 1990), compared with only 500 million m^3 for the Luvhuvhu (Louw 1995), although flood peaks are similar. A peak of 3570 m^3/sec has been measured for the Tana, compared to 11000 m^3/sec for the Phongolo, 3150 m^3/sec for the Mkuze, and 3400 m^3/sec for the Luvhuvhu (van Bladeren 1996). From a tree population perspective, the effect of these massive floods and their frequency is unknown. Similarly, the incidence and effect of mid-size floods in tree germination requirements, and water table recharge is also similarly undetermined.

3. AIMS AND OBJECTIVES:

With the primary aim being to contribute to the knowledge of riverine forest systems, and their conservation in a management context in South Africa, the goals of my thesis are the following:

1- Test paradigms or working hypotheses that assist in understanding the dynamics of floodplain forests. If we have a better understanding of the dynamics of these systems, river managers and conservationists could possibly identify problems threatening the persistence of tree populations forming floodplain forests, or the effects of other abiotic factors on their functioning. Four working hypotheses are elaborated on below.

2- Determine to what extent these are event driven systems, and which features of the events are important in structuring forest communities. If these forests are not in equilibrium with reigning environmental regimes, then this poses significant challenges to stable state ecosystem management that might be dominated by equilibrium principles. Alternatively, if environmental or climatic events are important in structuring floodplain forests, and features of these events can be manipulated, then managers have the ability to ensure that vital features are not removed from flow regimes. Events resulting in recruitment or mortality would probably be visible in the populations structures of long-lived trees.

3- Investigate which biophysical factors are limiting forest expansion or tree recruitment. Experimental evidence of environmental variables' influence on tree populations is crucial to support hypotheses concerning floodplain forest functioning or proposed management actions that would alter flow regimes.

4- Infer vegetation change from an understanding of the influence of hydrological regime on plant recruitment and forest succession. By analysing past distributions of forests, the effect of specific events, and of the influence of abiotic variables, it would be possible to make predictions of the likely impacts of future changes in these governing factors on forest distribution and population dynamics.

3.1 Working hypotheses:

Riparian communities and their dynamics are a complex interaction between their history (including successional stage) and the environmental determinants of a floodplain (including flow and hydrological regime, sediment characteristics, water availability and herbivory). The following hypotheses for riparian vegetation pattern and process are drawn for South African floodplain forests:

1. Adult distribution and niche differentiation will be dependent on dry season water availability and water stress tolerance.
2. Distribution patterns may be determined by flood tolerance, with sensitive species only found at high elevations on the floodplain.
3. Recruitment of pioneer colonising species is dependent on hydrological constraints and sediment conditions in semi-arid areas.
4. Forest dynamics will be determined by geomorphological factors in dry or actively eroding areas, and by biological processes in stable or mesic areas.

4. THESIS STRUCTURE:

This thesis is divided into 5 chapters, beginning with this Introduction. Each of the chapters is meant to stand alone, so there is some measure of repetition, and abstracts for each in place of a thesis summary. Figures in a chapter are referred to in **bold**, and figures elsewhere in normal type.
In Chapters 2 and 3 vegetation communities are described for the Mkuze and Luvhuvhu Rivers, respectively, and correlated with environmental variables. Certain dominant canopy species are linked with specific factors. The communities described provide a backdrop to investigate vegetation dynamics or succession. Analysis of demographic replacement patterns determine if fluvial geomorphic features or successional processes determine community patterns.

Chapter 4 investigates the coexistence of four Acacia species on the Luvhuvhu floodplain at Pafuri. Life history traits are invoked to explain distribution patterns. Abiotic controls on tree distribution are studied using the water relations of dominant trees and their flood tolerance.

The final Chapter synthesises our current understanding of the functioning of these floodplains, their governing environmental factors and dynamics. The effects of altered flow regimes are then considered and recommendations made for floodplain management and instream flow requirements of floodplain vegetation.

5. APPROACH AND METHODOLOGIES.

This study has employed a hierarchical approach that aims to bridge the gap between systems understanding (*i.e.* landscape level abiotic determinants), community dynamics (*i.e.* looking at distribution and succession) and population biology (*i.e.* investigating limiting life-history factors). This can be used to test the predictions of the working hypotheses by determining which level of understanding best describes observed tree community patterns.

Riparian vegetation is often described in relation to surrounding upland communities, which necessitates a coarse sampling approach (*e.g.* Smith 1998). I chose to only examine those communities under direct riparian influence and situated on alluvial sediments.

Monitoring and goal driven management aims in conservation require simple techniques that can be deployed rapidly to ascertain ecosystem integrity or the outcome of a specific management action or natural event. My study, wherever possible, uses methodologies that are easily adopted by river or conservation managers. The methods used for determining tree population dynamics and community structure are uncomplicated and easily replicable, but the tests for abiotic factors governing tree growth rely on technology unavailable to field personnel and conservation managers. Rule based models are being developed for other rivers in the Kruger National Park (McKenzie J. *pers comm.*). This thesis, however, concentrates on collecting baseline ecological data to aid in a more complete understanding of the system, and subsequently, to feed into those models.

6. TERMINOLOGY

Many different researchers in different systems have used terms in subtly different ways. I have defined or explained them upfront to avoid confusion.

- Forest and woodland will be used loosely as the distinctions are not important for this study.
- "Riparian", "riverine", "gallery" are terms used to define vegetation in all reaches of the whole catchment, whereas "alluvial", "bottomland" and

"floodplain" refer to true floodplains, usually in the lower reaches of a river (Hughes 1988).

- "Habitat" is used in a broad sense to incorporate any specific environmental requirements of a particular species.
- "Dynamics" and "succession" both refer to vegetation change. However, the latter term is used in this thesis to denote seral replacement of communities, while the former describes physically or geomorphologically mediated change in community or species composition.
- "Events" are defined as important changes in the baseline characteristics of a dominant abiotic variable over a relatively short time. A flood, an aseasonal drought, or flow cessation for whatever reason, are classified as events.
- Different spellings of river names result from colloquial usage. There is no accepted form for each, but consistency will be applied.

7. NOTATION

- Discharge (Q) of rivers is measured in cumecs ($m^3.s^{-1}$) or million cumecs ($Mm^3.s^{-1}$).
- Delta notation (δ) is used for isotopic concentrations and is defined as the proportion of the isotope in question to that occurring naturally in a fixed standard (usually Standard Mean Ocean Water, (SMOW) for H and O; and Pedee Belemnite (PDB) for C) and is denoted by δH, δO and δ^{13}C respectively. It is measured in parts per mil ($^{o}/_{oo}$).

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Chapter 2: THE MKUZE FIG FOREST.
TREE COMMUNITY DESCRIPTION AND DYNAMICS.

ABSTRACT:

To investigate floodplain tree community structure and regeneration patterns, twenty-five transect plots were sampled in the Mkuze Fig Forest, Maputaland. Classification and ordination of transect data both revealed four major community types; *Acacia xanthophloea* woodland, regenerating *Ficus sycomorus* stands, mature *F. sycomorus* forest with evergreen understorey and a diverse Evergreen forest. Detrended Canonical Correspondence Analysis (DCCA) revealed weak environmental correlates of the community types. This could be due to low variation in sediment types and landform height above the river. However, a strong indication of succession was noted, with regenerating stages of one community type being found underneath mature stages of another type. Previously published floodplain forest determinants, such as stand height and sediment type, were poor predictors of vegetation patterns observed. Distance away from the river did explain some variation, but this could be spurious because the channel has recently switched from a previous position. Evergreen forest represents a climax or late successional stage.

Large flood events appeared important to initiate establishment of *F. sycomorus* and *Acacia xanthophloea*, and their effects are indicated by the occurrence of early seral stages of these species in previously flood-affected areas.

INTRODUCTION:

Floodplain forests and associated woodlands have been described by several authors on the alluvial areas of the Maputaland coastal plain (De Moor *et al.* 1977, Pooley 1978, Furness and Breen 1980), and elsewhere in Africa (Hughes 1988, Dunham 1989, Bredenkamp and Van Rooyen 1993).
The Mkuze river forms an alluvial fan on a large broad floodplain (8km X 4km wide) where it meets the Maputaland coastal plain (27° 40'S, 32°20'E). It lies only 15 km South of the Phongolo River floodplain, but flows in the opposite direction to empty into Lake St Lucia. This fan appears to be stable or aggrading and therefore provides scope for forest development after initial sediment colonisation (Watkeys *et al.* 1993). The climate is sub tropical with an average 650 mm rainfall p.a. and mean maximum temperatures of 27°C (Mkuze Game Reserve research office records).

The forest occurs on the fan where the river enters Nsumu pan and is dominated by tall *Ficus sycomorus*, underlain and interspersed with other broad-leafed species. At the edges of the fan, groves of *Acacia xanthophloea* mark the limits of relatively recently deposited alluvium and inundation. The river once meandered through the forest but has now re-occupied an original channel on the western edge. The channel in the middle of forest was abandoned during cyclonic flooding in 1984. There is little lateral erosion and thus a lack of meandering disturbance. Almost all forest North of the river and outside the Mkuze Game Reserve has been burnt, felled or cleared for agriculture.

The ecological processes responsible for structuring riverine forests are important to understand if we are to manage the catchments and rivers that sustain them. Among the factors considered most important in delimiting forest communities are stand height above a river (which can be construed as flood return time), soil type and sediment age (Hughes 1988, Dunham 1990).

Riverine vegetation classifications of Maputaland conducted thus far describe two canopy tree communities consisting of a microphyllous association (usually *Acacia xanthophloea*, the fever tree) and a broad-leafed forest often including *Ficus sycomorus* (Pooley 1978, Furness and Breen 1980).

Furness and Breen (1980) hypothesised that there is very little sediment control of vegetation type on the Phongolo river, and showed communities were best correlated with height above a maximum retention level on this storage floodplain, and less well with height below a maximum flood level. This implies that duration of flooding is crucial, with *A. xanthophloea* more tolerant than *Ficus sycomorus*. Hughes (1990) and Dunham (1989) corroborate this for other *Acacia* and riparian species. De Moor *et al.* (1977) undertook a quantitative physiognomic survey of the Ndumu Game Reserve, on the Phongolo River, and therefore their forest communities did not correspond with the floristic approach of Furness and Breen (1980).

Hughes' (1990) study of the Tana river in Kenya shows that forest type is well correlated with flooding frequency and duration, and underlines the importance of landforms or geomorphological units (*e.g.* active levees, point bars, oxbows) in the spatial distribution of forest types. Dunham (1990) confirms this by showing that floodplain woodland type is closely related to frequency of inundation and sediment (topsoil) characteristics. He noted *Faidherbia albida* (syn. *Acacia albida*) saplings recruiting in the lower lying sandy bars, and mixed woodland with canopy *Faidherbia* further away from the river.

Studies of floodplain forest dynamics elsewhere in the world have centred on Europe (see Schnitzler 1997 for review, Nilsson *et al.* 1991), the USA (Hughes and Cass 1997) and the Mississippi drainage in particular (Everitt 1968) and Alaska (Walker *et al.* 1986, Walker and Chapin 1986). Terborgh *et al.* (1996) showed through canopy tree frequencies that Amazonian floodplain forest communities were not a random assemblage of species, intimating that successional features, and competitive exclusion, were important in structuring tropical floodplain forest communities. Jones *et al.* (1994) showed that seedling survival was dependent on time of germination in relation to the flood regime, and seedling distribution was determined by shade tolerance.

As regards dynamics of African floodplains, Hughes (1988, 1990) and other authors (*e.g.* Davies *et al.* 1993) have noted the lack of data on regeneration and, in particular, pleaded for more information on succession. Dunham (1989) recorded, from point photographs, the loss of *F. albida* canopy individuals on the

Zambezi in the post Kariba dam period from 1963 to 1989, but could not link seedling establishment to a previous flood regime.

Schnitzler (1997) proposed a classification of fluvial driven forest dynamics in a mosaic of 5 stages: The **innovation** stage is the colonisation of newly deposited or opened substrates. A **pre-equilibrium** stage, up to canopy closure, the duration of which depends on site stability. An equilibrium or **climax** stage, which may persist for thousands of years in Europe, where internal forest processes are dominant. An **elimination** stage where mature trees senesce and die back and finally a stage of **collapse**, where the area is opened up for further invasion. These stages will be alluded to later in the context of successional seres.

The aims of my study were:

1- Describe the canopy tree communities in the Fig Forest, Mkuze Game Reserve. This would determine if the physiognomic investigation of previous authors would result in similar floristic assemblages, and would provide useful communities for an analysis of successional tendencies in the forest ecosystem.
2- Determine any correlation of these with environmental factors. If specific communities could be related to governing variables or certain elements of flow regimes, then an understanding of their response to changes in the hydrological system could be gained. If little correlation is found, then other forces, possibly biotic, could be responsible for determining forest and community structure.
3- Collect and analyse regeneration data to determine successional tendencies. Regeneration data could be used to identify the effect of climatic events on certain tree populations in the forest or different species' seedlings' response to limiting factors such as light availability. This would influence forest structure through altered successional patterns.

METHODS:

Sampling:

The reserve managers (KwaZulu-Natal Nature Conservation Services) have established a grid system of cut-lines through the fig forest, for alien plant monitoring and control (**Photograph A**). I sampled 27 randomly selected transects, each 50m by 20m long, 10m in from each cut-line. This size ($1000m^2$) was chosen to exploit the linearity of the grid system, and to avoid crossing potential tree community boundaries.

In each transect all woody individuals, regardless of their origin (*i.e.* seed or suckering), were enumerated and grouped into the following functional size classes:

Table 1: Size class groups and their definitions used in all transect sampling.

Class 1	Germinants and seedlings, less than 20cm high and apparently reliant on seed reserves only (*i.e.* showing thin stems and short internodes)
Class 2	Seedlings and suckers over 20cm but less than 1m high, which appear to have survived at least one dry season. Fast growing species (*F. sycomorus* and *A. xanthophloea*) may reach this stage in one growing season.
Class 3	Saplings between 1 and 3m high, which have survived several dry seasons.
Class 4	Saplings greater than 3m high, but less than 10cm diameter at breast height (dbh).
Class 5	Small trees between 10 and 20 cm dbh
Class 6	Young trees between 20 and 30cm dbh
Class 7	Trees between 30 and 50 cm dbh
Class 8	Mature stems between 50cm and 1m dbh
Class 9	Mature stems over 1m in dbh

Figure A: The Mkuze Fig Forest, showing the thicket understorey layer and open canopy of the *Ficus* community.

Figure B: The author and Andrew Skowno on one of the transect cutlines in the forest.

Canopy cover was estimated for each plot, and ground cover was determined through 5 (one metre square) subplots in each transect. An index of shrub density was determined as the percentage of a 1m square card obscured when viewed at 2m above ground from the end of the transect.
The height of each transect above the nearest section of river was determined from the accurate 1:10000 orthophoto map of the forest (Map 2732CB nos.17, 22. Dept. Surveys and Mapping, Mowbray, Cape Town). As there is very little topographical variation in the forest, height levels were corroborated with an inclinometer and measuring staff to a known base level of the river. Soil texture in each transect was determined by a simple moist rolling test and recorded as sand, clay or silt.

Analysis:

To determine replacement patterns and if succession is occurring, size class data per species per transect were allocated to one of three demographic groups:

- Recruiting individuals- size classes 1 to 3, *i.e.* up to 3m tall and less than 10cm diameter at breast height (dbh).
- Sub-canopy and replacement size classes 4 to 6, *i.e.* between 10 and 30cm dbh.
- Canopy trees- classes 7 to 9, *i.e.* over 30 cm dbh.

Exceptions to this were *Ficus sycomorus*, where the lower limit for mature trees was raised to 50 cm dbh, (Mature trees in size classes 8 and 9 only). For *Celtis durandii* the limit was lowered to 20 cm dbh, *i.e.* mature tree were in size classes 6,7,8 and 9. This was felt to be a more accurate reflection of each species' growth pattern.

I considered cohortedness (a predominance of one size class or group) to indicate event-driven recruitment. A species was recognised to be cohorted by counting the number of times the proportion of stems in each demographic group was greater than 80% of that species' total in each transect, and if this occurred in at least 70% of transects in which that species occurred. Transects with less than 10 individuals of that species were omitted to avoid small sample biases.

Two Way Indicator Species Analysis (Hill 1979) was used to classify the grouped transect data into woody vegetation communities. The number of stems in a transect was used as species importance values, and cut levels were set at 0, 20 and 80 for the algorithm. Division of groups was done using the following parameters: a minimum group size of 3 sample transects and up to 10 indicator species per division, with only 3 levels of division.

Indirect gradient analysis was used to ordinate the grouped data (*i.e.* recruiting, sub canopy and canopy individuals- after the methods of Everard *et al.* (1995) and van Wyk *et al.* (1996)) and to identify any correlation between vegetation type and environmental variables. Detrended Canonical Correspondence Analysis with down weighting of rare species was performed using the software program Canoco for Windows (ter Braak and Smilauer 1999). The variables considered were sediment type, height above and distance away from the river, and the percentage of ground cover. No down-weighting of rare species or data transformation was used. One group (*Acacia xanthophloea* seedlings) significantly altered the relationships between the remaining groups. As these samples were located on the very fringe of the forest they were omitted from the analysis.

Community dynamics.

Size class distributions were constructed in each of the different community types by summing the transect data for each species in that particular community. Community successional patterns (after Everard *et al.* 1995) were inferred from a perusal of the ordination plot and the size-class distribution data (recruiting, sub-canopy and canopy individuals) in each community.

Once each transect was allocated to a tree community (see Appendix **Table B**), further environmental data were collected for each community. Photosynthetically active radiation (PAR) was recorded at ground level with a SKYE Instruments SKP 200 light meter, using its PAR quantum sensor in the 400-700nm band. Ten measurements in each community in summer (February) were taken between 11h00 and 13h00 and the highest and lowest discarded. For each shade tolerant species, ambient light levels were measured at ground level alongside 3 different clusters of seedlings in the darkest shade to determine the minimum requirements for survival.

RESULTS:

Classification analysis revealed four major tree community types. *Acacia xanthophloea* woodland; immature *Ficus sycomorus* stands; Mature *F. sycomorus* forest with a deciduous and evergreen understorey and a broad-leafed, evergreen forest with evergreen understorey (Appendix **Table A**). The first division (Eigenvalue = 0.495) separated transects dominated by *Acacia* and recruiting *Ficus* from all others. The second division (Eigenvalue = 0.159) further separated recruiting and sub-canopy *Ficus* from *Acacia* dominated areas. The broad-leafed groups were separated into canopy *Ficus* (with *Celtis* and *Rauvolfia* in the understorey) and *Blighia* and *Trichilia* canopies (Eigenvalue = 0.320).

The ordination plot (**Figure 2**) confirmed the segregation of communities clustering them in ordination space, and displayed rather weak environmental correlates. As the gradient lengths tended to approach 4, a DCCA was considered justified. Axis 1 (Distance away, Eigenvalue 0.735) separates the broad-leafed from the *Acacia* and young *Ficus* communities, and this explains 32% of the variation. The communities did not correlate well with other environmental factors. There was no significant correlation with soil type. Predictably, percentage ground cover decreased with greater evergreen species abundance and must be seen as a co-variable in older stands as it is heavily influenced by canopy structure.

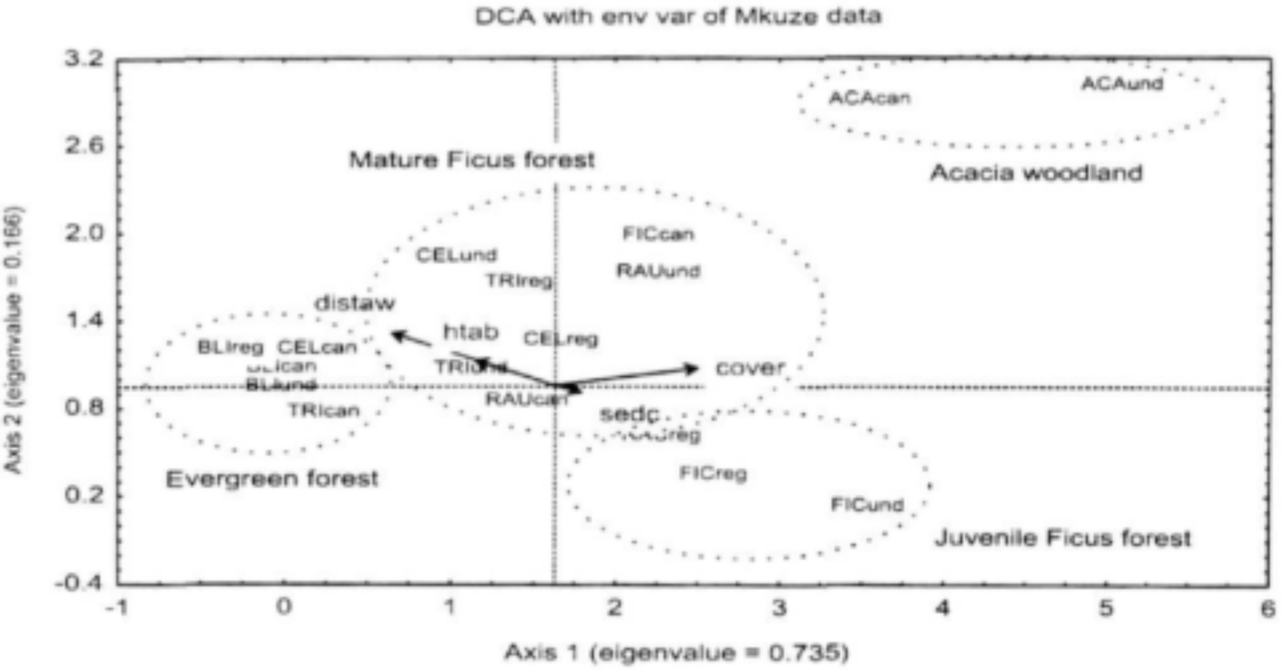
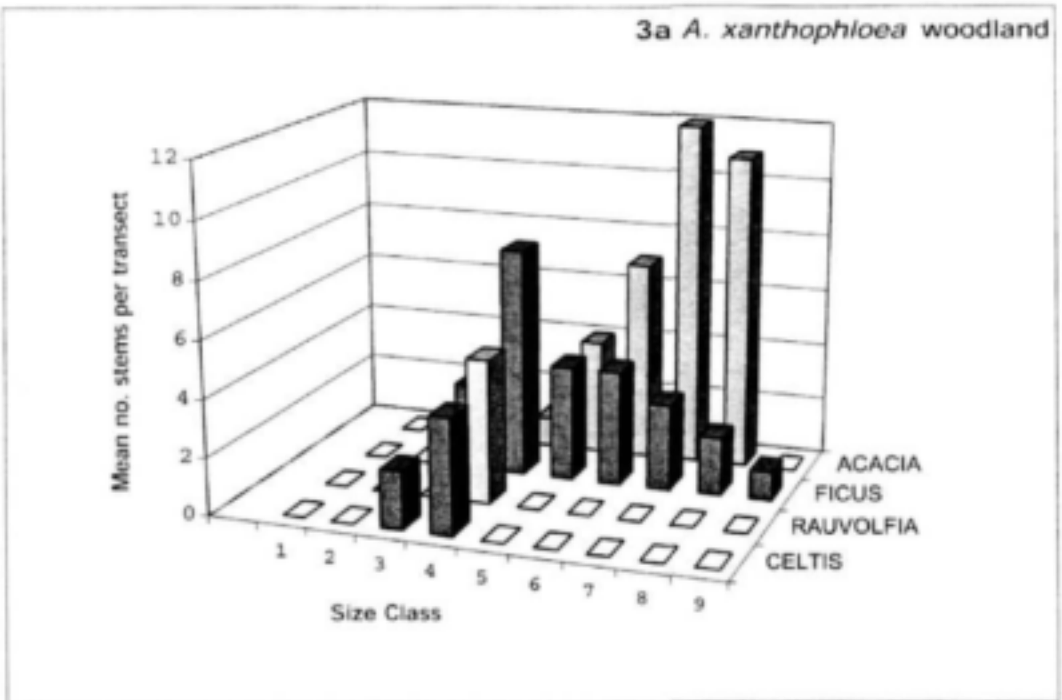


Figure 2: The four communities in ordination space. Species are denoted by the first three letters of the Genus name, and demographic group by regenerating (reg), understorey (und) and canopy (can). A successional trend is evident from regenerating *Ficus* stands through adult *Ficus* with an evergreen understorey, to a mixed evergreen broad-leafed forest, with *Blighia unijugata, Trichilia emetica* and *Celtis durandii*.

Acacia xanthophloea showed a narrow range of size classes in any single community type (**Figure 3a**), and adults were cohorted according to the definition above. The only other demographic groups that can be classified as cohorted were Understorey *Ficus* (**Figure 3b**) and Regenerating *Blighia*. The latter can be omitted, however, as many of the small stems are resprouts and the high numbers of shade tolerant seedlings distort the analysis.

Broad-leafed and shade tolerant species, particularly *Blighia unijugata, Celtis durandii* and *Rauvolfia caffra* displayed a more typical inverse J distribution (**Figure 3c and 3d**), with the recruiting classes (*i.e.* 1, 2 and 3) contributing up to 80% of total number of stems.



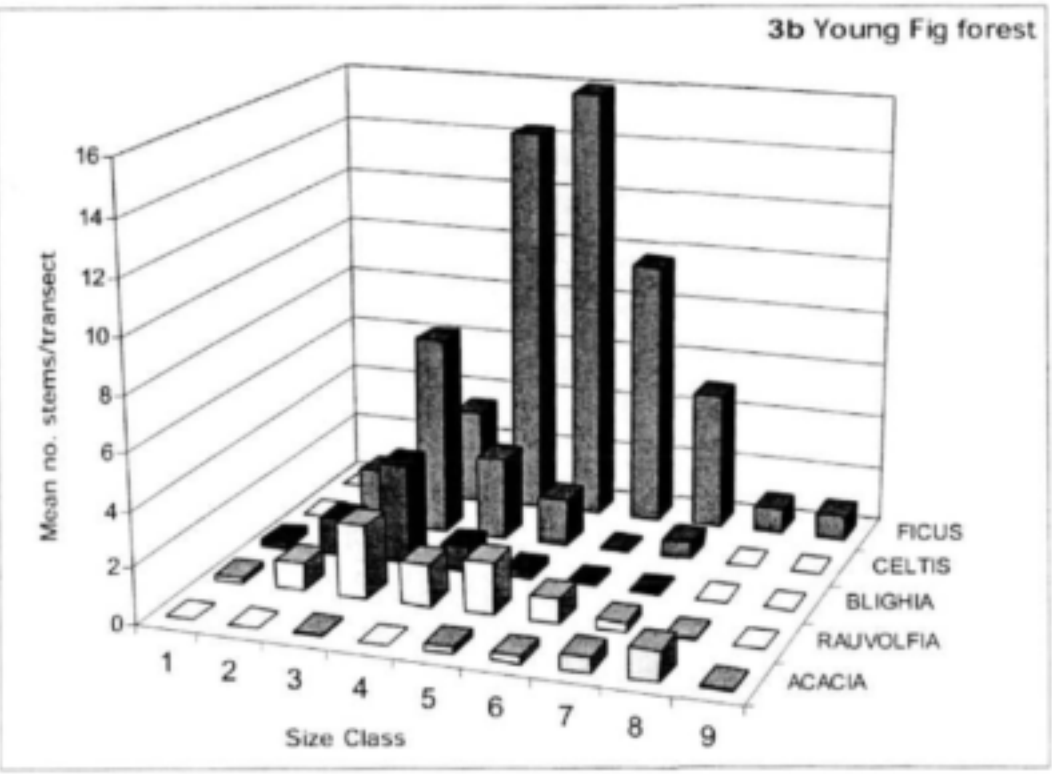
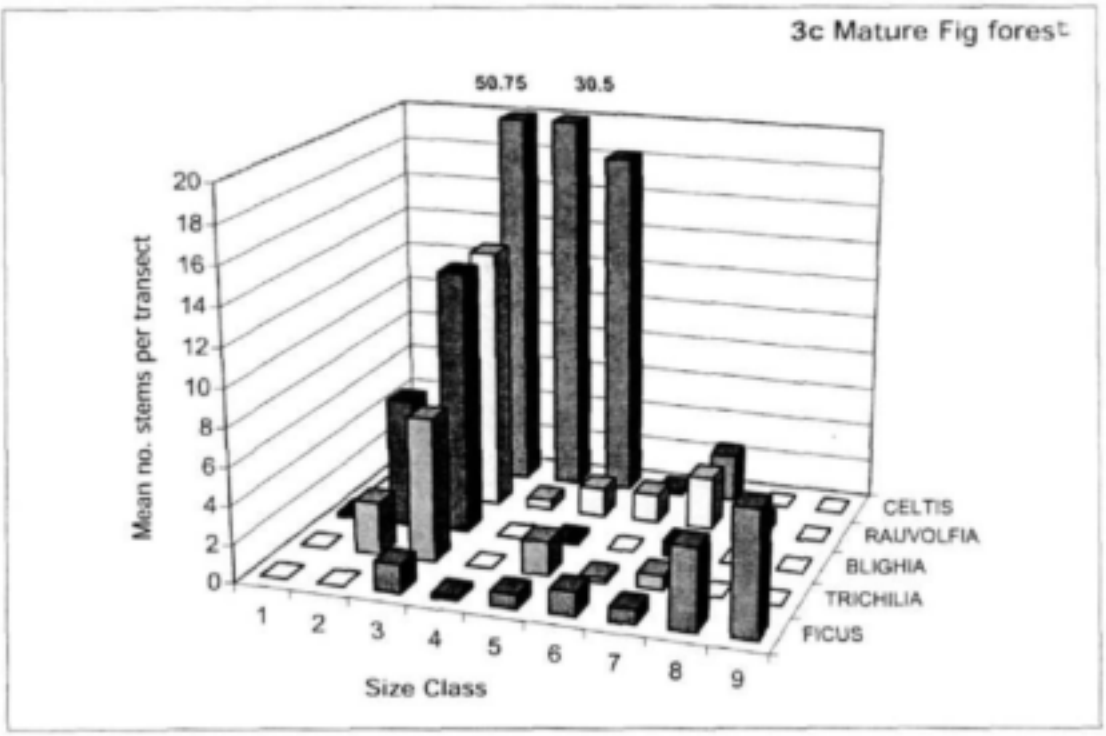


Figure 3: **(a)** The average number of stems of each canopy tree species in a transect in *Acacia xanthophloea* woodland and **(b)** Regenerating Fig forest.



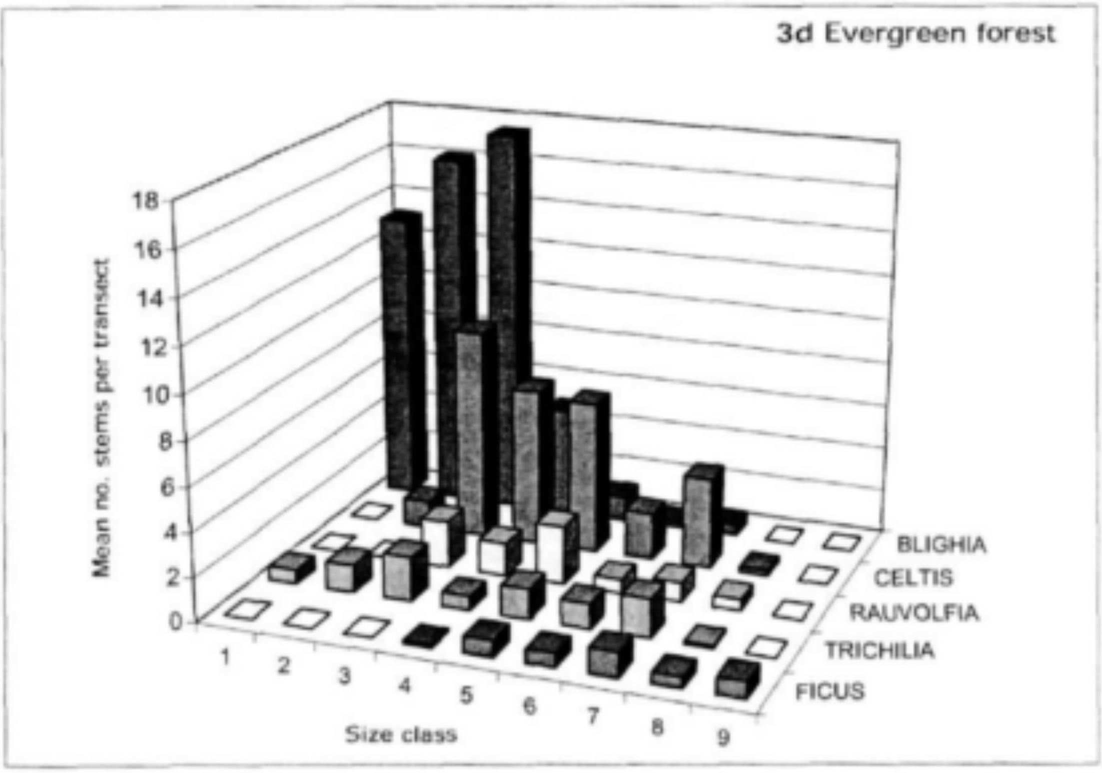


Figure 3: **(c)** The average number of stems per transect of canopy tree species in Mature Fig forest and **(d)** Evergreen forest.

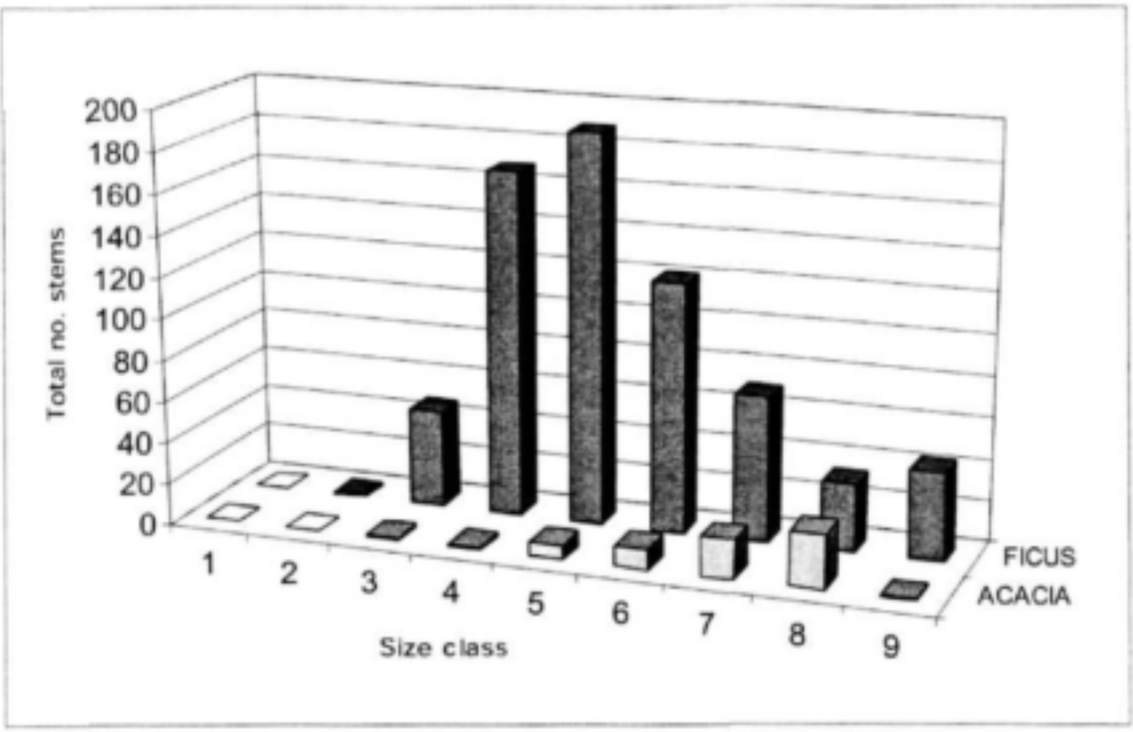
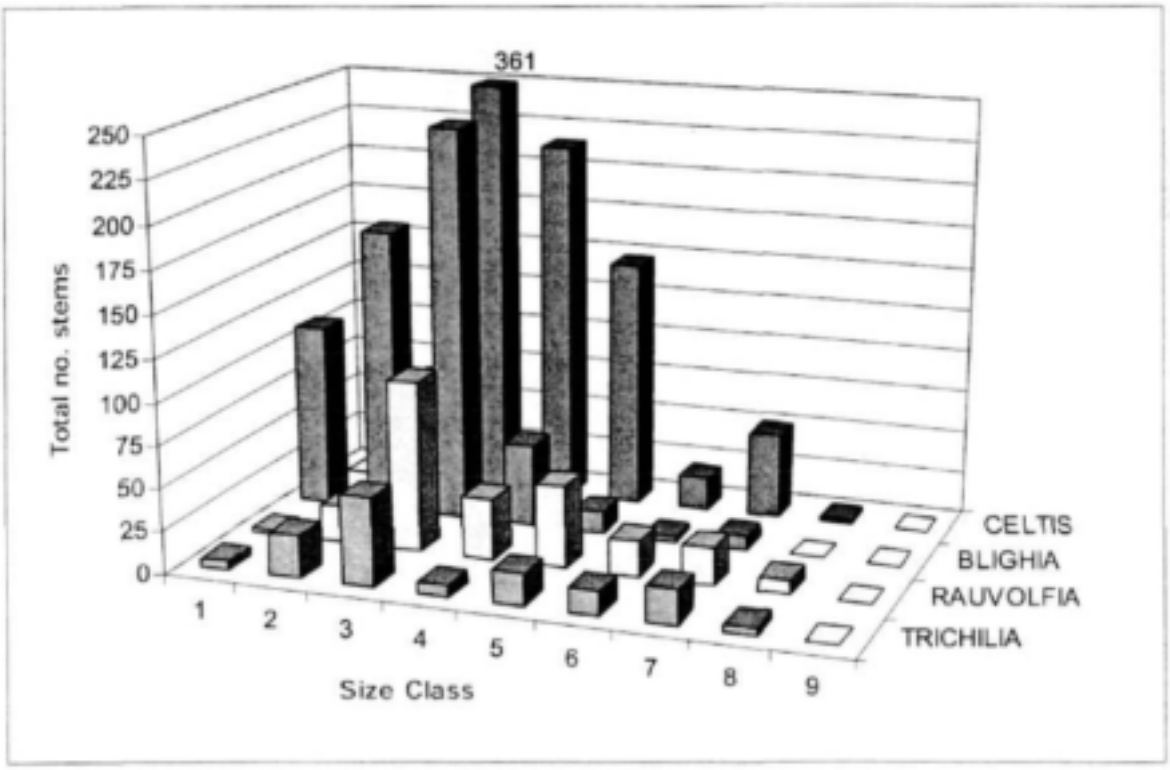


Figure 4: Total number of stems (cumulative demography) for Ficus sycomorus



and Acacia xanthophloea in the Mukze Fig Forest.

Figure 5: Cumulative demographies for evergreen species in the Mkuze Fig Forest.

The only species with young (size class 1 and 2) recruiting individuals in the study area were evergreen or broad-leafed species, but very seldom *Ficus* and never *Acacia* (**Figure 4**). Cumulative demographic profiles of the four common evergreen canopy species from all transects (**Figure 5**) display a predominance of saplings less than 3m tall (size class 3), and appear to be typically shade tolerant.

Light meter readings varied from low in the Broad-leafed forest to high in the *Acacia xanthophloea* woodland. Levels in the *A. xanthophloea* stands ranged between 6.28% and 23.72% (mean = 15.46, S.D.=6.31) of full sunlight (2150 μmol.m^{-2}.s^{-1}), while the Evergreen communities ranged from 0.33% to 0.95% (mean = 0.63, S.D.=0.17). Mature Fig forest averaged 3.52% (S.D.=0.72) of ambient and immature fig stands 4.11% (S.D.=1.32).

DISCUSSION:

Communities:

The communities described here conform to the basic microphyllous/broadleaf split noted by De Moor *et al.* (1977), but with an additional evergreen type. Formation 1 of De Moor *et al.* (1977) corresponds with the mature *F. sycomorus* community, while formation 2 corresponds to *A. xanthophloea* woodland. Juvenile *F. sycomorus* occur in such large stands, for reasons given later, that they warrant inclusion as a vegetation association in their own right. They are often monospecific, but sometimes are interspersed with the occasional *A. xanthophloea*. Only *A. xanthophloea* and *F. sycomorus* are riparian or floodplain specialists (Coates Palgrave 1977); the species constituting the evergreen community are all derived from sub-tropical or tropical forest associations (Pooley 1993). Although described as such, *Rauvolfia* and *Celtis* are not strictly evergreen, being deciduous for a short time at the end of the dry season.

Photo C: Laurence surveys a stand of young *Ficus sycomorus* that established after cyclone Demoina in 1984. Note the shallow lateral roots.

Photo D: *Ficus sycomorus* root profile. There are a multitude of very shallow roots, with few probing deeper than 2.5m.

Although the distance away from the channel explains a significant portion of the species variation observed (**Figure 2**), this must be spurious, as the channel has recently switched from a more northerly course during Cyclone Demoina. Other environmental correlates of the four community types are weak and I hypothesise that the differences between this and other floodplains are (in order of priority) due to:

- The elevation gradients at Mkuze are too low, ranging to a maximum of only 3m above the riverbed. This reduces the range of differences in response to hydrological factors, *e.g.* flood return time. Sufficient slope (1:800) exists for floodwaters to drain away from the main body of forest reasonably rapidly compared to the Phongolo storage floodplain.
- The geomorphic environment is too stable to develop significant levees or undercuts, thus not creating landscape heterogeneity that may be exploited as different niches by trees.
- The climate is sufficiently mesic, and groundwater relatively accessible, to allow forest succession to dominate over environmental constraints in structuring communities.

The implications of these features of the Mkuze Fig Forest are that (1) a lack of disturbance will allow the forest to develop into a closed broad-leafed canopy community wherever soil moisture is sufficient and (2) alien forest-invading species will be heavily favoured by prevailing climatic conditions. The lack of correlation of elevation and community type suggests that stand height above the river must not be used as a surrogate for flood return time, without first being interrogated as such. It must be also be seen in its appropriate climatic and geomorphic context, and direct measurement of receding flood levels at certain discharge rates may be the best indicator of flooding frequency.

Succession:

The results suggest a successional trend from *A. xanthophloea* woodland or young fig forest, to mature canopy figs to mature evergreen, broad-leafed forest (**Figure 3a-d**). *F. sycomorus* and *A. xanthophloea* appear to be pioneers in the system and show strongly cohorted demographies. All recent recruits of both species were either near channels (with higher light regimes) or in open areas, and none in closed stands with evergreen or broad-leafed species. This is in line with their small seeded, fast growing and shade intolerant habit. Factors separating these two species spatially are not readily apparent in this study, but could be due *A. xanthophloea* being more tolerant of saturated soils and longer flood duration than *F. sycomorus* (Furness and Breen 1980). The lack of recent cohorts of *A. xanthophloea* in the forest is notable, as several large stands are visible elsewhere on the Mkuze floodplain system (but outside the study area) that were initiated after Cyclone Demoina (1984). This contrasts with the large areas of young fig trees immediately upstream of the forest and along the channel edges, which regenerated after the 1984 floods. Cyclone Demoina (January 1984, 600mm of rain over 48 hours, 3450 $m^3.s^{-1}$ flood) initiated large-scale recruitment of *F. sycomorus* in certain areas of the floodplain (Pete Goodman KwaZulu-Natal Nature Conservation Services *pers comm.*).

In the tall, open canopy mature fig stands, the early invaders are *Rauvolfia caffra* and *Celtis durandii*. This is confirmed by the proximity of these pseudospecies (demographic groups) in the ordination plot (**Figure 2**) and the fact that understorey species in one community are regularly found in the canopy of the next (**Figure 3a-d**). These species, along with subsequent evergreen shade tolerant species, both have small fruits and are primarily bird dispersed (unpublished notes). As canopy closure becomes more complete, more shade tolerant bird-dispersed species such as *Blighia unijugata* and *Trichilia emetica* establish. These two species are able to recruit in the dense shade underneath themselves (size classes 1 and 2) and probably represent a climax stage for the forest.

The five stages defined by Schnitzler (1997, being "innovation", "pre-equilibrium", "climax", "elimination" and "collapse") for succession in riverine systems cannot be easily interpreted for the Mkuze forest. They appear better suited to describing a stand development (or maturation) cycle, than true successional replacement of species. The **innovation** stage corresponds with the early colonisation by *Ficus* and *Acacia*. However, owing to the rapid growth rates in sub-tropical Africa (compared to cold temperate N Europe) both the **innovation** and the **pre-equilibrium** stage will be short-lived as canopy closure can be completed in less than 10 years. It would seem best to alter the definition of the **pre-equilibrium** from one of canopy closure, to one of a middle successional sere, equivalent to mature *Ficus* forest with an evergreen and deciduous understorey. The **climax** stage is applicable to the evergreen component, but not the **elimination** stage, as these species replace themselves *in situ*. The elimination stage is visible in some stands of *A. xanthophloea* (and noted elsewhere in Africa- Vesey- Fitzgerald 1973) at Mkuze where 70 year old adult trees are senescing and little understorey of evergreens is present to replace them. The **collapse** stage is possibly not relevant to Tropical African systems as areas are usually opened up for further invasion by large flood events or cyclones, and this may be of too short a duration to be called a stage.

Demographies:

The narrow distribution of *Ficus* stems between 12 and 16 cm dbh (**Figure 4**) is due to the massive recruitment event following cyclone Demoina. These tree have a mean dbh of 16 (S.D.=3.4) cm and a height of 12 to 15 m, suggesting a growth rate of 1m per year. This comprises cohorts in several different areas of the Mkuze floodplain, which correlate with others found in reserves on different rivers in northern Natal, dating from 1984 (**Figure 6, Photo C**, unpublished data). In all cases, large adult trees that survived the flooding were present in or adjacent to younger cohorts, suggesting that short distance dispersal is important for mass seedling survival.

The strongly cohorted demography of *Ficus* and *Acacia xanthophloea* (**Figure 4**) implies that these species respond to specific cues for germination, establishment or escape into adult classes (**Figure 3a** and **3b**). The evidence from Mkuze is that the cue is flood triggered germination and establishment. The apparent lack of response of *A. xanthophloea* to cyclone Demoina in the forested areas of Mkuze is notable. There are areas of young Fever trees outside the reserve and away from the Fig Forest, but the cohorts that may have followed Demoina are possibly absent here because of a lack of suitably open areas to colonise or because *Ficus* was better prepared to occupy those areas. I hypothesise that *Ficus* was able to colonise newly opened areas or deposited silt as it has seed available almost throughout the year, and has better seed dispersal through birds. *A. xanthophloea* has a semi-recalcitrant seed that ripens early in the season (November in Mkuze), suffers a high predation rate and is only viable for a short period after maturity (unpublished notes and see Chapter

4) and it is possible that sufficient viable seed was not available immediately after the late January flood.

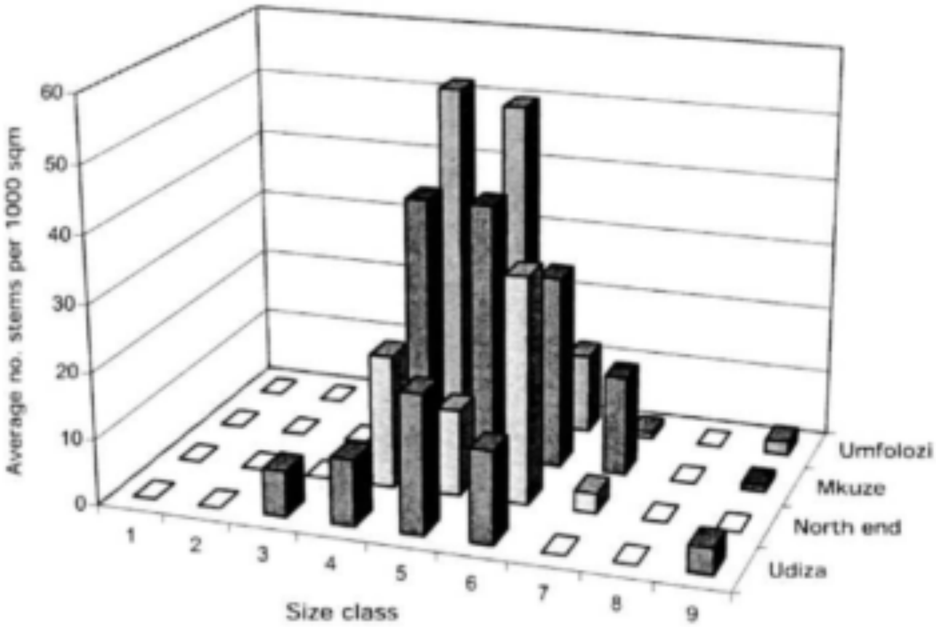


Figure 6: Transect demographies showing post-cyclone Demoina recruitment cohorts of *Ficus sycomorus* from four other floodplain sites in northern KwaZulu-Natal.

The low light conditions prevailing under canopies of *Trichilia* and *Blighia* appear to exclude all other species in the forest, except for the seedlings of themselves. This, and the latter's ability to resprout, would explain the pseudo-cohortedness displayed by *Blighia*. Only when large tree-falls or storm damage disturb the canopy or open the forest completely can light be available for recolonisation by pioneer species.

Forest dynamics.

In the Mkuze Fig Forest, several waves of expansion southwards over the alluvial fan have similar sized individuals of *A. xanthophloea* (Transects 18, 19 and 20, 21).

The northern most area comprises individuals from 70 to 100cm in dbh; further south is a 400m wide group of trees of 50 to 80cm in dbh. At the pan margin, representing the final expansion sometime in the late 1950's (the large flood in 1958?) are a group from 30 to 52cm in dbh (Transects 7 and 11). Similar sized cohorts are evident on the Usuthu and Phongolo rivers (unpub. data). The 70-100cm group are not visible in the 1937 aerial photos (*pers* obs) and must have been absent or rather small. It appears, therefore, that forest initiation is not continuous, but dependent on specific conditions consistent with large floods.

In conclusion, it is apparent that floods are a crucial event in this system, allowing establishment of pioneer species and resetting the successional cycle. If floods are removed (such as below large dams) then an invasion of these riverine forests by shade tolerant evergreen species is predicted. Further there will be a significant reduction in the recruitment of *Acacia xanthophloea* and *Ficus sycomorus*. As these are often pioneers in the forest system and probably shorter lived than other species, an absence of floods will gradually eliminate them. Many bird species in the Fig Forest rely heavily on *Ficus sycomorus* both for fruit, attendant insects and nesting sites (unpub notes), and these can be expected to leave the forest with the decline of mature figs. Managers of large impoundments should be aware of this in the need for and timing of any releases.

Therefore to maintain a viable floodplain system, I suggest that any dams envisaged for this river, especially off-course storage for sugar-cane irrigation upstream, must be compatible with large flood pulses at regular intervals to maintain a mosaic of different age stands of pioneers and evergreen, climax communities.

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CHAPTER 3: THE PAFURI FLOODPLAIN: TREE COMMUNITIES, ENVIRONMENTAL CORRELATES AND FOREST DYNAMICS

ABSTRACT:

An investigation of tree community structure, distribution and environmental correlates was carried out along the Luvhuvhu River in the Pafuri region of Kruger National Park. Thirty-four transects were sampled for species, size class, landform, soil type, and other environmental factors.

Two-way indicator species analysis revealed four canopy tree communities. These were *Acacia xanthophloea* woodland, *Faidherbia albida* woodland, *A. tortilis* woodland and Broad-leafed forest. These were correlated, in order of importance, with distance away from the river, alluvium type and landform. Broad-leafed dominated communities were present on high levees nearest the river. The *Acacia tortilis* community was restricted to the drier outer edges and *A. xanthophloea* woodland was primarily located on clay and silt substrates on lower lying areas of the extensive floodplain, away from the main channel. *Faidherbia albida* woodland occupied sandy terrace and channel sediments close to the river.

Analysis of canopy and understorey species relationships did not reveal any successional patterns and an ordination of species size class distributions in their respective communities showed no obvious successional trajectories.

Geomorphological changes in the river channel have been minimal in the last 50 years.

Demographic investigation of dominant trees revealed cohorted recruitment in *Acacia xanthophloea*, and to a lesser extent *Faidherbia albida*, suggesting the event driven nature of recruitment in these species. Current recruitment failure observed in several tree species (particularly *Ficus sycomorus*) is ascribed to a recent drought and altered flow regime. A planned dam will have significant consequences for forest persistence if it cannot emulate crucial aspects of the natural flow patterns, specifically medium sized floods for seedling establishment and aquifer recharge.

INTRODUCTION:

The Luvhuvhu River floodplain at Pafuri is the only floodplain ecosystem in the Kruger National Park and as such supports a diverse array of plant and animal communities. I was interested to investigate what information the tree communities and their demographies could yield regarding forest functioning, dynamics and the impact of floods and droughts.

Many different approaches have been adopted in understanding riverine ecosystems. Traditionally, riparian vegetation has been viewed in relation to dominating physical variables, but in isolation from structuring processes (Gregory *et al.* 1991, van Coller *et al.* 1993, and Schnitzler 1997, but see Hughes and Cass 1997). Studies have focussed on ecosystem components such as nutrient cycling (*e.g.* Frango and Lugi 1985), hydrology (Bate and Walker 1993, Birkhead *et al.* 1996) and geomorphology (Everitt 1968, Walker *et al.* 1986). These components of the riparian system have been analyzed in a hierarchical framework (van Coller *et al.* 1993, Rogers *et al.* 1997) and this can serve to link various components. However, this often ignores biological processes (such as competition and succession) responsible for vegetation pattern. Recently, a systems view of river functioning has been promoted by ecologists (Gregory *et al.* 1991, Ward 1998) and this has influenced investigation of riverine community structure.

Demographic (life history) approaches to understanding processes have been neglected tools in riparian forest investigation (Hughes 1988, Streng *et al.* 1989). A few recent studies have concentrated on potential floras (seedbanks) and other seed related demographic aspects (Streng *et al.* 1989, Jones *et al.* 1994, Hughes and Cass 1997), but few studies have linked life history traits with community structuring processes (*e.g.* Bradley and Smith 1985, Chapin *et al.* 1986). Succession, in particular, has been neglected in the study of riparian forests (Walker *et al.* 1986), particularly in Africa (Hughes 1988).

Environmental variables governing riverine vegetation

Factors governing the distribution of vegetation on riverine, and particularly floodplain ecosystems, have been given as height above river level (Furness and Breen 1980, Hughes 1990), sediment type and stability (Dunham 1990, Gregory *et al.* 1991), and ground water availability (Hughes 1989). Carter and Rogers (1995) provide a thorough review of all vegetation determinants. Ground water availability has also been cited as a controlling factor of riverine forest development in arid areas (Hughes 1988, Ward and Breen 1983).

Hughes (1989) found a good correlation with community type and stand height above a minimum base level on the Tana River in Kenya. She measured absolute height above river surface, translated into an upstream weir gauged height, as a primary determinant of tree distribution above an annually flooded forest in Kenya. Broad-leafed forest could only persist on levees above a certain height not too frequently inundated. Further down the profile were other species that could tolerate submergence, particularly at the juvenile stage. Furness and Breen (1980) noted a similar pattern for the Phongolo River, where woody communities only persisted above a minimum pan retention level on this storage floodplain. Van Coller *et al.* (1993) found that vegetation type on other non-floodplain Kruger National Park rivers was well correlated with height above water level.

Dunham (1989) analysed plots along the middle Zambezi floodplain correlating communities with various environmental variables (*i.e.* soil nutrient status, sediment type) and found that the best correlate of woody plant diversity was a stand development gradient (succession) with increasing height above the Zambezi River. The seven vegetation types he describes could be separated on the basis of topsoil texture (sediment type) and flooding frequency (of which height above river is a surrogate). These results indicate that dominating physical constraints operated on both juvenile and adult stages.

Dominating processes on floodplains.

Everitt (1968) determined an accurate historical perspective of floodplain dynamics by coring and ageing cottonwoods (*Populus deltoides* var.

occidentalis), and hence computing rates of channel migration and sediment movement. He showed 100% sediment turnover per century in one reach of the Little Missouri River and that tree life histories were adapted to regenerating in this dynamic environment. Bradley and Smith (1985) showed that lowered rates of sedimentation and meander migration impaired recruitment of cottonwoods and thus predicted the consequences of upstream dam construction on floodplain tree communities. Hall and Harcombe (1998) provide one of the best studies bridging the approaches of life history stage characters and physical determinants, and show the interactions between some environmental variables and seedling and sapling characteristics.

Vegetation dynamics or stand development can be classified in two types: seral community replacement (typical succession) and geomorphologically induced change (*i.e.* new landforms resulting in new colonising opportunities). I chose to concentrate on the former, as the evidence is more readily obtainable, can be interpreted from community patterns and demographies, and does not rely on, often incomplete, aerial photo series.

Previous Work on the Luvhuvhu River

Bredenkamp and Van Rooyen (1993) use Decorana ordination techniques, augmented with Braun-Blanquet methods, to define the vegetation communities of the Luvhuvhu River in the Kruger National Park. Their analysis focuses on defining and correlating three regional vegetation units, and does not elucidate the relationships between the 12 communities within these broad types. They determine the forest types of the floodplain reaches as:

1- *Acacia tortilis* dominated savanna: association 4
2- *Acacia xanthophloea* woodland: association 5
3- Mixed riverine forest with *Faidherbia albida* and *Ficus sycomorus*: association 6
4- A Broad-leafed forest dominated by *Diospyros mespiliformis* and *Acacia robusta* subsp. *clavigera*: association 7

This descriptive study determines useful river reach and vegetation management units and identifies areas for further research, specifically that focussed on the forest communities. The communities are not correlated with any environmental variables, and no hypothesis of forest dynamics is presented.

Carter and Rogers (1995) used a Markovian modelling approach to investigate landscape change along the Luvhuvhu, and other rivers in the Kruger National Park. They found that the Luvhuvhu displayed the least variability in landscape change over its length, compared to all other major rivers analysed, had the lowest flow variation (CV =95.8), but had a low minimum monthly-flow despite high rainfall in the catchment (ave. 997.2mm.yr^{-1}) due to heavy abstraction. The river also showed the highest woody-vegetation cover of all rivers. However, their state and transition model assumed some steps in the development of plant communities that were probably not valid in all reaches of this system, (*e.g.* the transition from reeds to forest) and thus is limited in understanding vegetation dynamics.

Van Coller (unpub) collected (in March 1994) data on tree mortality after the 1991/1992 drought on the lower reaches of the Luvhuvhu River. A helicopter transect revealed that only 0.5 individuals of *Faidherbia albida* died per km on the floodplain, compared with 0.7 in the higher rocky reaches. *Ficus sycomorus*, however, showed 20.8 dead trees/km on the floodplain as opposed to 6.4 for the upstream stretches of river. Very few *Trichilia emetica* and no *Diospyros mespiliformis* died on the floodplain during this worst recorded drought.

Aims of this study:

This work looks at the Pafuri floodplain system on the Luvhuvhu River from a demographic viewpoint to highlight environmental correlates, and at succession to determine its role in structuring riparian systems.

1- Describe tree communities, relate these to previous work and determine environmental correlates. Physical environment determinants of forest type, in particular height above channel bed and sediment characters, will be investigated. This will verify if functional tree communities relate to floristic studies, and if specific abiotic variables or biotic processes determine these.
2- Investigate tree demographics, community dynamics and succession. Tree demographics may yield clues as to population stability, effect of or reliance on aseasonal and stochastic events, and other possible limiting factors. Community dynamics will be important to determine both for long term

monitoring, and to predict the conservation status of other species or relationships that may rely on one specific community type.

3- Relate communities and dynamics to specific properties of the flow regime. Infer possible effects of predicted changes in flow. If specific communities, and their dynamics or transitions can be related to specific hydrological features, and if these can be managed by catchment agencies, then the chance of losing important ecosystem elements can be minimised.

METHODS:

Study site:

The Luvhuvhu River forms a floodplain 16 km long and 4 km wide before its junction with the Limpopo River in the far north-eastern corner of the Northern Province, South Africa (**Figure 1**). This, the Pafuri region of the northern Kruger National Park (Photographs 1 and 2; 22°26' S: 31°15' E), usually receives less than 400mm rain annually and has a summer mean maximum temperature over 30°C (Tinley 1976). The alluvium is over 30m deep across much of the floodplain and consists of a highly complex layering of coarse and fine sediments (Dept. Water Affairs and Forestry borehole reports); bedrock control of flow is thus negligible. Rainfall is almost exclusively in summer in large storms, which result in local floods.

Large floods are generated by late season cyclonic ingression from the Moçambique channel (Louw 1995) and occur from both the Luvhuvhu River and back flooding from the Limpopo.

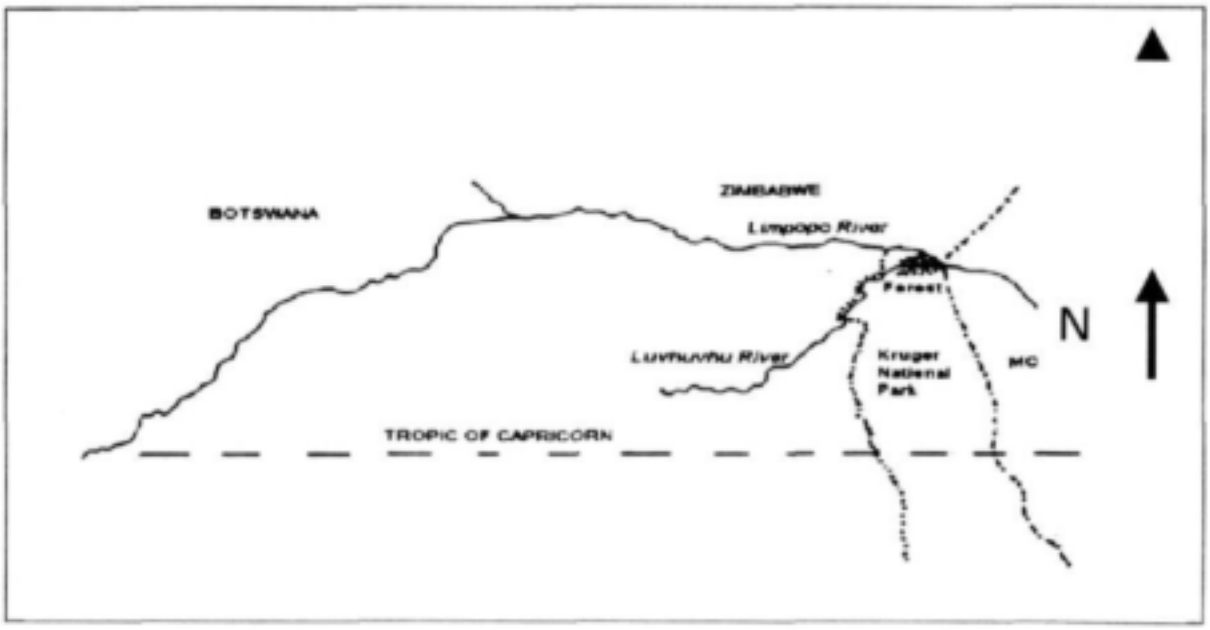


Figure 1. The Luvhuvhu floodplain forest at Pafuri in the far North-Eastern corner of the Kruger National Park, South Africa. The forest occurs on the 16km of floodplain before the Luvhuvhu joins the Limpopo River and flows into Mozambique.

Due to the relatively small catchment (5110 km^2), flood recession is usually rapid (*pers* obs.). *The first recorded instance of the river drying up at* Pafuri occurred in 1965 (Louw 1995), and it has been seasonal ever since, only flowing all year round in years of above average rainfall *e.g.* 1998. Abstraction for irrigation is the major water loss in the catchment, and together with forestry and domestic consumption, accounts for 80.4 million m^3 or 20% of the virgin mean annual runoff (571 million m^3, Louw 1994). Three sites have been selected on the River to determine the Instream Flow Requirements (IFRs) for the Luvhuvhu, and as monitoring sites following the construction of a large dam on the river.

The North bank of the river was subject to clearing for small-scale agriculture until 1967 and therefore avoided for sampling transects.

Sampling:

Sampling occurred from May 1997 to October 1998.

Communities

A total of 34 rectangular transects/plots (70m X 20m) were located approximately every 300m on the south bank of the floodplain, away from any possible human disturbance. Transects were laid out parallel to river flow, and did not cross landforms. This length was chosen as it usually encompasses at least 10 mature tree canopies. It was considered that longer transects may have included subtle variation in sediment types, and therefore obscured possible community boundaries. In each transect, all woody stems were identified and allocated into one of 9 functional size classes as in Chapter 2 Table 1.

Only tree data were collected as herbs, grasses and annuals persist on different temporal and spatial scales, are thus more determined by prevailing or immediately preceding conditions and therefore less likely to yield any useful long term information regarding ecosystem dynamics.

Environmental correlates

Landforms. Plot elevation above river channel has been shown to be important in determining vegetation communities as this provides an indication of inundation frequency and flood submergence (Hughes 1988). On the Luvhuvhu, this height is often difficult to assess effectively because the floodplain widens considerably towards its confluence, and local topographic features can affect water movement. Further, levee height decreases (from 9.5m to 3.5m) downstream towards the confluence and inundation can be greatly affected by the level of the much larger Limpopo River.

It was decided that a landform classification (**Figure 2**) would constitute the best expression of height of a transect above the channel floor for two reasons: landforms are an integrated expression of river functioning and flow, and they usually display consistent characteristics, particularly sediment type (Carter and Rogers 1995).

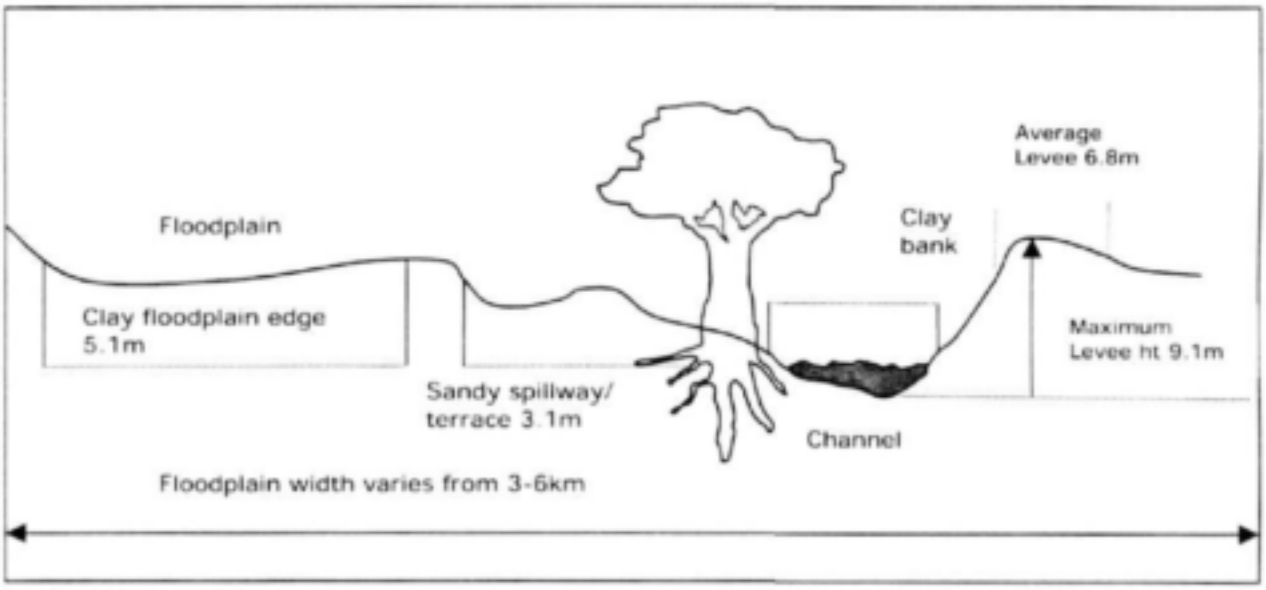


Figure 2: A stylized cross section of the Pafuri floodplain, showing the location and average height above base flow of the landforms described. (vertical exaggeration = 1:70)

A subjective landform classification was adopted incorporating all easily recognisable components of a floodplain channel (**Figure 2**). Five were chosen as readily distinguishable; channel, sandy spillway terraces, clay banks and terraces, higher silty levees and the heavy clay edge of the floodplain. Relative landform height above an averaged river base flow level (0.1 cumecs) was determined at three localities by inclinometer and measuring staff, and referenced to gauge plates of known height, and surveyed flood heights on a pump house on the floodplain. The base flow rate was derived from weir discharge records (Dept Water Affairs and Forestry weir nos. A9h012 and A9h013) as the most frequently occurring, persistent low flow in the dry season. Previous surveys and the gauging plates have used the channel bottom underneath the Road Bridge as baseline, which corresponds to 2m below the base flow rate. By using a base flow height, landform elevation could be determined more accurately upstream and downstream of the bridge.

Habitat data were collected in each transect to relate patterns of seedling survival to vegetation structure. These consisted of canopy cover, ground cover and an index of shrub density and light availability. Canopy cover was estimated for each plot as the proportion of shade on 5 one metre square subplots in each transect. Ground cover was determined visually by allocating a coverage rating out of 5 to any vegetation less than 50cm in the square metre subplots. An index of shrub density was determined as the percentage of a 1m square card obscured, when held at 2m above the ground and viewed from the end of the transect.

Light availability was recorded at 0.5 m in each transect with the quantum sensor (400-700 nm) of a Skye Instruments SKP 200 Light Meter. Full sun was recorded at 13:00h as 2180 $\mu mol.m^{-2}.s^{-1}$.

Sediment. Two 500g soil samples were collected from each landform (n=5) uing a steel tin and trowel, bulked, and analysed for particle size distribution through a series of sieves. Clay and silt fractions were determined by standard solution tests. This gives an indirect indication of permeability, water retention capacity (thus desiccation time after floods or rain) and nutrient status.

Water Table. Depth to water table in several different landforms was gauged from boreholes in different seasons. Owing to the incomplete borehole records, their distribution and relative scarcity on the floodplain, a complete picture of the floodplain water table dynamics did not emerge.

Flooding frequency. The nearest gauging stations to the Pafuri study site have incomplete records that are too short to construct accurate flow frequency curves (Louw 1994). Flood return time for the different landforms in Pafuri was determined by indirect methods; the stage- discharge curves calculated by Louw (1996) and Van Bladeren (1996), and the flood frequency tables given in the IFR workshop reports (Louw 1994). Although this may not be absolutely accurate as some coefficients have been inadequately confirmed (D. Louw, *pers comm.*) they are sufficient for this investigation given the method of landform height derivation.

Community profiles

Size class distributions of the dominant species in the canopy tree communities were constructed from all transects that fell in that particular type. These were used to determine if there were obvious successional patterns based on the relative location of recruiting, understorey and canopy individuals of the same species.

Demographic profiles

Population structures of important canopy species were constructed by summing all individuals across all transects in all communities. Species were grouped according to the presence (Size class 1 and 2 comprising >5%) or absence (<5% size class 1 and 2 in the population) of recruitment, and whether recruits appeared to progress to larger size classes (Presence of classes 3,4 and 5). These groups were then used to examine the influence of environmental factors on demographic status.

Analysis:

Stems of dominant species in all transects were grouped into one of three demographic categories:

- *Recruiting individuals*- size classes 1 to 3, *i.e.* up to 3m tall.
- *Sub-canopy and potentially adult*- intermediate size classes 4 to 6, *i.e.* 10 to 30cm dbh.
- *Mature trees*- classes 7 to 9, *i.e.* over 30cm dbh.

Exceptions were made to this to account for different growth forms and maximum sizes of different species. The lower limit for mature trees of *Ficus sycomorus* was raised to 50cm dbh, (Mature trees in size classes 8 and 9 only). In *A. tortilis, A. xanthophloea, A. robusta,* and *Croton megalobotrys* the limit was lowered to 20 cm dbh, *i.e.* Mature tree were in size classes 6,7,8 and 9. This was felt to be a more accurate reflection of each species' phenology and growth patterns.

I considered cohortedness (a predominance of one size class or group) to indicate event-driven recruitment. A species was recognised to be cohorted by counting the number of times the proportion of stems in each demographic group was greater than 80% in each transect, and if this occurred in at least 70% of transects in which that species occurred. Transects with less than 10 recruiting individuals of that species were omitted to avoid small sample biases.

Two Way Indicator Species Analysis (Hill 1979) was performed on the transect data thus categorised to elucidate community associations on a functional and not floristic basis. All algorithm defaults were used and cut levels for the divisions set at 0, 20 and 80 stems per plot.

Indirect gradient analysis of the grouped transect data was used to identify any correlation between vegetation type and environmental variables using the Detrended Canonical Correspondence Analysis function of CANOCO for Windows (ter Braak and Smilauer 1999) with no downweightings or transformation of data. The ordination plot was scrutinised for possible successional relationships by noting the relative position of recruiting and canopy trees of the same species. The sample of recruiting *Ficus* seedlings skewed the relationships between the remaining groups unacceptably. As the recently germinated seedlings were located in unusual places (in damp hollows in the evergreen forest and in *Faidherbia* woodland) and were probably ephemeral, they were excluded from further analysis.

Community dynamics

Recruitment dynamics and succession were investigated through patterns of regeneration, recruitment and replacement stages in tree populations *sensu* Walker *et al.* (1986B), Vesey-Fitzgerald (1974) and Everard *et al.* (1995). This involved perusal of the community grouped size class data to check if recruiting species in one type occurred in the understorey or canopy of another type and if these were linear transitions. This was corroborated by measuring the distance in ordination space of the demographic groups relative to each other and looking for repeated patterns of juvenile and adult associations.

RESULTS:

Communities and Correlates:

Canopy tree communities at Pafuri consisted of *A. xanthophloea* woodland (Photographs 5 and 7), *Faidherbia albida* woodland (Photograph 3 and 4), *A. tortilis* woodland (Photograph 9) and Broad-leafed forest dominated by *Diospyros, Acacia robusta* and *Ficus* (**Figures 3**, **4** and see Appendix **Table C**).

The first division, between *Acacia tortilis* and *A. xanthophloea* dominated communities and the others, returned an Eigenvalue of 0.755. This was further divided into *A. tortilis* woodland and *A. xanthophloea* woodland (Eigenvalue = 0.393). Division 2 revealed a community of broad-leafed and mostly evergreen species as distinct from *Faidherbia* forest with an understorey of *Croton megalobotrys* (Eigenvalue = 0.195). These communities correspond well with the phytosociological associations of Bredenkamp and van Rooyen (1993) (**Table 1**).

Table 1: A comparison of the phytosociological associations previously determined by Bredenkamp and van Rooyen (1993) and the tree communities in this study. Site refers to the predominant landforms where these were found.

Site	Bredenkamp & van Rooyen	*This Study*
Floodplain edge	*4. Hyphaene coriacea-Acacia tortilis* savanna	*Acacia tortilis* woodland
low lying areas & pans	*5. Acacia xanthophloea- Azima tetracantha* floodplain forests	*Acacia xanthophloea* woodland
Sandy terraces	*6. Acacia albida-Ficus sycomorus* riparian forest	*Faidherbia albida* forest with *Croton* understorey.
Levees	*7. Setaria sagittifolia-Croton megalobotrys* riparian forest	*Diospyros, A. robusta*, forest

Photo 3: *Faidherbia albida* woodland on sandy terraces with an understorey of *Croton megalobotrys*.. Note the trees are in leaf at the end of the dry season and the lack of ground cover. October 1998

Photo 4: Mature *Faidherbia* near the Limpopo/Luvhuvhu confluence. John indicates the level of the 1996 flood.

Photo 5: *Acacia xanthophloea* stand that emerged in a cohort after the 1987 floods. Note the even sized stems, lack of leaves. October 1998.

Photo 6: A cohort of *A. xanthophloea* seedlings that emerged after the 1996 floods, taken when the trees were 2 and a half years old and 3m high. October 1998.

Surveying revealed differences in landform elevation down the floodplain of up to 3m (**Figure 2** and **Table 2**). Landform and sediment type correlated consistently down the entire floodplain (similar Axis 1-direction and values in **Figure 3**, see Appendix **Table C**). Distance away from the river had the highest correlation (Eigenvalue = 0.809, 18% of the variation) followed by sediment type (0.527, combined, 42,8% variation explained) and landform occupied (**Figure 1**).

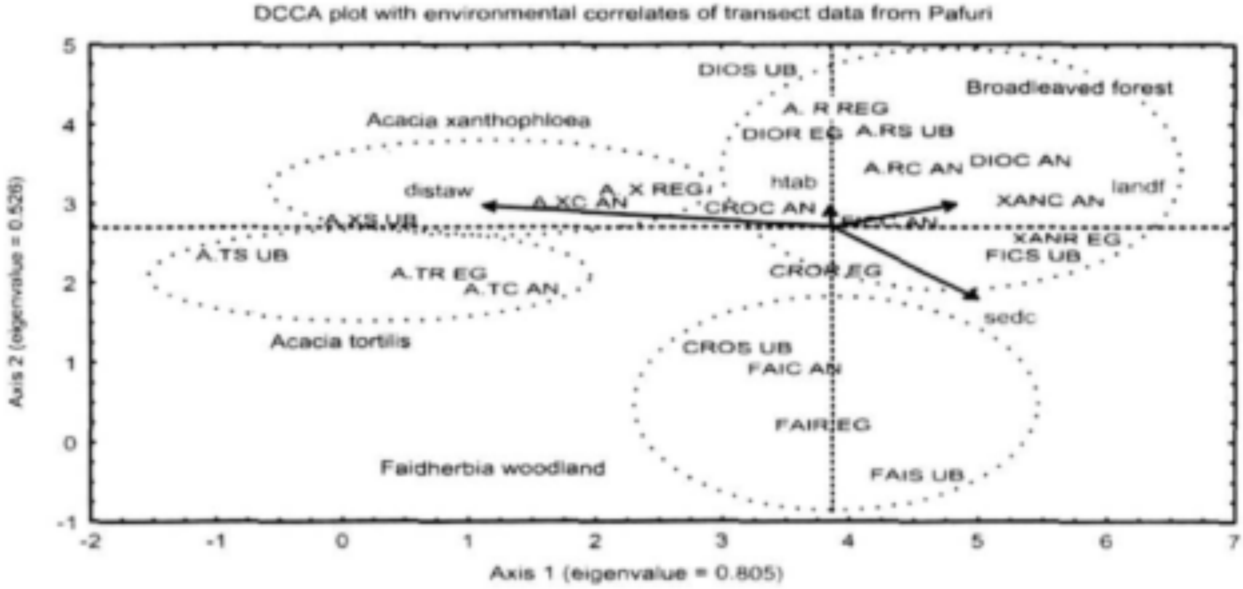


Figure 3: The four communities produced by Decorana analysis of demographic groups in each transect, displayed in ordination space. The strongest environmental determinants are shown with the length of the arrows indicating their correlation coefficients (*distaw* being greatest with Eigen value of 0.809). (FAI = *Faidherbia* woodland, AT = *A. tortilis* savanna, AX = *A. xanthophloea* woodland and the remainder fall into the Broad-leafed Forest. For data see Appendix **Table C**)

Table 2: Identified landforms, maximum and minimum measured heights above a baseflow river level of $0,1m^3.s^{-1}$, predominant sediment, and particle size distribution. Balance is made up of fractions >2mm diameter and organic matter. Values are means (S.D.) with n=5, except for channel and high terrace (n=2).

Landform	Max height	Min height	Sediment	% Clay <0.02mm	% Silt 0.02-0.2mm	% Sand 0.2-2mm
Channel	1.4m	-2m	Sand	0	12.8	79.6
Flood spillway	3.2m	1.3m	Sandy silt	6 ± 4	16.4 ± 6	65.3 ± 18
Levee	7m	4m	Clay silt	26 ± 2	39 ± 5	22 ± 2.3
High terrace	4.2m	3.5	Silty clay	29.7	32.1	7.5
Floodplain	6.8m	3.8m	Clay, clay silt	34.5 ± 5.3	39 ± 8	9 ± 2.1

Faidherbia woodland was always found on sandy soils (mean particle size >0.2mm: **Table 2**, Appendix **Table C**) on or adjacent to spillways and lower terraces. *A. tortilis* and *A. xanthophloea* stands were correlated with clay soils on low lying portions of the floodplain, See **Figure 4** and Chapter 4. Broad-leafed forest (incorporating *A. robusta*) was invariably associated with higher silty levees, usually in close proximity to the active channel. All demographic groups of each of the above microphyllous species occurred on only one sediment type (Appendix **Table C**). For example, both recruiting and mature *A. xanthophloea* only occurred on silt/clay substrates, regardless of height above the river.

Light readings taken in the different communities reveal a gradient from high light under *A. xanthophloea* (30% of full sunlight 660 $\mu mol.m^{-2}.s^{-1}$) and *A. tortilis* (318 $\mu mol.m^{-2}.s^{-1}$) to full shade in the Broad-leafed forest (34$\mu mol.m^{-2}.s^{-1}$ or 1.5% of full sunlight). *Faidherbia* was intermediate at 143$\mu mol.m^{-2}.s^{-1}$ (**Figure 5**).

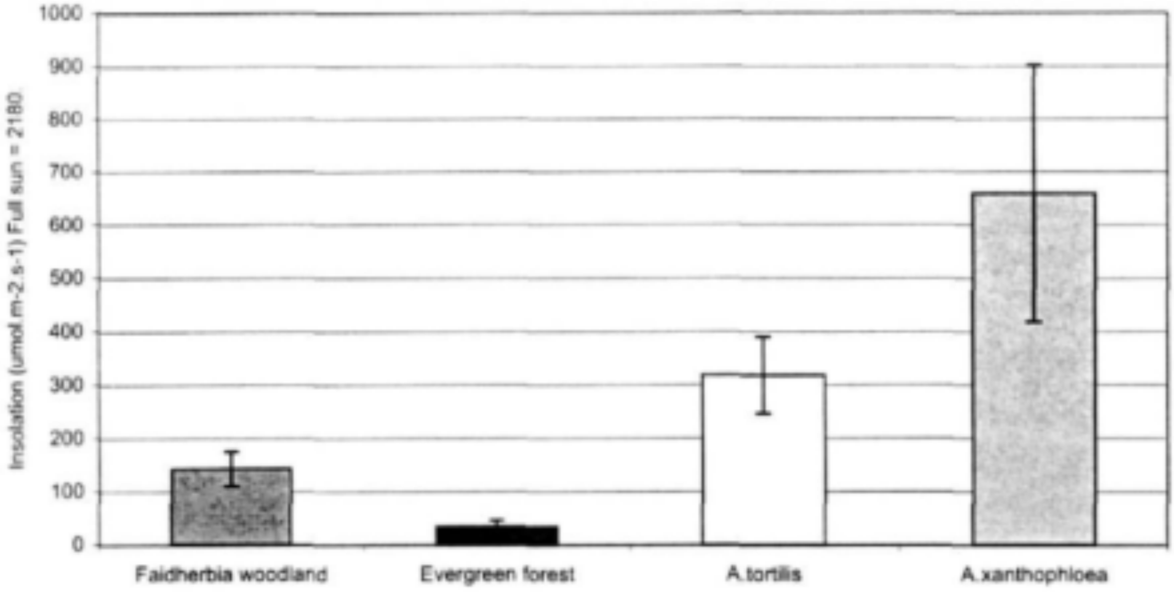


Figure 5: Light availability at ground level in 4 floodplain tree communities (n= 10, bars are one s.d.)

Succession and Dynamics:

Recruits of canopy species of one community were seldom found establishing in the understorey of another (**Figures 6a-d**), but, rather, were either regenerating *in-situ* (**Figure 3**) or as cohorts (**Table 3**). Adult (climax) and recruiting communities of the same species were also found in close proximity in ordination space (**Figure 3**). Of the actively recruiting species in the evergreen forest, only *Diospyros mespiliformis*, *Croton megalobotrys* and *Acacia robusta* can be considered shade tolerant as they have numerous saplings in size classes 2 and 3.

Demographic profiles:

Of the microphylls, only *Acacia xanthophloea* and *Faidherbia albida* were cohorted (**Table 3**). No obvious cohorts were visible in the size class structure of *A. tortilis*, *A. robusta* or other dominant canopy species (**Figures 7a-d**), although only very large specimens of *Kigelia africana* and *Xanthocercis zambesiaca* were noted.

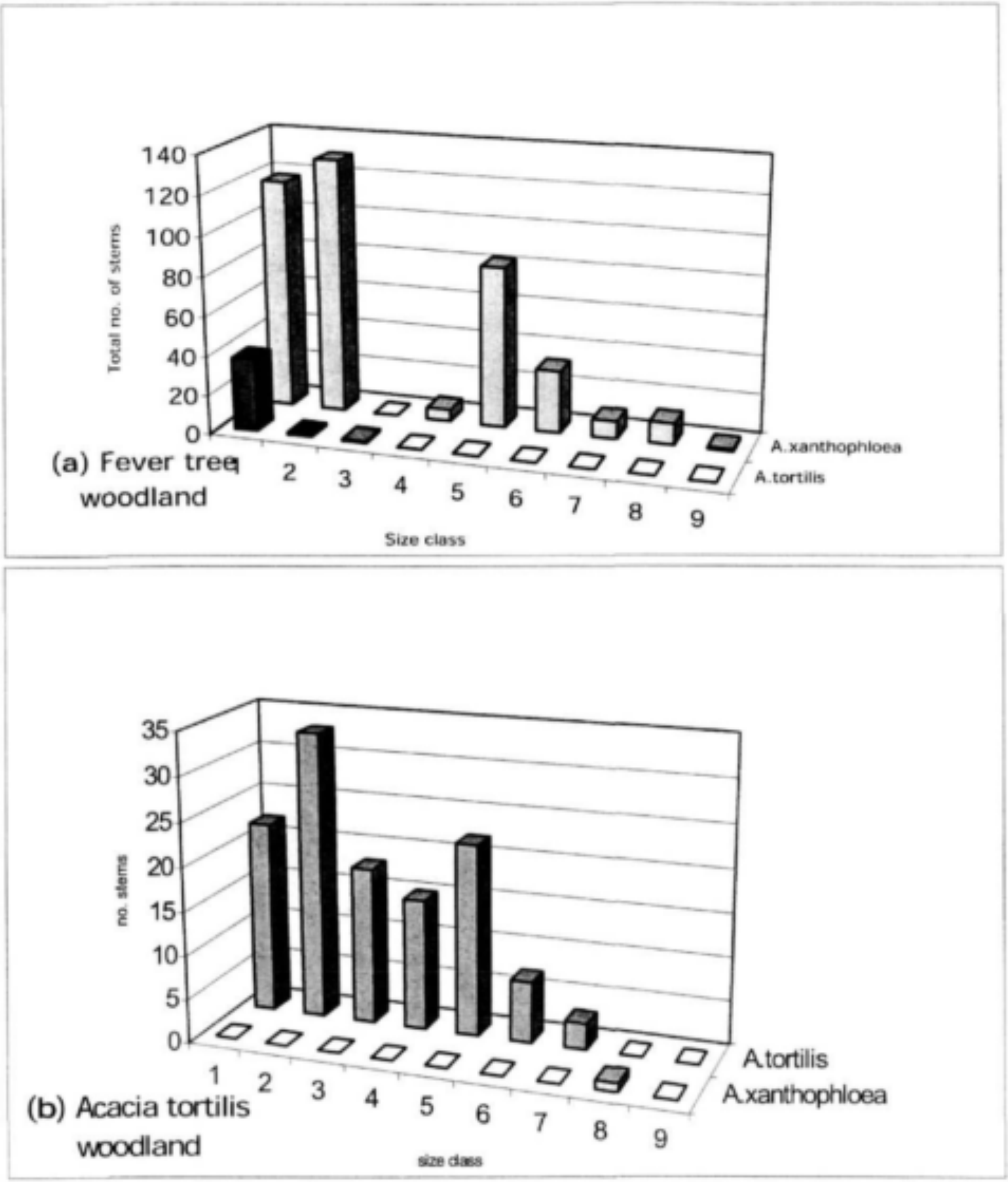
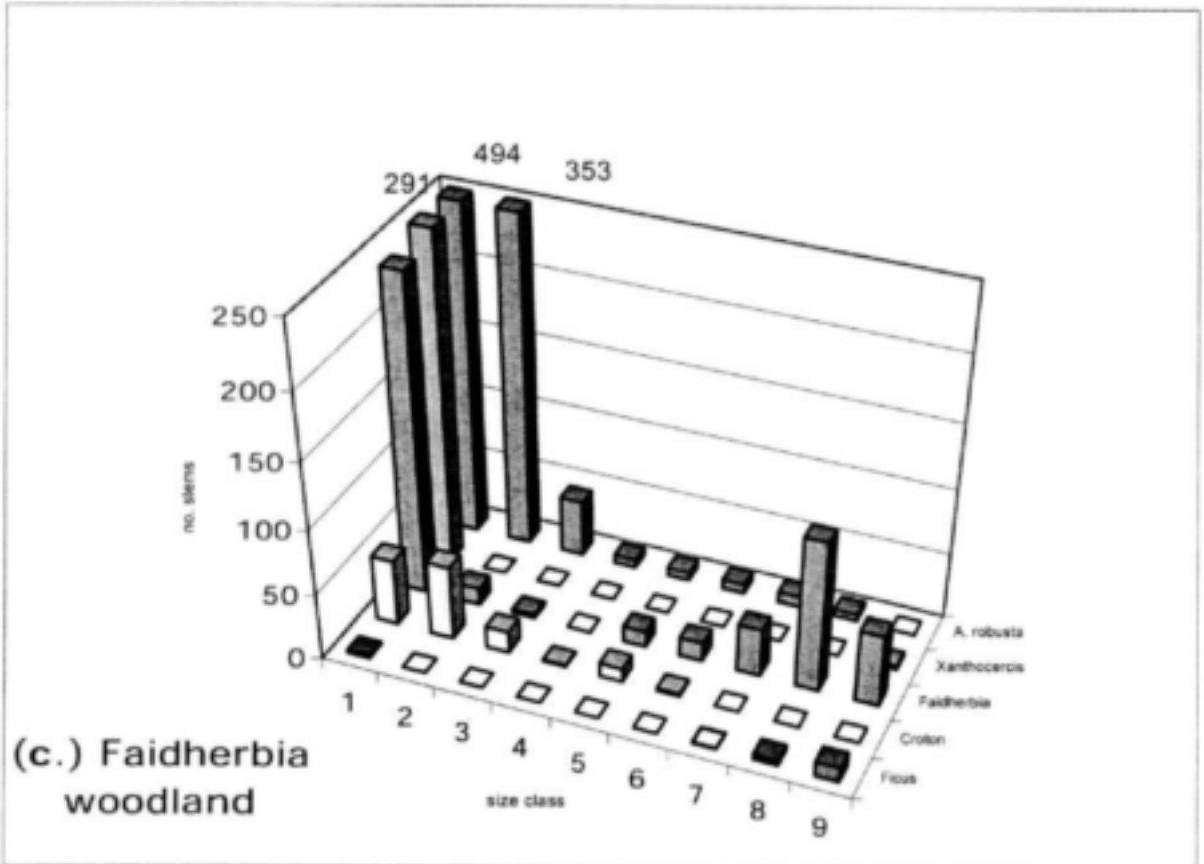


Figure 6: Size class distributions of dominant canopy trees in four communities at Pafuri: **(a)** *A. xanthophloea* woodland, **(b)** *A. tortilis* woodland.



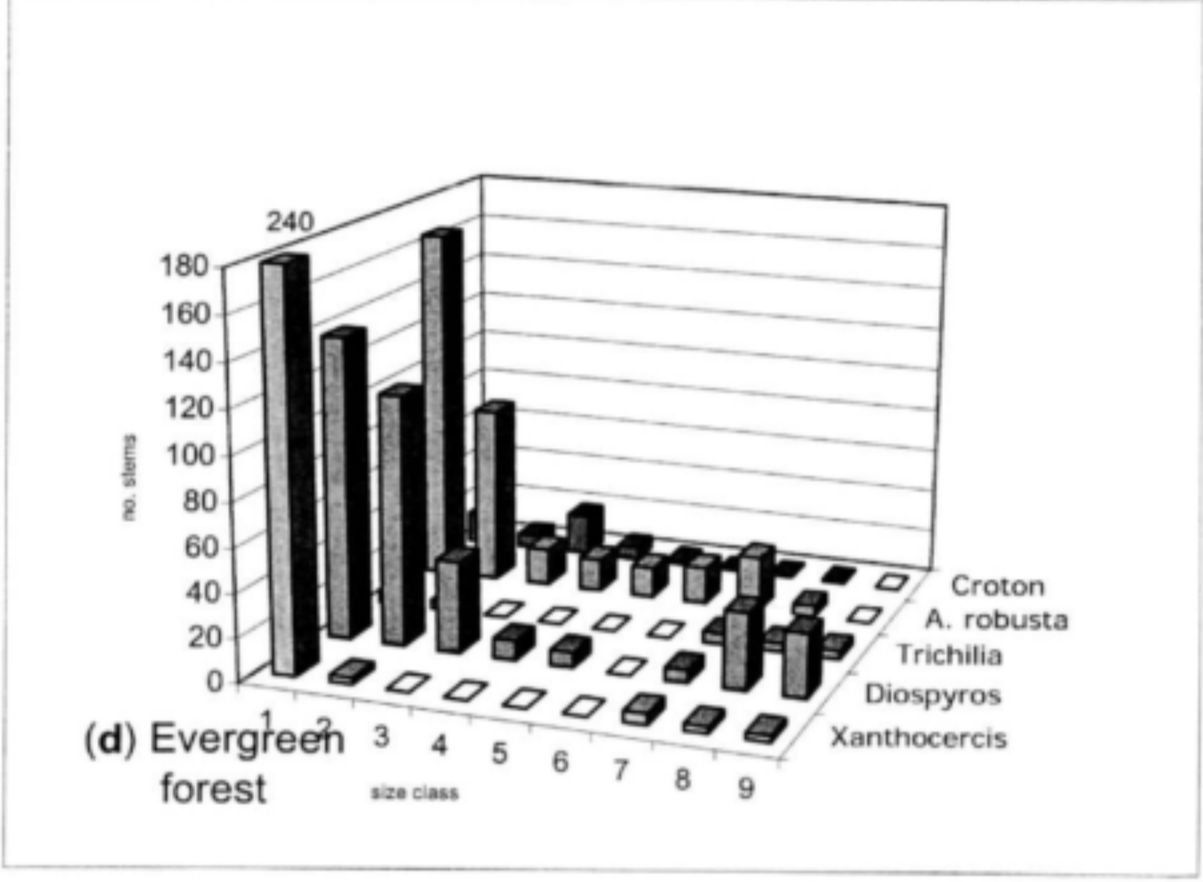


Figure 6: Size class distributions of dominant canopy trees in four communities at Pafuri: **(c.)** *Faidherbia* woodland and **(d)** Evergreen forest.

Table 3: The degree of cohortedness of four microphyllous species on the Pafuri floodplain. See text for explanation of method. The number of transects shown is for the most commonly occurring demographic group. **Acacia robusta* only just misses the arbitrary cutoff line of 70%, but this is considered reasonable as it is biased by very high number of germinants, (size class 1) than do not make it through to larger size classes.

Species	Number of Transects of commonest group	Number transects with > 80% stems in one demographic category	Degree of Cohortedness (>70% transects have more than 80% stems)
Acacia robusta	16	11	68% – No*
Acacia tortilis	6	3	50% - No
Acacia xanthophloea	8	6	75%- Yes
Faidherbia albida	15	11	73% - Yes

Cumulative size class distributions of all species sampled reveal 3 groups in the canopy tree species (**Figure 7a-c**). Microphyllous species are treated separately (**Figure 7d**), as each is found in a different community and will be subject to other, subsequent, analyses.

Complete recruitment failure (no seedlings or saplings in classes 2, 3, 4 and 5 evident), is apparent in *F. sycomorus, Kigelia africana* and *Xanthocercis zambesiaca* (**Figure 7a**), despite several recent years of above-average rainfall, large flooding in 1995, 1996 and a mid-size flood in 1998. The second group (**Figure 7b**) shows good recruitment but very low juvenile survival, and is typified by *Xanthocercis zambesiaca*. The final group (**Figure 7c**) shows good recruitment and survival, resulting in stable population structures.

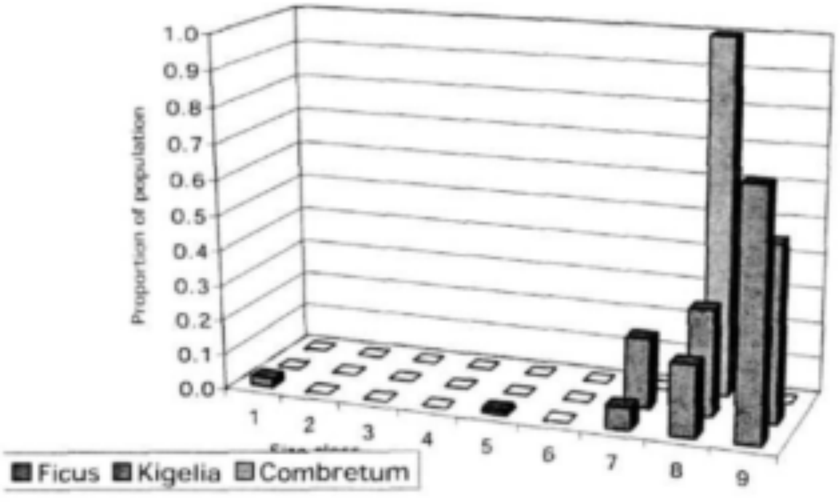


Figure 7a: Cumulative demographies of all transects of three species showing almost complete recruitment failure on the Luvhuvhu River at Pafuri.

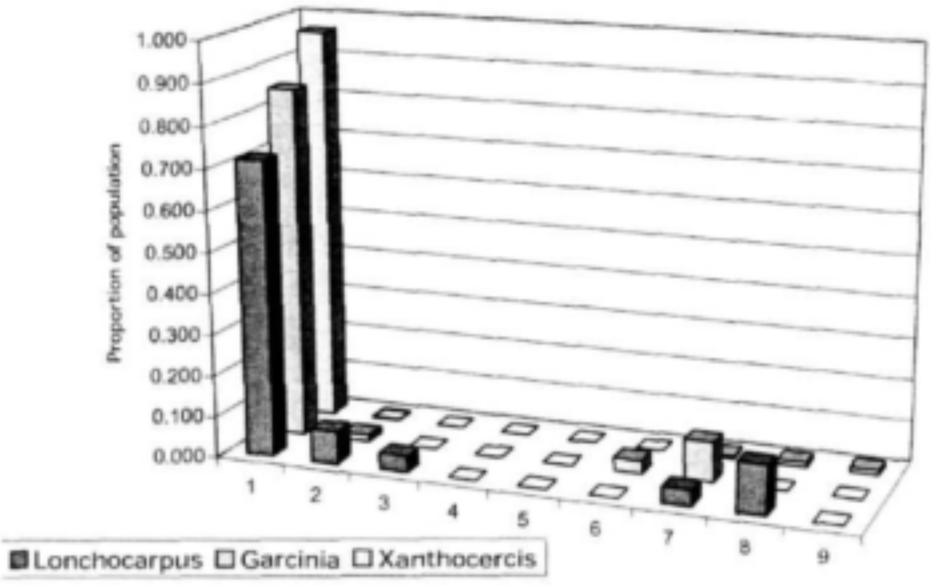


Figure 7b: Demographies of three species showing significant recruitment, but very low survival. Values expressed as a proprortion of the total population

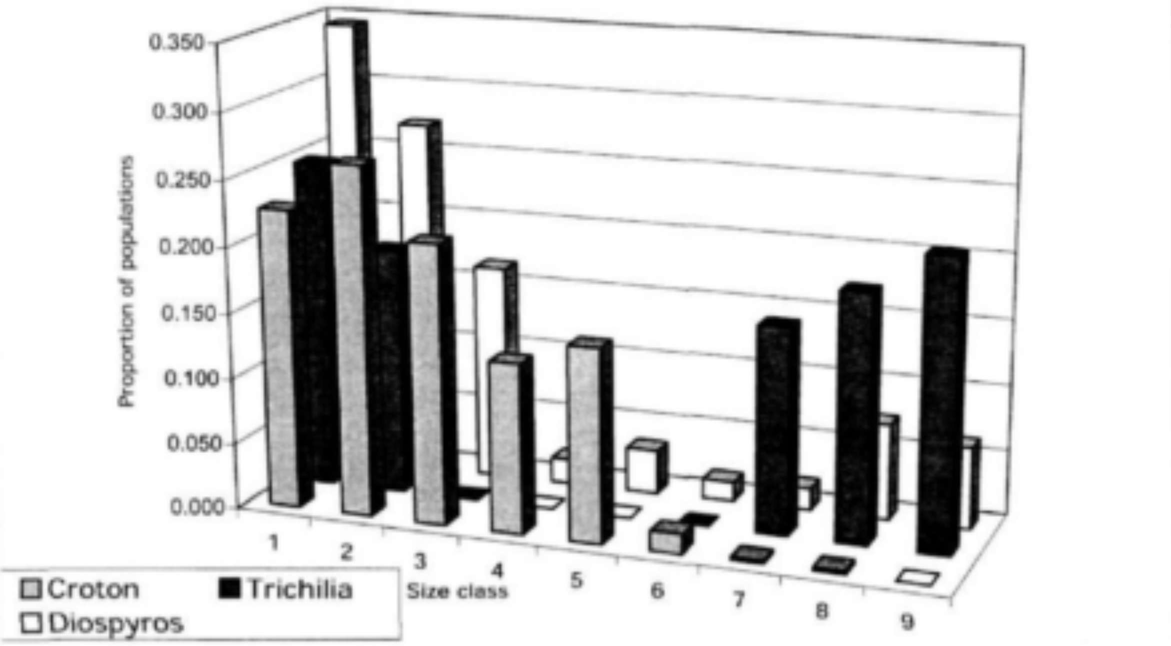


Figure 7c: Demographies of three dominant species with stable population structures

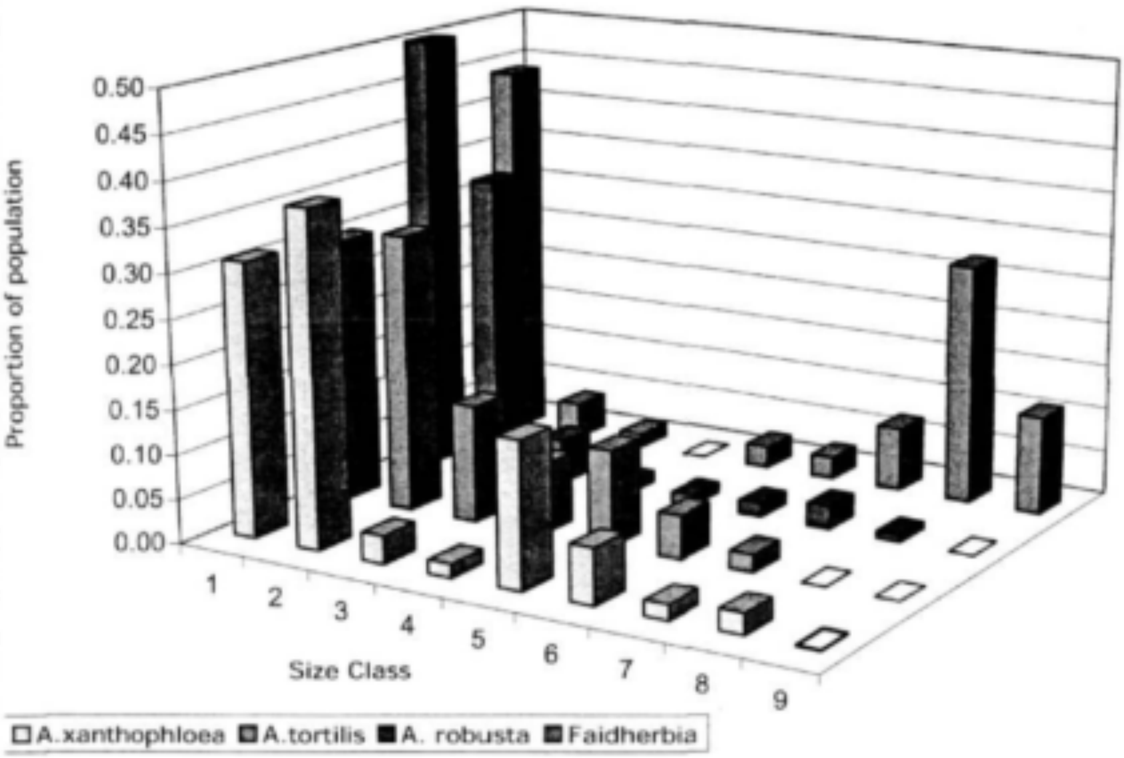


Figure 7d: Demographies of four microphyllous species on the Luvhuvhu floodplain at Pafuri.

Flood regime:
Discharge magnitude.

Flood peaks are large for such a small catchment, the maximum recorded being 3450 $m^3.s^{-1}$ (1977) with peaks over 2000 $m^3.s^{-1}$ occurring roughly every 10-12 years (Louw 1996).

Frequency.

Gauging weir data and flood tables revealed that floods between 5-20 cumecs occurred 97 times (from 1930-60) and 47 times (1963- 1993) in 30 year periods. An annual flood may be expected to be between 30-40 cumecs. Floods greater than 200 cumecs occur once every three years. (**Figure 8**).

Season.

Almost all large floods occurred in February, with occasional discharges >1000 cumecs in January and March. Smaller floods were spread throughout summer, but were also concentrated in February.

Inundation heights:

Stage discharge curves for the Luvhuvhu in its lower reaches are given in **Figure 9** (after Louw 1996 and Louw 1994). The lowest lying sandbars and sandy terraces are activated by a flow of 20-50$m^3.s^{-1}$. Bankfull conditions equivalent to a discharge of between 200 and 390 $m^3.s^{-1}$ will activate all remaining terraces and lower lying channels less than 4.2 m above base level. The outer lying edges of the floodplain are only inundated during relatively large floods of 700-1000$m^3.s^{-1}$ (stage height = 6.8m at the bridge), or when the Limpopo River is in flood.

DISCUSSION:

Communities and correlates:

The congruency between the tree communities described here and the phytosociological associations of Bredenkamp and van Rooyen (1993) is surprising given that their communities were differentiated on the basis of herbaceous species,

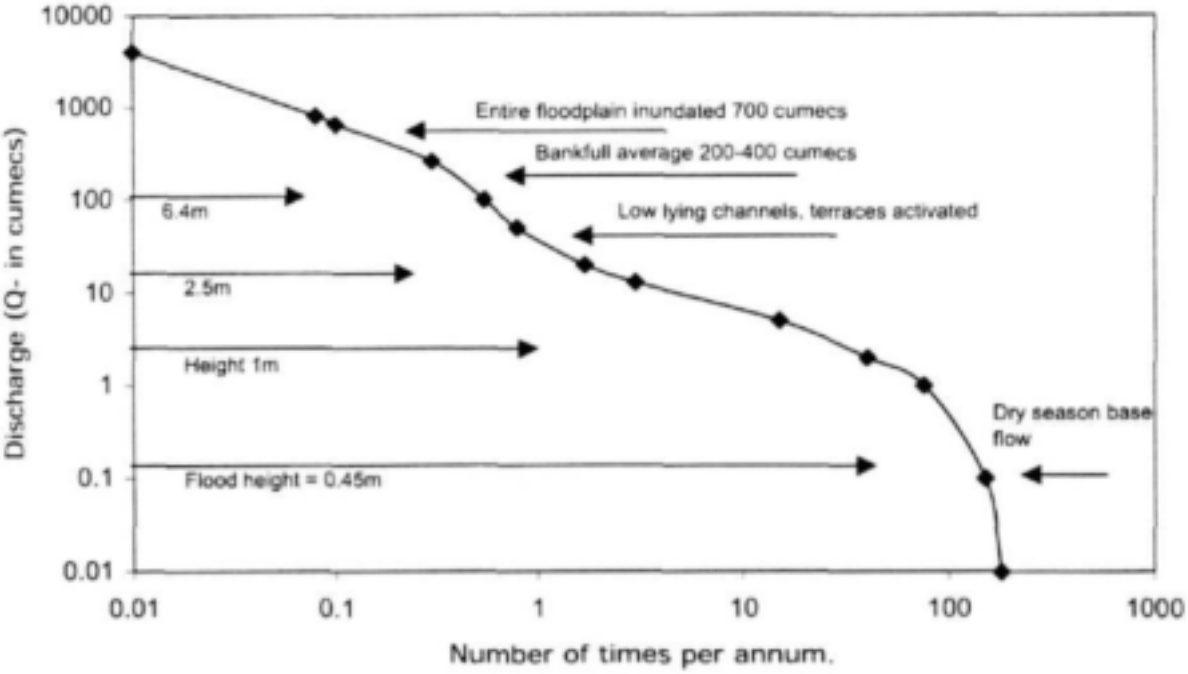


Figure 8: Flood frequency and inundation heights for the Luvhuvhu River at Pafuri

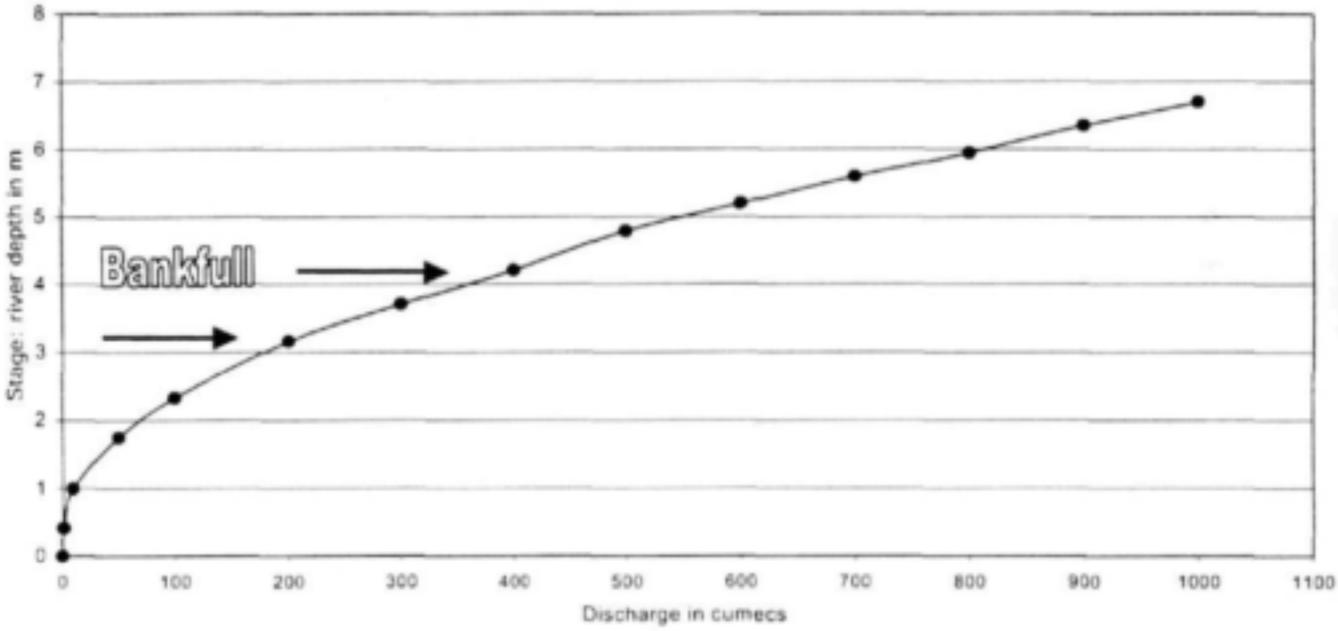


Figure 9: Stage/ discharge curve for the Luvhuvhu River at IFR site 3. Redrawn from Louw (1996) and van Bladeren (1996)

whereas I only used woody species. This suggests that both woody and herbaceous species distribution is determined by similar environmental variables, despite obvious differences in life histories. Distance away from the river and sediment-type appear to be the strongest determinants of forest type and may explain the associations of both woody and herbaceous species.

Transect height above the river was not as well correlated with community type (**Figure 3**), contrary to findings on the Zambezi and Tana Rivers (Dunham 1989, Hughes 1990). This could be due to the unusual floodplain structure at Pafuri where it is deeply incised at the top, broad in the lower reaches and interacts with the Limpopo at its mouth. I suggest, therefore, that height above the river is not a good surrogate for flood return frequency on highly heterogeneous floodplains. Confirmation of this would require a detailed analysis of floodwater rise or recession (and heights marked at specific discharges) to determine which landforms in different parts of the floodplain were subjected to similar inundation periods. Landform was more strongly correlated with forest type than height, and on highly variable floodplains seems justified for rapid and inexpensive flood return frequency determination.

Although I suggest that sediment type is important in delimiting vegetation communities at Pafuri, and this has been found in other arid areas (Dunham 1989), it may not be valid for all sites. For example, *Faidherbia* is found on clay and silt sediments elsewhere in Africa (*e.g.* Roupsard *et al.* 1999). Its absence from these soils along the Luvhuvhu is noteworthy and may be due to the much lower rainfall (less than half that on the Burkina Faso clay site, Roupsard *et al.* 1999). Similarly, *A. xanthophloea* is found on sandy sediments elsewhere in Africa, (*e.g.* Young and Lindsay 1988, Vesey-Fitzgerald 1974), but these also experience far higher rainfall. This implies that sediment type *per se* may be less important than its impact on local soil moisture regime.

Forest Dynamics:

Seral community replacement (such as occurs on Mkuze River floodplain- see chapter 2) does not seem to be occurring at Pafuri. Recruitment seems to be either cohorted (after events open up areas or permit drought safe establishment- *A. xanthophloea* and *Faidherbia)* or occurs *in situ* (Broad-leafed species, shade tolerant *A. robusta*, and open woodland *A. tortilis*). This also suggests that communities are self-replacing at the transect scale, otherwise the different demographic categories (Recruiting, Understorey and Canopy) should have shown up as separate groups in the ordination. At Mkuze, understorey species were frequently different to canopy species in a particular transect. Also, regenerating *Ficus* was identified at Mkuze by classification analysis (TWINSPAN) as a distinct community. The lack of succession on the Luvhuvhu River may be explained by the correlation of sediment type and landform with tree community. This would restrict certain dominant species to specific sediments on certain landforms. Sediment was not correlated with forest community type in Mkuze.

Both *Acacia xanthophloea* and *Faidherbia* show cohorted recruitment (**Table 3**). Also, sediment has been shown to determine tree distribution (**Figure 3**). I hypothesise that this is evidence that floods *and* depositional events are necessary for their recruitment. Large areas of relatively uniform aged stands of *A. xanthophloea* (photographs 5 and 7) appeared after a 1987 flood (Scott Ronaldson- Section ranger *pers comm.*.) and large areas of seedling recruitment occurred after the 1996 flood (photograph 6). These were on the North bank and hence not sampled in transects. *Faidherbia* recruitment is cohorted elsewhere and this is also linked to floods (Jobst 1996).

Photo 7: Surface erosion has exposed the root profile of these Fever trees. Note large investment in lateral roots and lack of a deep root crown.

Photo 8: The Massive trunks of *Xanthocercis zambesiaca* dot the floodplain, and although seedlings are abundant, almost no saplings were found. These trees are highly palatable

Demographies:

Demographic determinants include seed production and dispersal, germination, and survival (Jones *et al.* 1994). *Combretum imberbe*, *Kigelia africana* and *Ficus sycomorus* represent a group that has only adult trees and very low recruitment. The first two are savanna species, and *Kigelia* has unusual pollination, disperser and germination syndromes (unpub data), which may explain their lack of recruitment in the presently light limiting environment of the floodplain forest. *Ficus* usually produces massive amounts of seeds throughout the year, and these are well dispersed by many animal vectors. A few seedlings were found, but these were almost certainly ephemeral and located in shady parts of the floodplain. Elsewhere, *Ficus* seedlings require a high light environment to establish (Mkuze, Chapter 2; Phongolo River in Ndumu Game Reserve, and Olifants River in Kruger National Park- Unpublished data). I suggest that the recent severe drought eliminated most juvenile trees from all but the most mesic areas of the floodplain, and that recent floods have not resulted in establishment because adults have become too scarce in the system for adequate seed supply for recruitment (Galil and Eisikowitch 1968, Anstett *et al.* 1995).

The absence of any recruiting classes of *Ficus* from Pafuri is disturbing as many frugivorous species rely on the large amounts of fruit produced throughout the year. Low recruitment can be offset by adult longevity in a stochastic environment (Higgins *et al.* 2000), of which floodplains are a good example. Although *Combretum*, *Kigelia* and *Ficus* are known live over 300 years (Stephan Woodburne, CSIR dating laboratory *pers comm.*), any increase in adult mortality may cause local extinction. Further droughts, especially man induced through dams or abstraction, would thus be disastrous for the persistence of fig trees along the Luvhuvhu at Pafuri.

The second group (**Figure 7b**) shows recruitment, but relatively low juvenile survival and thus an absence of intermediate sized individuals. *Xanthocercis zambesiaca* showed massive recruitment from seed every year of this study but abundant signs of intense herbivory (browse lines on adult trees and all basal shoots eaten) suggests that herbivores limit sapling banks and juvenile escape (**Photograph 8**). Very high Impala and Nyala populations over protracted periods (in excess of several hundred years) may have a detrimental effect on *Xanthocercis* recruitment, although this is unlikely in an area where Anthrax is known to be endemic (Tinley 1976).

The final functional group shows relatively stable community structures, with a flat size class distribution, as illustrated by *Croton* and *Diospyros*. These species are relatively unaffected by drought or herbivory, or are resprouters (pers obs.). *Diospyros,* in particular, resprouts from broken or buried stems and, sometimes, exposed roots. *Croton* showed no signs of mammal herbivory in any transect. These species should be relatively unaffected by changes in flow regime.

Acacia and *Faidherbia* display adequate recruitment in both the seedling and intermediate size classes. Nevertheless, the cohorted nature of two species indicates the importance of events, such as large floods, in regeneration. In one area, *A. xanthophloea* occurs in three large stands, all of different sizes and even aged, and probably less than 80 years old as 1942 aerial photographs (job 165A-nos. 63089-092 Dept Surveys and Mapping, Mowbray Cape Town) show no large trees. Fever trees are unlikely to live longer than a century (Vesey-Fitzgerald 1974, Young and Lindsay 1988). As succession is not apparent, I suggest that these communities require regular floods to provide new sediments and open environments to initiate establishment.

F. albida appears to occur in bands of different ages, which become progressively younger towards outside of point bars or aggrading meanders (1963, 1970 and 1987 aerial photograph nos. 558, 652 and 908 respectively), similar to that found by Dunham (1989). Because transects ran parallel to the river, this data was not collected and the relationship only noted during sample collection for plant water relations (see Chapter 4).

Flow regime:

As mentioned earlier, flood regime has often been invoked as important in determining forest structure (*e.g.* Streng *et al.* 1989). In particular, flood frequency and height, and sediment movement are paramount in influencing tree establishment. However, there appears to be far less geomorphological activity on the Luvhuvhu River at Pafuri than elsewhere. For instance, compared to one North American floodplain, where a 100% sediment turnover per century was calculated for one reach of the Little Missouri River (Everitt 1968, ave. Q = 18cumecs, gradient 1:1170), there is remarkably little geomorphological activity (*e.g.* channel and sandbar migration) visible from aerial photo sets (numbers above), despite several significant floods.

The ecological effects of large floods (>1000 cumecs) are still not clearly understood, but they must have important implications for soil and bank aquifer recharge and seedling establishment. The canopy tree communities (except *A. xanthophloea* and *Faidherbia*) appear not to have responded to these events (1975,1977,1978,1988, 1996 floods- van Bladeren 1996) with increased seedling establishment which would have been detected as cohorts of intermediate size. By contrast, in northern KwaZulu-Natal *Ficus* showed various cohorts on several different river floodplains (Chapter 2 Figure 6).

The incidence of medium sized floods is low (and may be declining as further impoundments are built upstream) and this, combined with rapid flow recession, may mean that flood induced mortality at low elevations may not be a factor limiting adult survival as in other African systems. This is in contrast to Hughes (1988) who found on the Tana River in Kenya that Evergreen Forest, and *Acacia robusta* (subsp. *clavigera*) communities were only found above a height of 4m on the levees. This height was only flooded infrequently (on average every two years) and the longest duration being for 28 days over the entire 50 year data set for the Tana.

The effect of smaller floods may, however, be on recruitment, preparing soil and providing sufficient water for initial establishment. Unlike other floodplains with prolonged flooding (see Furness and Breen 1980, Hughes 1988, Dunham 1989), no grass or sedge community is visible at lower elevations at Pafuri. This indicates that either flooding time is insufficient to preclude tree growth, or that low lying tree species are sufficiently adapted to withstand the reigning flood regime. Prolonged submergence therefore does not appear to be a common feature of this floodplain. The effect of short-term submergence on the distribution of dominant species in each of the communities is discussed in Chapter 4 on Acacias.

Flood Recession time is undocumented on the Luvhuvhu, but a return to base flow conditions occurs within 3 weeks of a flood peak (Pafuri Section rangers Scott Ronaldson, Kobus Wentzel *pers com.*). Only very low-lying areas dominated by *Acacia xanthophloea* toward the confluence will retain water for longer periods. On the Tana River, and in the USA, prolonged flood recession is crucial for *Populus* seedlings to establish before the sediments dry out (Hughes 1990, Bradley and Smith 1985). While this notion is intriguing and worth investigating, it is remarkable that "drought safe" seedling establishment could be possible in such a short time after one flood. It may be that several smaller floods would be necessary over one season to maintain soil moisture at sufficient levels for seedling survival.

CONCLUSIONS:

Pafuri differs from many other African floodplains in being drier, geomorphologically stable and having large flood peaks with rapid recession. Communities are depauperate and characterised by episodic or *in-situ* replacement for many species. Distribution of canopy tree communities is strongly determined by the distance away from the channel and sediment type. Although community dynamics are not pronounced, demographic analysis suggests that some populations are certainly unstable, while others respond significantly to stochastic events.

The altered flow regime appears to have affected regeneration of *F. sycomorus* to the extent that its persistence in the system is in jeopardy.

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CHAPTER 4: DISTRIBUTION, RECRUITMENT AND WATER USE OF 4 ACACIAS ON A SEMI-ARID TROPICAL FLOODPLAIN:

DETERMINANTS OF THE PAFURI SYSTEM.

ABSTRACT:

The environmental correlates of four different Acacia species were studied on the Luvhuvhu River floodplain in the Kruger National Park with the aim of explaining observed distribution patterns and identifying limiting life history stages. Greenhouse experiments were also conducted to determine factors affecting establishment success and the effect of morphological differences on survival and water use. Water relations of *Acacia* and other reference tree species were examined using xylem pressure potentials, water use efficiency ($\delta^{13}C$) measures and tree water source analysis (δD and $^{1}\delta^{8}O$ ratios) for the Pafuri area in the dry season.

Germination and growth experiments showed that all species could establish on all sediment types (except pure sand, which only *Faidherbia* tolerated), but this was not borne out in the field. The growth experiment indicated significant differences in seedling rooting strategies. *Faidherbia* displayed strong taproot development, in contrast to *Acacia robusta, A. tortilis* and *A. xanthophloea* that showed lateral rooting. This was corroborated by field measurements of adult root architecture. Root to shoot ratios of greenhouse seedlings indicated a stronger relative root investment in *F. albida* than in the other species. Difference in height attained by the study species was low, except in *A. tortilis*, which had the slowest relative growth rate. *Acacia xanthophloea* and *A. robusta* displayed the greatest biomass accumulation after 4 months.

All species survived experimental flooding for periods in excess of the greatest of natural events in the system. Observed distribution patterns are thus probably a result of sediment mediated water availability, and not flood induced seedling mortality as reported elsewhere.

Some species were transpiring freely in the driest season, indicating access to either ground- or river bank water (*Faidherbia*). In contrast, *Acacia tortilis* and *A. xanthophloea* had noon pressure potentials approaching those of desert adapted plants. Water use efficiency did not vary among microphyllous species, but

decreased with increasing size within the *Acacia* species. Only *Faidherbia* did not show any decrease in efficiency with increasing diameter. Tree water source (*i.e.* ground water versus river or bank aquifer) could not be determined by isotope typing due to insufficient differences between environmental pools.
Each species' degree of drought-stress tolerance partly explains its distribution patterns, although it appears that substrate and the seedling stage are more important limiting factors.

INTRODUCTION:

Four different microphyllous tree species (three *Acacia* spp. and *Faidherbia albida*) occur on the Luvhuvhu floodplain at Pafuri. Here, the river flows through an arid system and forms different microhabitats with relation to sediment type, height above the river, distance away from channel, and time since last inundation or depositional event. In Chapter 3, tree community distribution was correlated with various environmental factors. This chapter explores the relationships between these physical factors and biological attributes of the different species. In particular, what factor explains why *Faidherbia* is restricted to sandy substrates, low down on the river profile?

Factors that limit *Acacia* populations have been given as seed predation, soil nutrient status, fire and herbivory (Midgley and Bond *in press*). However, the importance of regeneration site and water utilisation has seldom been studied in determining *Acacia* distribution (Midgley and Bond *in press*). Important species attributes influencing recruitment and distribution are differences in seed biology, seedling growth characteristics, adult rooting morphology and leaf physiology, flood and drought tolerance, and phenology. On floodplain systems, height above the river (as a surrogate for flood return time) and sediment type are the most commonly cited abiotic factors influencing tree distribution (Hughes 1988, Dunham 1989, Hall and Harcombe 1998)

Seed biology.

Establishment patterns could be determined by either the presence of seeds or specific germination requirements. In some areas, seed bank decimation by

Bruchid beetles (Miller 1996) or fire germination cues (Mucunguzi and Oryem-Origa 1996) are critical limiting factors. In this context, I questioned what the differences in seed characteristics are that might affect availability and germination in the floodplain environment. For example, if a species is shown to have low seed dormancy, this might explain its response to ephemeral events, and affect its distribution by limiting it to specific areas that suit establishment when seeds are viable. The different species' seeds' abilities to resist germination was used as a surrogate for their propensity to form seed banks.

Seedling morphology

Microphyllous and compound -leafed species' seedlings are light demanding (Givnish 1979). Seed mass is used as a surrogate for degree of shade tolerance (Salisbury 1942, Jones *et al.* 1994). Small seeded species may have difficulty establishing in coarse sediments as small embryonic roots are more vulnerable to nutrient and water limitation in sands, and light limitation in shaded habitats. I wanted to determine the effect of sandy and clay sediments on seedlings growth and biomass allocation patterns, and if ambient light was correlated with seedling establishment in different habitats.

Rooting

It is known that *Faidherbia albida* (syn. *Acacia albida*) has a very deep root system in many arid areas (Wickens 1969, Roupsard *et al.* 1999). However, in other areas this species persists in mesic and temporarily flooded paddy systems and floodplains (personal observation) which would seem to militate against having deep roots in all conditions. Roupsard *et al.* (1999) record that *F. albida*'s roots vanish in the vicinity of the permanent water table at 7m in Burkina Faso on heavy clay soils. I needed to know what the differences in seedling and adult rooting patterns were, and if they affected distribution patterns at Pafuri. Floodplains provide a useful location for studying root architecture as lateral riverbank incision exposes almost complete root profiles.

Phenology and flood and drought tolerance

Acacia xanthophloea (the Fever tree) possesses significant stem photosynthetic tissue (its characteristic green bark), not observed in other species, and is the first species to lose its leaves with the onset of the dry season (pers obs.). Does this influence its ability to withstand moisture stress, or prolonged flooding?

Peculiarly, *Faidherbia albida* is wet season deciduous (Wickens 1969), with all other species being to a greater or lesser degree facultatively drought (*i.e.* Winter) deciduous (unpublished data). Roupsard *et al.* (1999) investigated this reverse phenology at length, and determined that *Faidherbia* is facultatively phreatophytic, using surface soil moisture only when it is freely available, otherwise transpiring freely using ground water. However, they make no attempt to explain the adaptive significance wet season deciduousness. I investigated two alternative hypotheses for this trait.

1. *Faidherbia* avoids summer flooding by being wet season deciduous as it does not have to maintain a full canopy when its roots are partially oxygen starved. It has to utilise deep ground water to grow during the dry season and therefore has a deep taproot.
2. *Faidherbia* has to avoid summer heat stress by photosynthesising in the cool dry season. To do this it invests heavily in root resources to tap ground water, and is thereby able to expand its potential niche to include sandy substrates unavailable to other species.

Flooding has also been shown to alter a species' position on a light gradient, (Hall and Harcombe 1998), and reduce transpiration rates (Birkhead *et al.* 1996). Does flood tolerance explain the distribution patterns on the Pafuri floodplain observed in Chapter 3? Are *Faidherbia* and *Acacia xanthophloea* more tolerant of submergence than *A. tortilis* or *A. robusta* as they are found on landforms lower down on the river profile?

Water relations

The water requirements of floodplain trees, water limitation in establishment and persistence and water movement in floodplain sediments are poorly understood (Hughes 1988, but see Birkhead *et al.* 1996). Little work on the ecological significance of *Acacia* water relations has been published for southern Africa (Bate and Walker 1993). Dunham (1990) could not determine the role of flooding in the initiation of *Faidherbia (=Acacia) albida* woodland, but suggests that climate and edaphic factors play a major part in seedling establishment. Jobst

(1996) suggests that *Faidherbia* mortality increases with declining water tables, and populations are adversely affected by a decrease in floods that facilitate establishment.

I wanted to investigate what aspect of tree water relations affected distribution patterns and at what life history stage the effect is strongest. In particular, are there differences between species in adults' water use efficiency (WUE, *sensu* Zimmerman 1983), with those in arid sites having the higher efficiencies? Or, is there evidence that adults and seedlings of the same species experience different plant moisture stress (PMS) and how would this act as a selective pressure?

Water source.

The structure of the floodplain presents different possible water sources to trees, for example bank aquifers are accessible to riverside trees when young, while species at the floodplain margin must rely on soil water for establishment. White *et al.* (1985) showed that it was possible to determine plant water source from D/H ratios in tree sap. Differences in water source between neighbouring trees have been shown by Ehleringer and Dawson (1992) for streamside plants in arid areas, but its application to riverine trees is untested in South Africa.

A hypothetical suite of water sources available to a tree was determined from the literature (see Dawson 1993), and tested empirically through water isotopic characterisation. River water, the bank aquifer (from bores close to the river) and the levee water table were all sampled and tested. If local water in the form of summer thunderstorms (highly depleted in Deuterium (D or ^{2}H)) or, alternatively, river water penetration (usually D enriched through longer evaporation) were important contributors to ground water (see Verhagen *et al.* 1974, Vogel and Van Urk 1975), it should be possible to distinguish them through the highly fractionated isotopic signal they would impart. An indication of plant water source was attempted by mechanically extracting xylem water from fully suberised stem sections, and analysing it for Deuterium. I asked if the signals in environmental pools are different, and is this reflected in the various species' xylem water.

Plant moisture stress.

Water stress studies help to reveal degrees of stress (midday values) and rates of rehydration (*e.g.* Birkhead *et al.* 1996) in different plants. Pressure bombing is an instantaneous indication of PMS, whereas ^{13}C ratios are indicative of integrated water use of the previous growing season of the plant (Ehleringer and Cooper 1988).

Different size trees (varying root depths and canopy sizes) growing on different landforms and sediments would experience very different soil moisture regimes. I compared species and life history stages in the driest months to determine their drought stress and indicate any correlation with tree age and efficiency.

How all these factors affect the distribution and persistence of the microphyllous species is the thesis of this chapter.

METHODS:

Study site:

The Luvhuvhu River forms a floodplain 16 km long and 4 km wide before its junction with the Limpopo River in the far north-eastern corner of the Northern Province, South Africa (Chapter 3 Figure 1). This, the Pafuri region of the northern Kruger National Park (Photographs 1 and 2; 22°26′ S: 31°15′ E), receives an annual average rainfall of 362mm and has a summer mean maximum temperature over 30°C (Tinley 1976). The floodplain drops from an altitude of 210m.a.s.l. where it exits Lanner Gorge to 195m where it joins the Limpopo, a distance of 16 km. The alluvium is over 30m deep across much of the floodplain and consists of a highly complex layering of coarse and fine sediments (DWAF 1992 borehole reports); bedrock control of flow is negligible. Rain comes almost exclusively in summer in large storms, which result in local floods. Large floods are generated by late season cyclonic ingression from the Moçambique channel (van Bladeren 1996). Due to the relatively small catchment (5110 km^2), flood recession is usually rapid. The first recorded instance of the river drying up occurred in 1965, and it has been seasonal ever since, only flowing all year round in years of above average rainfall *e.g.* 1998. The North bank of the river was subject to clearing for agriculture until 1967.

Climatic data (supplied by the Weather Bureau of SA, Dept Environmental Affairs and Tourism) for the site are presented for the end of the dry season in the study year (1998). This data was collected to provide the climatic context for the water use analysis.

Rainfall measures were obtained from the Pafuri Ranger over the two field summers (October to February) in 1997/98 (270 mm) and 1998/99 (262 up to Jan 7, mostly in 3 storms).

Table 1: Mean temperature and humidity for three times of day in the two driest months at the Pafuri study site in 1998 (DEAT- Weather Bureau data).

	September		**October**	
Temperature °C	Mean	S.D.	Mean	S.D.
08h00	20.7	2.40	23.3	2.85
12h00	30.5	4.06	30.4	6.04
20h00	24.7	3.62	26.5	4.85
Humidity %	MEAN	S.D.	Mean	S.D.
08h00	69	7.8	77.5	9.19
12h00	38	12.0	53	4.24
20h00	47	13.0	68.5	4.95

Seed biology

Locally collected seed of the four study species and *Acacia nilotica* (as a hard-coated control species) was weighed. Soil sieving to quantify in-situ seedbanks was abandoned due to the heavy clay sediment being impossible to sort carefully.

Intact, first year, healthy seeds (n=50 for each treatment) were submerged in 50% H_2SO_4 for time intervals varying from 30 to 300 seconds, then washed and left to germinate on pre moistened filter paper treated with Capstan-C to prevent fungal contamination. Seeds were also physically scarified with sandpaper to check for imbibition and to act as a control for seed viability. A further control group were washed in water only and allowed to germinate. I conjectured that average annual seed exposure to scarifying factors is roughly equivalent to 90 seconds acid exposure. This was arbitrarily determined as it was the average time it took for 50% of seeds of all species to imbibe.

Seedling establishment

Five transects (average 500m long and 10 m wide) from the river to the floodplain's edge were searched for established seedlings (size classes 1,2 and 3) of all species at the end of the rainy season (February). Each seedling's location was recorded as being in full sun, semi-shade (mixed canopy) or full shade, and substrate as being predominantly sands, clay or silt by a simple moist rolling test. Similar search effort was expended in each area or landform (see Chapter 3) until 120 seedlings for the least common species (usually *Faidherbia*) were counted.

Growth rate and allocation experiment:

To confirm that seedling location in the field was either driven by sediment preference or water regime, germinated seeds were planted in a four-factorial experiment into two different substrates under two water regimes in 50-cm deep containers and monitored for seedling survivorship, and root and shoot growth rates. The two substrates used consisted of (**1**) 70% silt/clay and 30% fine river sand and (**2**) 80% river sand and 20% clay. This emulated the extremes of the major soil types found on the floodplain (see Chapter 3, Table 2) and all sediments were taken from under actively nodulating adult trees. Sixteen pots were kept in full sunlight in the UCT Botany greenhouse during summer and watered with an automated sprinkler system in two water regimes. "Moist" conditions consisted of a fine spray every third day for 3 minutes, while "wet" conditions required watering every second day for 5 minutes. Plants were harvested at 120 days to ascertain root and shoot biomass and length, and to examine morphological characteristics, in particular root behaviour on different sediments. Only data for the 70% silt and clay /30% sand substrate were used for root and shoot length and biomass determination, as survivorship was too low in the sand experiment.

Flooding experiment

Another factor which may delimit floodplain tree distribution is flood tolerance. To test each species seedling's ability to withstand complete root submersion, a further trial was initiated with only one substrate used (Moist Silt- 40%silt and clay and 60% fine sand) as seedling survivorship was not optimal in the predominantly clay or sand mixes. The four species were grown under a moderate water regime (every third day for 3 minutes), for 99 days after which time the pots were submerged for 3 weeks to simulate a natural flood. Eight pots were submerged in drums of water until the base of the seedlings was covered.

After a week, anoxic conditions were confirmed by the presence of H_2S in the sediment. The physiological impact of flooding was measured by relative decline of seedling photosynthetic rates in full sunlight (Blom *et al.* 1990). Although this was not ideal, other more expensive or technically challenging methods, such as chlorophyll fluorescence, were pragmatically avoided. Photosynthetic rates of each species were measured before, after 1,2,3,6,15 and 21 days submersion with a Licor 6400 Infra-Red Gas Analyser to determine if flooding had a significant impact on seedling growth potential. The percentage difference in maximum assimilation rate in full sunlight for the different species before flooding and after 21 days was used to determine if flooding had a significant impact on seedling photosynthesis. Three weeks was used as being the longest natural flood based on flood hydrograph records and observations of the resident section rangers (Scott Ronaldson *pers comm.*). Lower lying pans may experience longer submersion, but this is restricted to small areas of the floodplain.

Adult rooting architecture

Adult tree water requirements and flood tolerance may be reflected in root architecture. To investigate this, individuals of *A. robusta, A. tortilis* and *Faidherbia* were examined where root crowns were exposed on undercut levees, and where their rooting patterns were clearly observable (see Chapter 3, Photographs 7 and 10). *A. xanthophloea* (not usually found on levees) roots were counted where local subsidence had exposed the root crown (as happened after the 1991/2 drought) or where floods had toppled, by washing away sediment, several trees in one area. Architecture was examined by counting all roots greater than 50-mm diameter in different depths below the root crown. Categories of roots were lateral surface- (*i.e.* less than 1m deep), crown- (between 1 and 2m deep) and tap-roots (deeper than 3m).

Water relations

Several aspects of the water relations of dominant canopy trees (four study species and two reference species) were investigated at Pafuri in the driest season to determine phreatic water constraints on vegetation distribution. This was achieved in three ways:

Water source.

Tree xylem water samples were analysed to determine which possible source, or combination thereof, they were drawing on during the driest season. Xylem samples were taken low down on the stem of mature trees, immediately squeezed in a modified vice, and the resultant xylem sap immediately captured in an eppindorf tube, sealed with parafilm tape and refrigerated to avoid further fractionation. Unfortunately, several species' wood was too dense to express sufficient quantities of water rapidly except Faidherbia and Ficus, both of which yielded water freely. The expressed water was centrifuged to remove any solutes that could contaminate the D ratio. This method, although compromising precision, was used over cryogenic (freeze-sublimation-capture) or azeotropic (D-free solvent mediated) distillation due to their prohibitive cost and the absence of the correct laboratory set-up.

Deuterium analysis was performed by the Archaeology Department at University of Cape Town using the Coleman method of reaction with Zn at 500°C and the resulting H and D mixture was collected in sealed glass vials for analysis in a Finnegan MAT252 (Bremen, Germany) mass spectrometer.

Xylem pressure potentials.

To investigate plant moisture stress, fully -leafed cut shoots were sampled in October (driest month) at dawn and noon with a Scholander Bomb to determine their water or xylem pressure potential. Absolute values are strictly comparable only between closely related groups with similar leaf form, *e.g. Acacia* and *Faidherbia*, but the differentials can be informative across unrelated species. To determine any effect of distance from the river, *A. xanthophloea* individuals of similar diameter were sampled on the bank and on the levees, 60m away from the river. No other species' distributions permitted this. The effect of size on pressure potential was measured by pressure bombing young *A. tortilis* trees (<3cm diameter at ground height) where they occurred on the same landform near adult specimens.

Water use efficiency.

Pressure potentials give only an instantaneous measure of plant moisture stress, but integrated indices of stress may be more ecologically informative. Canopy branches representing the previous years growth were sampled for all the *Acacia* species, *Faidherbia*, *Ficus sycomorus* and *Trichilia emetica*. These were analysed for 91^{13}C to determine their water use efficiency (WUE), a measure of stomatal conductance, and thus, indirectly, water availability in the growing season. A Finnegan MAT252 mass spectrometer and Standards of *Nasturtium* spp. (known δ^{13}C of –29.65‰) were used. Standards were run every five samples and each sample datum was corrected with a moving average. A standard regression was constructed for each microphyllous species.

All statistical analyses were conducted using single and multivariate ANOVAs in Statistica for Windows (2000, release 5.5 Statsoft Inc, Tulsa OK). Root:Shoot ratios were first ln-transformed. Significantly different means were determined by a post hoc LSD test.

Water table measurements

An important determinant of tree distribution and adult persistence may be access to ground water (Hughes 1988). Ground water depth was sampled to determine the availability of water in relation to root architecture and water relations. Boreholes were sunk throughout the floodplain by the Department of Water Affairs after the 1991/2 drought. Water levels in several boreholes (Numbers 275, 276, 277, 281) were measured twice during the study to determine water table depth in late summer (February-March, wet season) and mid spring (September-October, driest season). Readings were then checked against known surveyed heights of the nearest river reach to give an indication of relative water table height, and thus the tendency for water flow to leave the channel. A water table lower than the riverbed would indicate a strong tendency for outflows, which would be expected during the dry season in an arid area, but may well be reversed after summer rain, or a large flood event (see Figure 2 in chapter 3).

The phreatic surface (the capillary zone above the water table available to trees) usually occurs above the permanent water table. This was impossible to measure without expensive technology (neutron probes) or major excavation and was ignored.

RESULTS:

Germination

Seed sizes (n=10 (s.d.)) vary from 0.034g (0.002) for *A. xanthophloea*, 0.054g (0.01) for *A. tortilis*, 0.15g (0.03) for *Faidherbia* to 0.225g (0.08) for *A. robusta*. This suggests that *A. robusta* is most shade tolerant and *A. xanthophloea* the least.

Germination ability (**Figure 2**) of the four species differed markedly. *A. xanthophloea* showed almost no dormancy potential at all as a third of the seeds germinated without any treatment. Although *F. albida* possesses a tough leathery seed coat, it showed a relatively high germination percentage with little acid exposure. More than 65% of *F. albida* and 97.5% *A. xanthophloea* seeds germinated after 90 seconds acid exposure, compared to less than 19% for the other species and the controls. *A. robusta* and *A. tortilis* showed very little response to acid, but almost complete imbibition after physical scarification. The high percentage of all species that germinated with physical scarification implies that seed viability could not have influenced results.

Seedling location

Established seedlings of *Faidherbia* were almost exclusively (97%) found on sandy substrates, in high light environments (66% of all *Faidherbia* seedlings, **Figure 3**). *A. robusta* showed the greatest tolerance of both substrate and light environments, but was most abundant on clays in shaded areas (62%). *A. xanthophloea* was restricted to clay areas (100%) and were almost exclusively out in the open (97.3%). *A. tortilis* seedlings were found mostly in high light environments (80%) on clays (98.5%, and predominantly on Impala middens).

Growth experiments

Seedling survivorship in growth trials paralleled field observations of clay/silt substrate preference for *Acacia xanthophloea, robusta* and *tortilis* which were significantly different to *Faidherbia* (Kruskal-Wallis Anova by ranks, $\chi^2 = 34$, df=9, P<0.0001, **Figure 4**). For significantly different groups, each species on each sediment type and each water regime were compared. *F. albida* showed no significant difference on the two substrates or water conditions (Mann Whitney U test, U=1, P>0.1). *Acacia robusta* had significantly better survival on silts versus sands (U=0, p<0.028), and although better with a higher water regime, this was not significant (U=1.5, p=0.057). Even though *A. xanthophloea* showed better establishment on moist silt and wet sand to moist sand, this was also not significant (U= 6.5, P=0.686). *A. tortilis* did not survive in the sand trials.

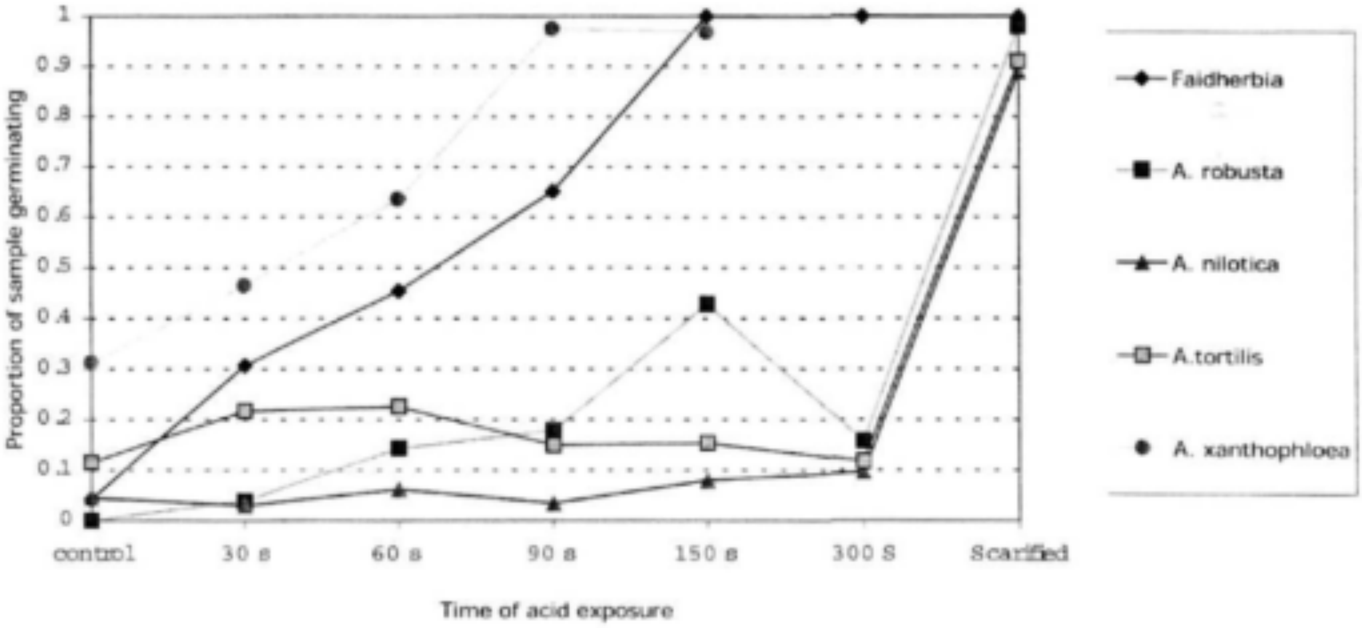


Figure 2: Acacia seed germination with acid exposure. Control seeds were only washed in water, scarified seeds had seed coat physically abraided.

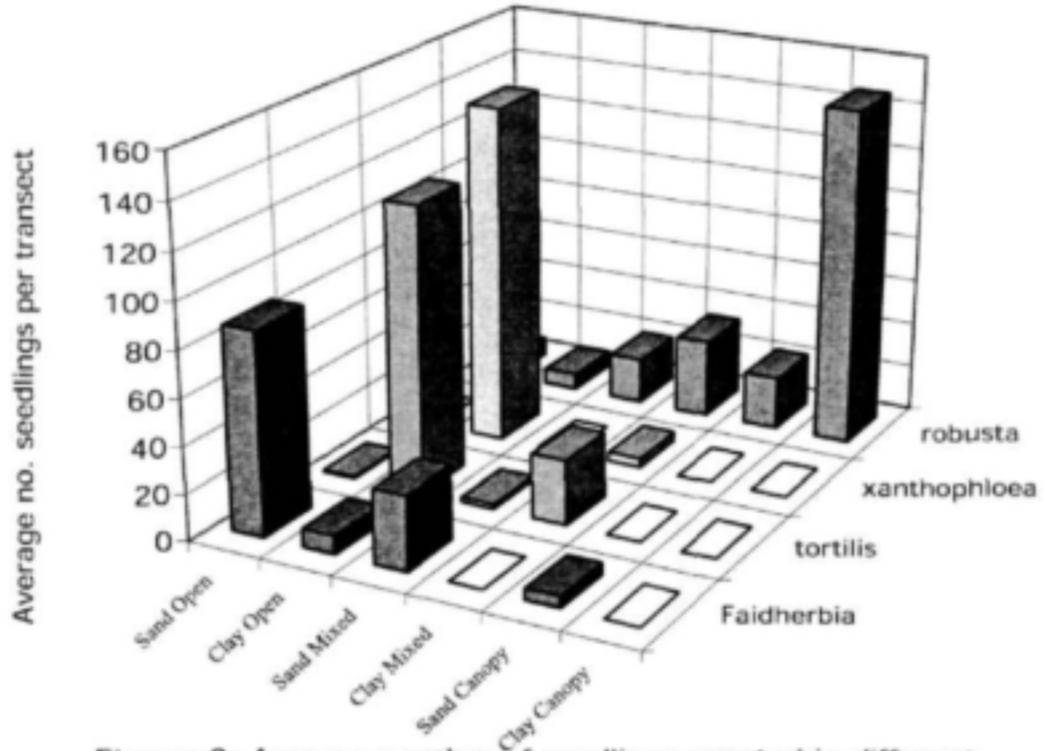


Figure 3: Average number of seedlings counted in different environments on the Luvhuvhu floodplain at Pafuri. Open, mixed and canopy refer to relative light availability. Only *Acacia* species epithets given.

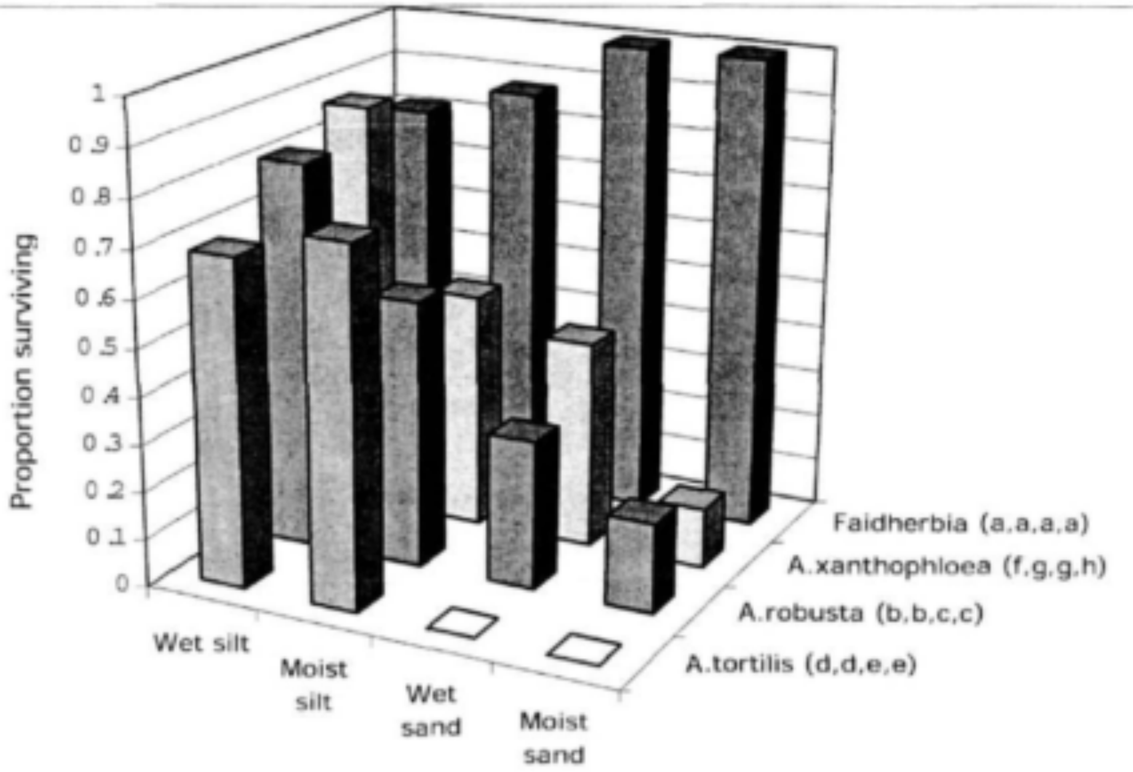


Figure 4: Establishment success of the four study species in greenhouse trials. Letters after species indicate if means are significantly different or not.

Root growth of *F. albida* was rapid and straight in sandy sediments (reaching the container bottom at 500mm in 61 days), but less so in silt and clay where root deformations were more frequent (64% of taproots were physically deformed by twisting). No differences were observed in the other species. Although *A. robusta* and *A. xanthophloea* had the most massive roots (**Figure 5a**), these were concentrated superficially and laterally, and only *Faidherbia* showed meaningful taproot development (**Figure 5b**).

Root:Shoot ratios were significantly different between species (Two-way ANOVA in a 4X2 design, F=75,67, P<0.000001), but not between moisture regimes within a species (F=0.76, p>0.4). The main affect for species was not qualified by moisture.

Root growth in *Faidherbia* occurred at the expense of shoot elongation and overall biomass accumulation. Root versus shoot allocation patterns clearly display the massive investment of *Faidherbia* in its water sourcing potential. *Faidherbia* was very significantly different to all other species (LSD test, p<0.00001, **Figure 5c**). *Acacia robusta* and *A. xanthophloea* invested heavily in shoot growth at the expense of deep roots. Although *A. tortilis* showed the poorest root development of all (**Figure 5a**) it allocated proportionally more to roots than did *A. xanthophloea* (**Figure 5c**). This was significant, and only marginally so, for the "moist" water regime (LSD post hoc test, p<0.05). All species nodulated.

Height measurements indicate the rapid growth potential of *A. xanthophloea, A. robusta* and *F. albida* under suitable conditions. *A. tortilis* showed the slowest growth rates under all conditions (**Figures 5b**).

Flood tolerance

Photosynthetic rates before and after experimental flooding of seedlings (**Table 4**) show that *A. robusta* and *A. xanthophloea* displayed no signs of photosynthetic inhibition. Only in *Faidherbia* and *A. tortilis* was a flooding effect noted (with a significant decline indicated by a dependent paired t-Test).

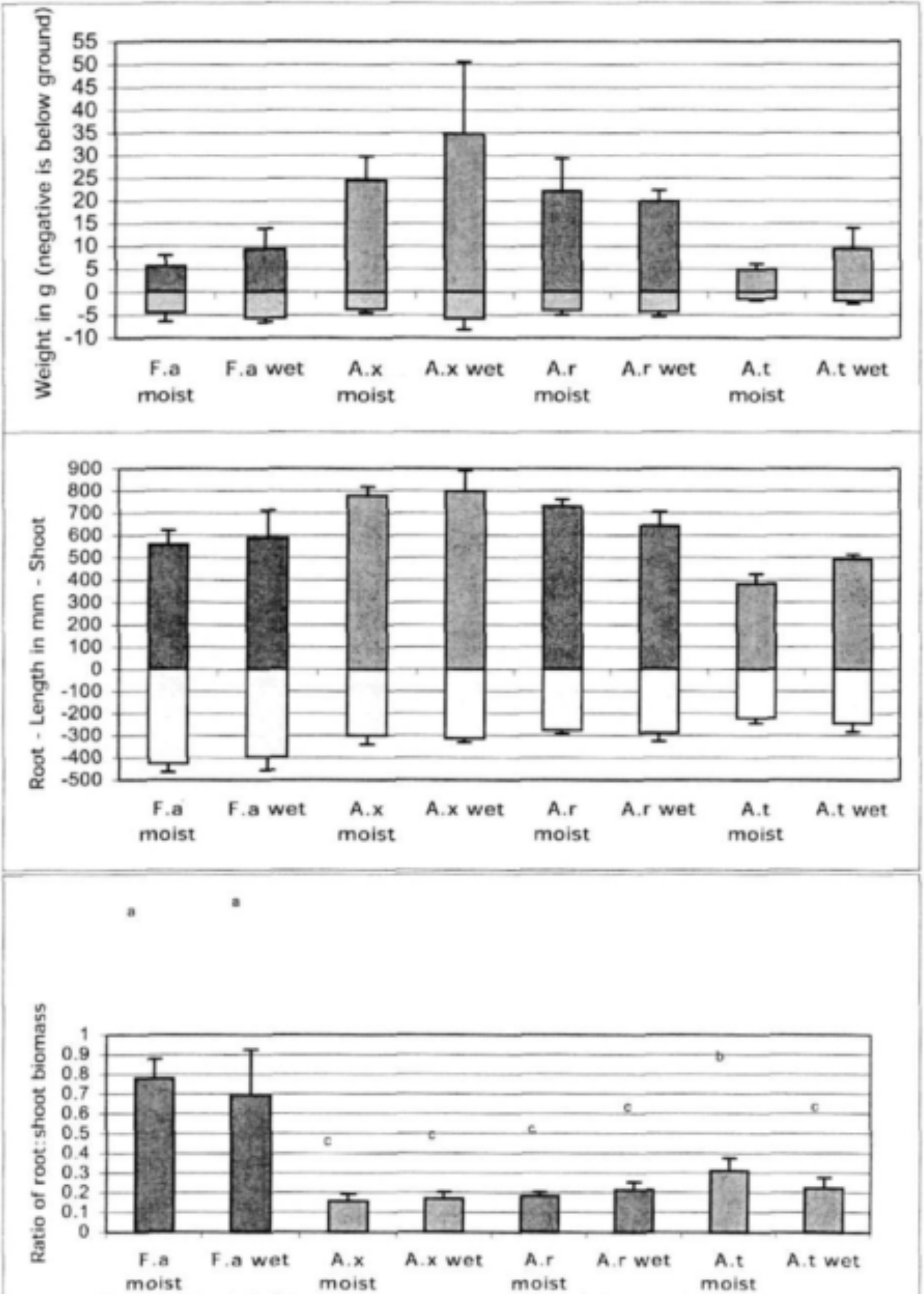


Figure 5: **(a)** Biomass in g dry weight, **(b)** growth in mm, and **(c)** root:shoot ratios for four microphyllous species on two water regimes in greenhouse experiments. Letters indicate significantly different means.

Table 4: Maximum photosynthetic assimilation rate (measured in $\mu mol.m^{-2}.s^{-1}$ + standard deviation) before a simulated flood, after 6 days and 21 days of being submerged (n=8).

Species	Before experiment Mean (s.d.)	6 Days submerged	21 days fully submerged	Percentage decline after 21 days	t-Test (df=4) significance	
					t=	P<
Faidherbia	16.92 (2.91)	15.76 (5.98)	4.57 (0.42)	72%	17.06	0.000069
Acacia tortilis	22.12 (5.05)	22.84 (2.74)	8.56 (2.34)	61.3%	6.2	0.0034
A. robusta	16.34 (3.91)	14.29 (5.53)	17.13 (1.64)	-4.8%	-1.25	n.s
A. xanthophloea	17.18 (2.85)	17.64 (2.13)	16.80 (1.89)	2.2%	0.693	n.s.

Adult root architecture

Acacia xanthophloea has very shallow roots, while *A. tortilis* and *A. robusta* have a spread of shallow and deeper roots (**Figure 6**). *Faidherbia* shows distinct taproot development and relatively fewer lateral roots.

Water relations

Water source

Limited environmental differences in δD and δ^{18}Oxygen between river and ground water sources in all but one site prohibited useful analysis of tree water source (**Figure 7**). As the simple extraction technique used involved errors in excess of 5‰ δD and 1‰$\delta^{18}O$, and maximum environmental differences only ranged from12‰ δD to 2‰$\delta^{18}O$, the analysis of xylem D was no longer considered worthwhile and was discontinued.

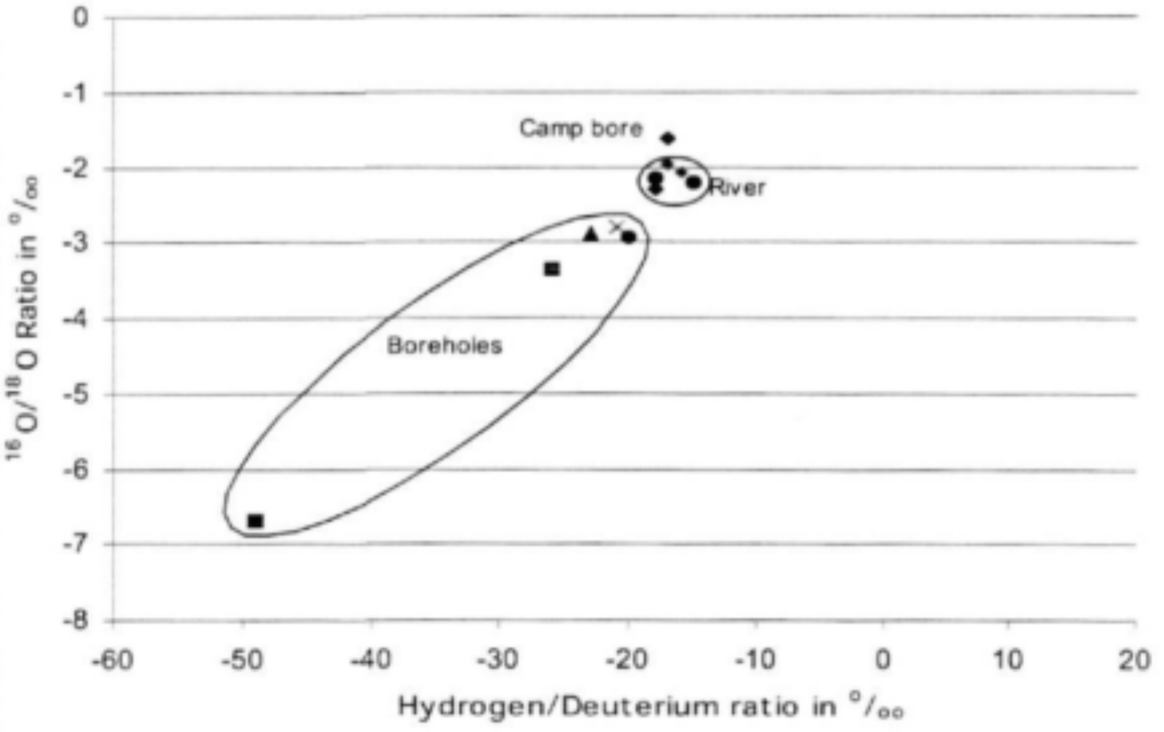


Figure 7: Isotopic signatures of environmental water sources.

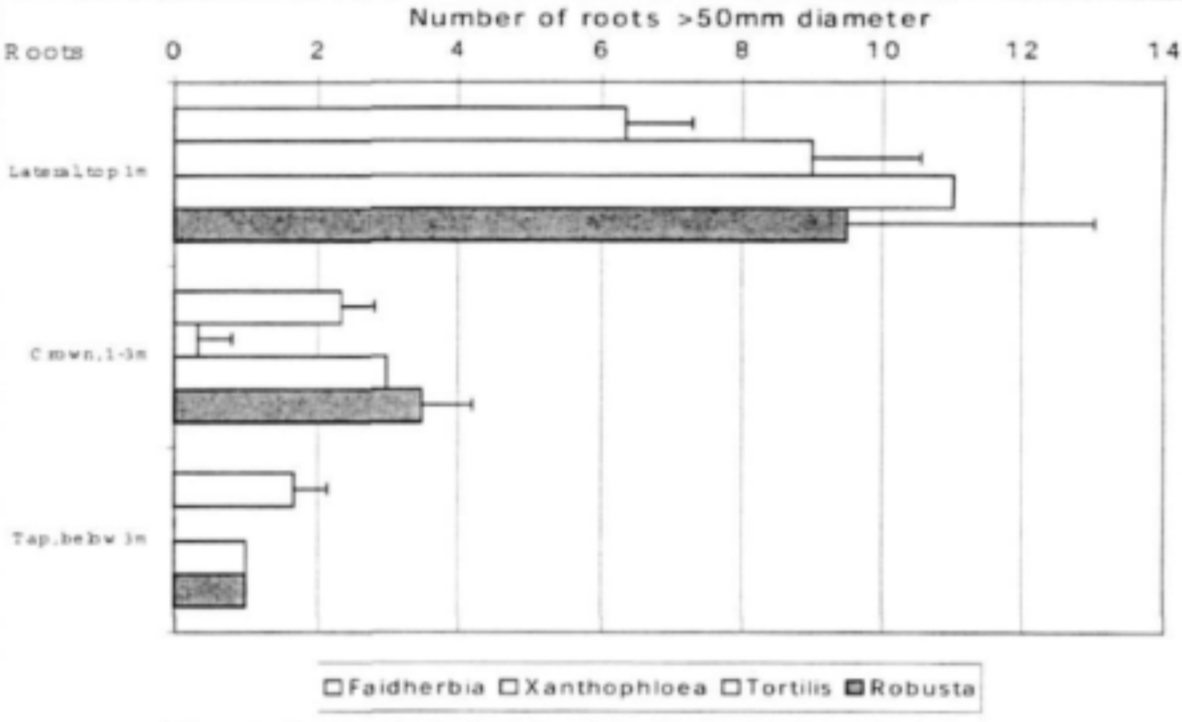


Figure 6: Vertical distribution of roots of adult trees on the Luvhuvhu floodplain.

Not surprisingly, the river samples clustered quite tightly due to rapid horizontal mixing, whereas the borehole samples were spread over a wider range owing to greater compartmentation (**Figure 7**). Boreholes situated close to the riverbank (Picnic, camp bores) and hence tapping into the bank aquifer, would be expected to resemble the river signature most closely. This was indeed the case in the camp bore, but no difference was noted between the picnic and other boreholes away from the river's edge. The Mangala bore (DWAF number G40- 281) showed the only quite distinct isotopic ratios.

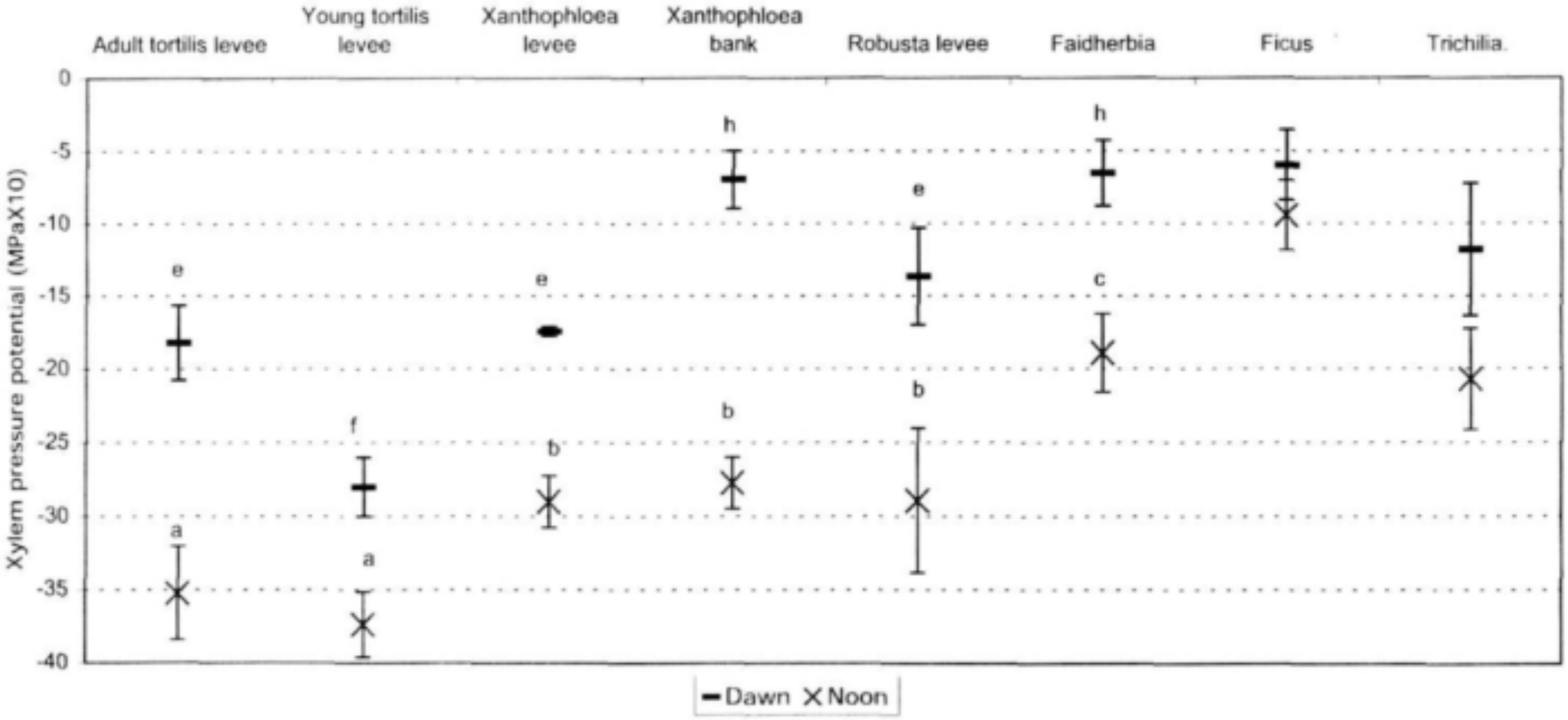
Xylem pressure potentials

The pre-dawn potentials (**Figure 8**) were highly significantly different between species (One-way ANOVA, df =(7,53), F=25.935, $p<0.0000001$) as were noon readings (df (7,53), F=30.229, $p<0.0000001$). A MANOVA (multivariate test, treating both as dependent variables) returned similar significant differences (Roa's R= 16.61, df1=14, df2=104, $p<0.0000001$), indicating that species has a highly significant effect on water potential. Significantly different means (using the post hoc LSD test at the $P<0.01$ level) are indicated by different letters in

Acacia tortilis showed very low water potentials (mean of –3.5MPa for adults, -3.7MPa for saplings). Younger trees were less effective at nocturnal rehydration, with dawn potentials of –2.76MPa compared to adults which had dawn potentials of –1.76MPa.

There was no difference between noon potentials of *A. xanthophloea* on the bank or levees (mean –2.78MPa versus –2.81MPa respectively). However, trees on the levee had dawn potentials (-1.69MPa) far below those on the bank (-0.7MPa). *Acacia robusta* on the levees had similar noon readings to *A. xanthophloea*, but dawn potentials were significantly higher (mean –1.4MPa).*Faidherbia* did not generate low pressure potentials during the day (maximum –2.2MPa) and had very high dawn potentials (mean –0.64MPa). *Ficus* showed the smallest diurnal fluctuation of all species, and the highest potentials with a total range of only –0.3MPa to –1.21MPa. *Trichilia* had a greater range than *Ficus*, and significantly higher noon potentials than all *Acacia* spp.

Figure 8: Dawn and noon water potentials (in MPa X10) of Acacias and reference trees. Letters indicate if means at similar times of day are significantly different.
Errors bars are one s.d.



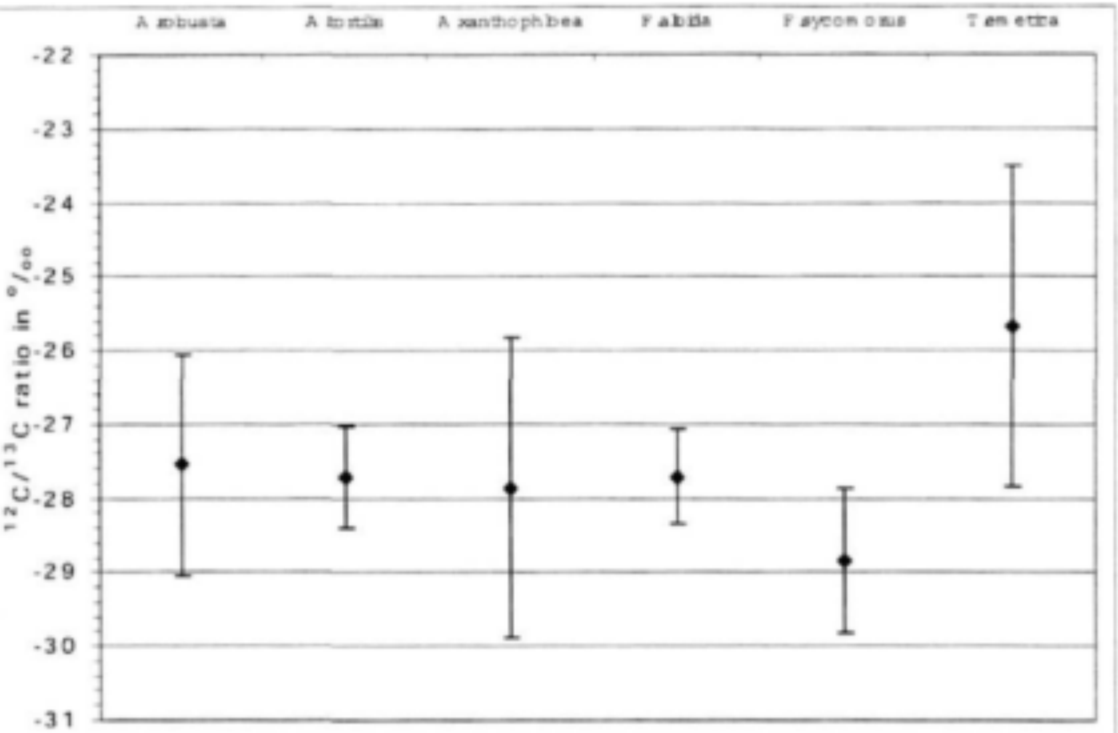


Figure 9a: Mean $^{12}C/^{13}C$ ratios for four study species and two broad leafed reference species in the dry season at Pafuri. Error bars are ± 1 s.d.

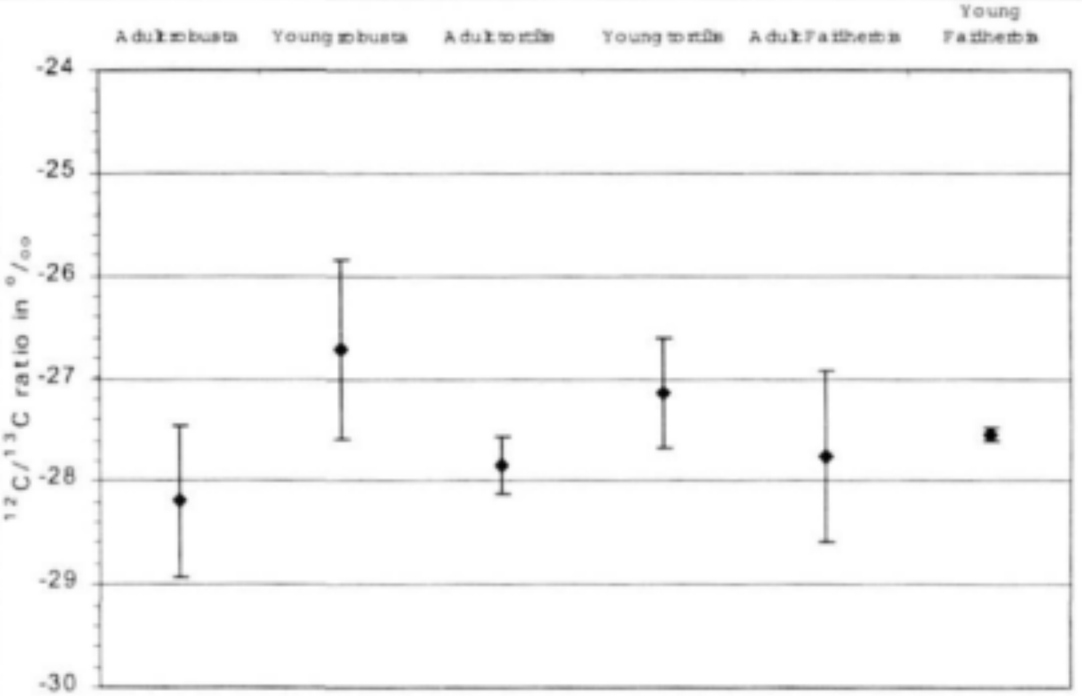


Figure 9b: Mean $^{12}C/^{13}C$ ratios for adult (>10cm dbh) and young (<10cm dbh) individuals of three of the study species. Error bars are ± 1 s.d.

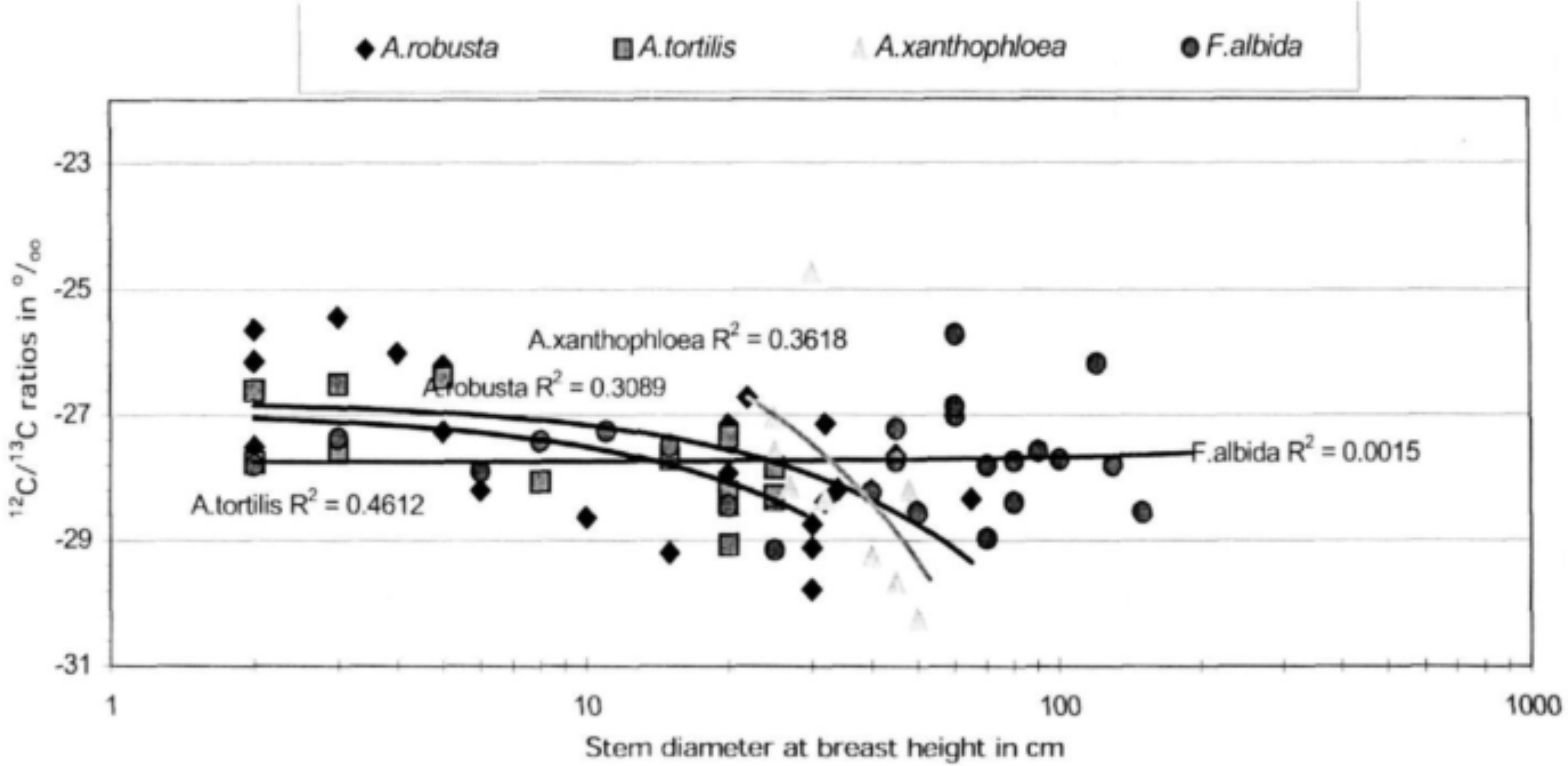


Figure 10: Water use efficiency of Acacias at Pafuri. Note log scale of stem diameter. Standard regression trendlines are shown.

Water Use Efficiency

Using a multivariate ANOVA, there was no significant difference in mean δ^{13}C values between any of the four study species (Factor 1, df=2,54, F=0.996, p>0.375. **Figure 9a**). Differences between adults and saplings in the same species were significant, however, with small trees (>10cm dbh) being more efficient than adults, except *Faidherbia* (Factor 2, df=1,54, F=13.756, p<0.00049, **Figure 9b**). The effect of species was qualified by size (interaction, df=2,54, F=4.277, p<0.018).

An increasingly negative trend with tree diameter was noted for *Acacia robusta, tortilis* and *xanthophloea*, but there was no downward trend in *Faidherbia* (**Figure 10**).

Ficus had the lowest WUE, particularly compared to *Trichilia*, which was the highest of all with an average of $-25.66\,^{0}/_{00}$.

Water Table Depth

Depth to the water table varied considerably over the floodplain, with the boreholes furthest away from the river being lowest (**Table 5**).

Borehole number G40-	Est. dist. away from river	November 1992 drought	October 1998	January 1999
275	190	10.37	7.81	6.84
276	720m	8.46	7.10	Not found
277	1.4km	11.41	11.05	9.49
Upstream				
281	120	11.59	8.72	8.66

Table 5: Measured borehole depths on the Luvhuvhu floodplain at Pafuri. Several other boreholes could not be located due to vegetation growth, and certain could not be measured due to physical obstructions. A total of 262 mm of rain was recorded from 1 November 1998 to 7 January 1999 when bores were re-measured, and the Luvhuvhu River did not cease flowing over this time.

Borehole no. 277 (sunk and measured in September 1992 after the longest flow cessation in the river and a serious drought in the catchment) was 11.05 m deep in 1998, only 36cm above where it was at the height of the 1992 drought. In

1999 it had risen 1.56 m compared to no. 275 (closer to the river) which only rose 0.97 m since 1998. This shows that boreholes nearer the river suffered much greater water table lowering than those furthest away, which has serious consequences for levee and bank aquifers.

DISCUSSION:

Seeds.

Acacia xanthophloea germinates relatively easily, implying that it will form feeble seedbanks and thereby limiting its ability to exploit temporal establishment niches such as floods which occur several months after seed fall. *Faidherbia* exhibits a range of seed responses to scarification, allowing a small percentage of seeds to respond to immediate germination cues but leaving most seeds in reserve for future opportunities. The strong resistance to germination observed in *A. robusta, A. tortilis,* and to a lesser extent *Faidherbia,* indicates an ability to lie dormant for extended periods and form seedbanks.

Acacia tortilis and *F. albida* both have indehiscent sugar rich pods which are animal dispersed (Seely *et al.* 1981,) while *A. robusta* and *A. xanthophloea* (dry dehiscent pods) rely on passive spread. Indications are that either physical scarification or herbivore gut digestion is necessary to break the tough-coated species' seed dormancy, and may therefore be important in initiating germination (Coe and Coe 1987). They are unable to react swiftly to colonising opportunities on newly deposited sediments relying instead on seedbanks or long seed viability. Only *A. xanthophloea* is likely to respond quickly to newly deposited sediment or open areas after a flood. This may explain the cohorted behaviour observed in Chapter 3 and shown in Photographs 5 and 6.

Seedlings.

Faidherbia displayed striking shoot and root elongation, being of similar length to *A. xanthophloea* and *A. robusta* despite having a much lower biomass. The single unbranched apical shoot and root may be adaptive in low elevation, sandy landforms where rapid escape above flood levels may be crucial. *Acacia tortilis* remained smallest and had small leaflets and canopies. These characters appear adaptive in the different seedling environments.

Pressure bombing revealed significant differences between species, and between adults and juveniles. From carbon isotopes, indications are that seedlings have higher WUEs than adults of the same species. However, there were no differences between species. Despite similar WUE, there are large differences in PMS. This could be explained by:

1- **Site factors**, *e.g. A. tortilis* was found on drier levees and the outer edge of the floodplain, therefore having less access to water and greater PMS at midday. *Faidherbia albida* grows on sandy substrates nearer the channel and has deep roots. It is therefore able to satisfy water demand and shows less negative xylem pressure potentials. *A. robusta* only grows on levees and banks near river and possibly has access to bank aquifer water to alleviate stress during nocturnal rehydration. The evergreen and therefore shaded habitat of *A. robusta* may also impose smaller transpiration demands on young plants.

2- **Morphology and plant response**. The lack of difference in WUE between species, indicates that they close their stomata for similar periods each day, despite growing in different moisture regimes. *Faidherbia* must then show some degree of stomata closure despite having free access to water, otherwise a far lower WUE would be evident. Reasons for this are given later under Water relations. *A. xanthophloea* may shed leaves with the onset of PMS and has photosynthetic bark to provide carbon for growth and maintenance. *A. tortilis* has very small leaflets compared to the other species (Coates Palgrave 1977) which may be adaptive in reducing evapotranspiration losses in hot dry areas.

Flood tolerance

In contrast to other systems (Phongolo River - Furness and Breen 1980; Tana River- Hughes 1988) average flood events (inundation for 3 weeks) do not appear to determine tree sapling distribution, as all species maintained effective photosynthesis in greenhouse trials. No significant change in photosynthetic assimilation was noted for *A. robusta* or *A. xanthophloea*. Although *F. albida* and *A. tortilis* did show a drop in photosynthetic rate after 3 weeks with roots under water, no leaf fall was noticed. Leaf abscission is an early indicator of flooding stress (Blom *et al.* 1990). Flooding may cause seedling mortality of if their canopies are completely submerged, but this was not experimentally determined.

Flooding may well cause mortality of adults, and not seedlings, as the former have significantly larger canopies to keep provisioned with water. Extended (six weeks) flooding has caused adult mortality in other river systems. Large stands of *A. xanthophloea* died on the Phongolo floodplain due to extended flooding that submerged some stands for over 30 days (*Pers obs.*, Furness and Breen 1980). The effect of a single long flood on adult trees is thus unknown although the floods of late summer 2000 may provide a chance to study this.

Water relations

The small ranges, relatively low efficiencies and lack of a significant difference in WUE in the four study species (**Figure 9**) indicates that water availability is not a major factor constraining adult persistence.

Although most flood intolerant in the greenhouse, *Faidherbia* occurs naturally in lowest landforms and sandy sediments (which may be most flood prone). The anomalous phenology of wet season deciduousness in *F. albida* as a possible adaptation to survive summer flooding seems unlikely, as young plants appeared tolerant of extended submersion, albeit with a reduced photosynthetic capacity. Further, young saplings do not display summer deciduousness, carrying leaves for several seasons, and would be vulnerable to annual summer floods during this time. The switch to dry season photosynthesis occurs when the plants are about 4-5m tall (*pers*obs) and presumably indicates reaching a permanent water table.

If adult *Faidherbia* trees are more susceptible to flooding than saplings, then they would be badly affected by aseasonal floods. Their pan-tropical distribution in Africa, through a wide range of climates and rainfall regimes appears to contradict this, leaving little support for the hypothesis that wet-season deciduousness is a means to avoid inundation induced stress.

Faidherbia showed the highest dawn and midday xylem pressure potential, despite varying distances of study trees from the river, indicating that they have access to water regardless of position on river profile. It does not seem to generate very low water potentials (**Figure 8**) and this confirms findings on the Kuiseb River, where minimum *Faidherbia* midday values were always greater than –2.4MPa and averaged –1.8MPa (Jobst 1996). This may limit its ability to extract water from dry, heavy clay sediments. An average WUE (**Figure 9**) indicates that either *Faidherbia* does not have easy access to water (but this is refuted by its very high pre-dawn water potential and massive root investment) or that it partially closes it stomata at noon. This would be further evidence for a strategy avoiding significant water stress despite having access to ground water.

Water conducting capacity increases with the 4th power of vessel radius, but so does the risk of vessel failure or cavitation (Zimmerman 1983). Bate and Walker (1993) found that *Faidherbia* had the highest transpiration rate (by 47%) of all riparian species on the Kuiseb River. *F. albida* also has much less dense wood than the other species. Van Vuuren *et al.* (1978) and Van Wyk (1984) give figures of 400-510 $kg.m^{-3}$ for *Faidherbia* as opposed to 880-910 $kg.m^{-3}$ for *A. robusta*, 910-980 $kg.m^{-3}$ for *A. xanthophloea* and 990 $kg.m^{-3}$ for *A. tortilis*. This, combined with the fact that *Faidherbia* wood yielded water freely in a vice (see methods for Water Source) whereas all *Acacia* species did not, points to either a high vessel:tracheid ratio or to wide vessel elements. It may therefore be susceptible to water stress induced xylem cavitation, because of (1) high noon water potentials, (2) its absence from clay sediments at Pafuri and (3) having a low density wood (*i.e.* large or numerous vessel elements). Young trees (>5m high) do not have very large canopies, and their short stature would also make them less susceptible to cavitation. This allows them to exploit surface soil moisture by photosynthesising during the wet season. These observations strongly support the second hypothesis for the reverse phenology of *Faidherbia*.

I predict that *Faidherbia* has large and/or long xylem vessel elements and this limits its distribution to sediments with readily available water and its growing season to less severe months (and therefore midday water deficits) when the risk of cavitation is significantly reduced.

The downward trend in WUE observed in the three *Acacias* in **Figure 10** suggests that older trees were less water use efficient than younger ones. Although Jobst (1996) found a weak negative trend with size in *Faidherbia*, this had a very low correlation coefficient (0.14) and was strongly influenced by a few large diameter outliers. The absence of any trend associated with *Faidherbia* is consistent with the hypothesis that *Faidherbia* taps into deep ground water sources and is not water limited, even from a very young age (diameters of 1-2cm, plant height of 2-3m). This is also consistent with the observation that *F. albida* starts becoming wet-season deciduous when it has established access to groundwater.

In **Figure 8** *Trichilia* and *Ficus* have the highest pre-dawn water potentials, and low differentials between dawn and midday. *Ficus* had by far the highest noon water potential, which is probably due to its position close to the channel or with good access to bank or ground aquifers. Most individuals away from the channel died during the 1991/2 drought. *Trichilia emetica* appears to have far better stomatal control (also evidenced by the high WUE in **Figure 9a**) and this explains the low mortality observed by van Coller (unpublished data) after the 1992 drought.

Implications for distribution on the floodplain.

Water use efficiency on its own does not explain distribution patterns of the microphyllous species in the floodplain. *A. xanthophloea* is restricted to low lying clay areas as it is able to colonise these before other species and avoids waterlogging through its shallow root system. It can tolerate the dry season by its facultative drought deciduousness, supporting itself through stem photosynthesis. Leaves are sometimes only present on the tree for 2 months after heavy rainfall events (*pers* obs.). Although it tolerates sandy substrates elsewhere in Africa (Vesey-Fitzgerald 1974), this is possibly due to a higher water table, or rainfall, or both.

Acacia tortilis's aversion to free draining sands (**Figures 3 and 4**) restricts its distribution to clays and silts on levees and the outer floodplain. Further, its slow growth rates and intolerance of low light makes it vulnerable to being out competed by evergreen and mesic species on the levees. However, with the drying out of the floodplain due to abstraction or reduced intermediate flows, *A. tortilis* might displace evergreen species and *A. robusta* from ever increasing areas of the levees.

The factor separating the distribution of *A. tortilis* from *A. xanthophloea* may be the formers' ability to withstand water stress (**Figure 8**), greater drought tolerance as evidenced by a higher root:shoot ratio in seedlings (**Figure 5b**) and deeper roots in adults (**Figure 6**). In addition, it did show reduced photosynthetic capacity under flood stress, and longer periods of inundation or sediment saturation may favour *A. xanthophloea*.

Acacia tortilis may invade the edges of seasonally saturated pans if river abstraction and diversion dry the floodplain out significantly.

Although *A. robusta* tolerates sandy substrates in the greenhouse, its absence from these in the field may be mediated by their rapid desiccation. This is the only species that appears to tolerate, when young, the low light levels of the evergreen community on the levees.

Through rapid root growth (10 $cm.wk^{-1}$- Bate and Walker 1993, this study), *Faidherbia* is able to tap deeper soil layers and the bank aquifer or water table while still young. In dry climates, it may only be successful at this on sandy substrates, as heavier soils may impede root growth (tap roots were deformed in clays in the greenhouse). More importantly, xylem cavitation on clay substrates may be a significant threat to large trees. This, and its strong taproot development, indicates that it is adapted to exploit sandy habitats, a niche unavailable to the *Acacia* spp. in this semi-arid environment.

It is unknown how a changed flow regime will affect sediment distribution in the channel, but this may be worth monitoring. Recruitment opportunities for *Faidherbia* may decrease if sand supply to and movement in the channel is interrupted.

Lateral ground water movement and tree distribution

Borehole levels below the river surface indicate that the river is mostly out-flowing (to the water table) in its lower reaches, even after a summer with above average rainfall and year round river flow. It appears that recharge from large events (storms or floods) is low as ground water is fractionated (closer to SMOW, **Figure 7**). This is possibly due to high runoff and the extremely low permeability of the clays on the floodplain. Birkhead *et al.* (1996) showed rainfall uptake only in the upper soil layers of sediments adjacent to the Sabie River in the Kruger Park, with no vertical movement into the intermediate soil layers, even though they were sandy. They also showed that lower soil layers (below 1.25 m) only obtained water from lateral seepage from the channel. Therefore, at Pafuri, the majority of water in the bank aquifer and water table will thus be derived from base flow and small or medium sized floods. This is corroborated by the small differences in isotopic signatures of bore- and river water.

Floods in the order of 50-200 cumecs might be crucial for soil water recharge because they activate sandy terraces and flood channels, and increase wetted perimeter and hydraulic pressure markedly. This would also allow more water to flow through sandy sedimentary facies into the bank aquifer.

The closer than expected correlation indicates that river flow and floodplain watertable are more closely linked than one would predict, thus raising the likelihood and severity of low flow impact on bank aquifers. Mangala (no. G40-281) and Bore numbers 275, 276 and 277 are not utilised or pumped, and should be regularly monitored, not just for depth, but also δD composition to further elucidate sub-surface water movement in different seasons and rainfall/flow regimes.

CONCLUSION:

Different life history stages of the four microphyllous study species respond to various environmental selective forces. Seed biology determines where species will be able to colonise and what environmental events they can respond to. Seedling and sapling characteristics (root:shoot ratios) correlate positively with sediment water availability, which determines each species niche substrate, and negatively with flood tolerance.

Despite very varied substrates and temporal water regime, adult persistence does not appear to be constrained by water availability. This indicates effective phenological and physical compensation mechanisms and that seedlings are the stage most vulnerable to selection.

Further flow reduction and elimination of flood recharge events will cause an expansion in the habitat occupied by *A. tortilis* at the expense of *A. robusta* and possibly *A. xanthophloea*. The distribution of *Faidherbia* is only likely to be affected if sediment deposition patterns change or sandy terraces are too infrequently activated for juvenile establishment.

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CHAPTER 5: SYNTHESIS, CONCLUSIONS AND FLOW REGIME MANAGEMENT

INTRODUCTION:

There is a pressing need for management of catchments and riverine ecosystems to replicate natural processes as closely as possible, especially in protected areas. Sound, proactive management requires goals, which may be in the form of some future desired state (Rogers and Bestbier 1997). However, there remains considerable difficulty in defining optimum states, as little baseline data are available, and the environment, climate and flow regime are inherently stochastic. Further, floodplains are often the endpoint of many rivers, and will inherit a suite of upstream problems that may affect their vegetation communities and geomorphological functioning. This study hoped to provide input into the flow management debate by testing some hypotheses regarding the determinants of floodplain forest structure and functioning. This final chapter draws out conclusions that may assist in determining those aspects of river flow that are vital for tree community persistence.

The two floodplains investigated display very different characteristics and tree distributions, determined by different processes. These will be summarised and drawn upon to interrogate the hypotheses put forward in the introductory chapter, viz.:

1. Adult distribution and niche differentiation will be dependent on dry season water availability and water stress tolerance.
2. Distribution patterns are determined by seedling flood tolerance, with sensitive species only found at high elevations on the floodplain.
3. Recruitment of pioneer colonising species is dependent on hydrological constraints and sediment conditions in semi-arid areas.
4. Forest dynamics will be determined by geomorphological factors in dry or actively eroding areas, and by biological processes in stable or mesic areas.

SUMMARY OF RELEVANT FINDINGS

Chapter 2- MKUZE:

In systems, such as Mkuze, that either sufficiently mesic (rainfall > 650mm p.a.) or where environmental gradients are not steep, biotic processes such as succession may predominate. In the Fig Forest, physical environmental variables such as height above the river and sediment did not dictate tree distribution, largely due to their uniformity over the floodplain. This differs from the neighbouring Phongolo floodplain where previous research has shown that trees only grow above a certain minimum height above the river, with lower elevations being dominated by flood tolerant herbaceous communities.

If succession is crucial in directing community structure, then any changes in flow regime that might arrest this succession can be expected to have ecological ramifications. The elimination of periodic large floods from the system (through off-course storage or large dam construction) will promote climax stages and reduce opportunities for pioneer species to colonise. Therefore, pioneer trees that have a critical role to play maintaining biotic associations, such as *Ficus sycomorus* in the case of frugivorous bird guilds, may be reduced sufficiently to cause the loss of other species. For example, large frugivores that depend on a continual supply of ripe figs may decline or migrate elsewhere.

The mesic environment coupled with small disturbances such as minor floods will make the forest communities at Mkuze highly susceptible to alien plant invasions. These may interrupt succession by choking out emerging seedlings, or being superior colonists of limited establishment sites. River management will have to involve removing upstream alien seed sources, and exploit all opportunities to control aliens at crucial stages, such as after floods.

Chapter 3- PAFURI:

Environmental factors have been shown to determine tree distribution in the arid environments of southern Africa. This is confirmed at Pafuri, where sediment type and distance away from the channel correlated with tree communities. Many researchers have invoked landform height as a crucial determinant, being a surrogate for flood return frequency and for mediating tree mortality. I postulate that, on the Luvhuvhu river at Pafuri, height above the river is less important for flood induced mortality than it is for aiding seedling survival. Throughout this thesis, flood events (and the cohorted tree recruitment that follows) have been alluded to as vital for the proper functioning of the floodplain system. In particular, floods of the correct frequency and magnitude are needed for seedling establishment, and soil water and bank aquifer recharge. Further, a reduction in these (40-200 $m^3.s^{-1}$) flows would mean that certain heights on the river profile would not be flooded or activated as often. This implies that groundwater infiltration may be affected, and site soil moisture may be too low or intermittent to allow successful establishment of seedlings.

Sediment type is imperative for determining seedling establishment success. Any change in flood regime that alters sediment distribution in the channel (for instance a decrease in the amount and mobility of sand) may be reflected in the decline of some communities, such as *Faidherbia* woodland. This could be mediated through reduced deposition of suitable sediment in establishment sites, or over-siltation of newly germinated seedlings.

Chapter 4- ACACIAS:

Environmental correlates of tree communities suggested that sediment and distance away from the river determine species distribution. Dominant microphyllous species in each community were investigated to understand environmental constraints. Height above the channel, as a surrogate for flood return frequency, was weakly correlated with communities due its variability over the floodplain. Some species, such as *Faidherbia* and *Acacia xanthophloea*, were only found lower down on the profile, and these should be most flood tolerant. Yet, experimental evidence showed the *Faidherbia* to be intolerant when young, and more so than the other species. All species did survive 3 weeks of inundation, longer than likely in the natural system.

Adult Water Use Efficiency (WUE), on its own, is relatively uninformative in explaining tree distribution. This is due to effective phenological and morphological compensation mechanisms. Of the microphyllous species, only *Faidherbia* did not show any decrease in efficiency with size, indicating that this species' saplings had access to ground water from a young age. Certain broad-leafed species with low WUE and high water potentials were heavily impacted on by the summer drought in 1991/1992. The large die-off of adult trees, particularly *Ficus,* is ascribed to a rapid water table drop resulting from almost complete rainfall failure and river cessation. This has manifested in a complete lack of seedlings almost a decade later, despite several flood events and above average rainfall during the study period.

It appears, therefore, that physical controls operate on the seedling stage, and that the effect of height above the river is merely an indication of soil moisture availability. It is crucial to maintain those aspects of the flow regime that replenish soil water for seedling establishment. However, certain species will probably not be affected by a reduction in the amount or frequency of the flow regime. *Acacia tortilis* is expected to expand into those niches previously occupied by others, especially *Acacia xanthophloea* on low lying portions and *Acacia robusta* on levees if the evergreen forest contracts. *Faidherbia* is only likely to be affected by changes in the sediment in the channel.

HYPOTHESIS TESTING

1: *Adult distribution and niche differentiation will be dependent on dry season water availability and water stress tolerance.*

It appears that, in Pafuri, adult distribution is not *primarily* determined by dry season water availability, as each species possesses sufficient compensatory mechanisms to deal with water stress.

Species distribution is only likely to be affected by seedling drought tolerance, and this appears chiefly mediated by sediment, and its impact on soil moisture.

Hypothesis 1 is thus rejected.

2: *Distribution patterns may be determined by flood tolerance, with sensitive species only found at high elevations on the floodplain.*

The effect of elevation differences in Mkuze was too small to elucidate fully, and would require direct measurement after receding floods. At Pafuri, however, there was only a weak correlation with height above the river and vegetation community. This could be ascribed to the changes in landform height (and thus flooding frequency) as the floodplain widened. There was weak experimental evidence that the certain species were negatively affected by flooding, but the most affected (*Faidherbia*) was found lowest on the river profile. Evergreen species were not tested. Flood tolerance, therefore, does not seem to determine seedling distribution, although its effects could be manifested by complete canopy submergence of juveniles or in adult stages.

It is difficult to reject this hypothesis based on the results obtained, but it appears that flood tolerance, *per se*, is not the main determinant of community distribution patterns.

3: *Recruitment of pioneer colonising species is dependent on hydrological constraints and sediment conditions in semi-arid areas.*

On both floodplains studied, establishment of colonising species was principally determined by specific components of the hydrological regime, being large flood events that opened up areas, deposited sediment or provided sufficient soil moisture in the correct season. Sediment was well correlated with communities at Pafuri.

Hypothesis 3 can be accepted, with the note that hydrological factors (in this case flood driven recruitment) also operate in the more mesic Mkuze floodplain.

4: *Forest dynamics will be determined by geomorphological factors in dry or actively eroding areas, and by biological processes in stable or mesic areas.*

Although geomorphological activity was minor in both floodplains, especially when compared to other published accounts, there was a reasonable correlation of community type to landform in the drier system (Pafuri). Community dynamics were not readily discernible here, compared to Mkuze where strong successional control on community type was noticed. By comparison, community type was most strongly linked to sediment type in Pafuri and this is be determined by geomorphological factors.

Hypothesis 4 can therefore be accepted, with the caveat that in semi-arid areas, geomorphological factors relate to sediment type and deposition, and not landform change and evolution as noted elsewhere.

How do these findings relate to informing an ecologically appropriate flow management regime? Firstly, we need a synthesis of these flow regimes and then some substantiated recommendations for vegetation requirements. This will only be attempted for the Luvhuvhu River, as the threats of flow alteration are far greater and potentially more pronounced in the semi-arid climate.

THE LUVHUVHU HYDROLOGICAL REGIME:

Significant changes have affected the Luvhuvhu River in the last four decades, not least of which are the reductions in intermediate flows and the onset of periodic flow cessation. Whatever the effects of the transition to this seasonal flow were, they are probably now not observable or quantifiable. However, the lack of recruitment of certain canopy species may be an important indicator of system failure. The tree communities may now be adapted to periodic flow cessation, as long as the bank aquifers and water table are maintained within reach of the sensitive species. This study has not dealt directly with all flood characteristics, such sediment load and frequency, but relevant insights will be highlighted where possible.

Borehole levels and isotopic signatures (Chapter 4, Table 5) indicate an outflowing river along the floodplain reach, with base flow contributing significantly to bank aquifers and ground water. Abstraction and flow reduction will affect infiltration rates and have important consequences for aquifer recharge.

Flood magnitude

Flood magnitude determines the maximum height of landforms submerged and the sediment deposition regime. Large floods open up canopies, remove ground cover, deposit silt and seed, and saturate the soil profile for long periods. Flow management ensuring that ground-water levels are maintained, that there are no summer droughts and that the river does not dry out in the growing season will be crucial to maintain healthy adult tree populations. These factors can be regularly monitored through borehole measurements. Specific features of the flood hydrograph, especially their erosive power, require further study.

New dams can be designed to release flows up to 20 $m^3.s^{-1}$, and can be expected to have significant negative consequences by removing or reducing medium size floods (40-200 $m^3.s^{-1}$), which are important for channel scouring and sediment deposition (Louw 1995). Medium sized floods are the most likely candidates for recharging the bank aquifer and soil water: both of which are linked to seedling establishment. How this has already been affected by abstraction, and to what degree will be further reduced by damming is unknown.

Frequency

Several observations regarding flood frequency have been made. If *Ficus* has a long juvenile phase, *e.g.* a minimum of 15 years (unpublished data), then successive erosive floods at shorter intervals will have disastrous consequences for the population. Alternatively, if establishment-enhancing floods decrease, no new cohorts of figs or fever trees may regenerate. *A. xanthophloea* does not appear to live more than a century, and if the large flood interval is too long, they may decline significantly because colonising opportunities become too infrequent. This may be a threat below heavily regulated impoundments but is considered unlikely.

Seasonality and flood duration

Flood seasonality might be important if seed availability is temporally limited. *Acacia xanthophloea* only has viable seeds in sufficient numbers to take advantage of a flood in mid-late summer. Trees have seed from mid-November until the end of January, suggesting that floods after March may not be sufficient to result in the large stands of Fever trees currently observed. Although *F. sycomorus* has viable seeds at almost any time of year, the summer fruiting peak from December to March yields the best chance for successful establishment. In several rivers, quickly dispersed seed falling onto fresh sediment may be the cause of all large fig stands found to date. Obviously, isolated seedlings will survive after flooding, but their high mortality rate (unpublished data) may preclude them from forming a sufficiently large population to maintain large frugivores.

Flood duration must be monitored, especially in low-lying areas, for effects on adults or completely submerged seedlings. However, it is unlikely to be long enough to warrant concern, unless there are sequential flood peaks in the Limpopo, Mutale and Luvhuvhu Rivers.

IN STREAM FLOW REQUIREMENTS (IFRS):

A regulated river's hydrological profile will only be successful in maintaining tree community dynamics if it retains the key events that drive succession or colonisation, and contributes significantly to groundwater aquifers. Rogers and van der Zel (1989) provide a brief introduction to floodplain requirements. Tharme (1996) pleads that IFRs should be considered for the entire riparian ecosystem. She argues that, in certain cases, the IF requirements of vegetation may be far greater than that of in-channel organisms, due to the former tending to persist at significantly greater distances from the water source. This is seriously under-researched in the South African context; and although this thesis did not attempt to address this comprehensively, several key findings are relevant.

Tharme (1996) reviewed methodologies for quantifying Instream Flow Requirements (IFRs), and highlighted the need for a holistic approach, building on requirements for different components of the river biota or functioning. This methodology has supplanted a species or individualistic approach which determine, for instance, single tree transpiration budgets and develop integrated community models from them. Insights from this study will follow a buildingblock approach, concentrating only on those aspects of floodplain forest ecology that have specific flow requirements.

Water flow to maintain riparian vegetation may be required for 3 reasons:

1. Site preparation; including a nutrient flush and seed germination
2. Seedling establishment and growth; including the ability to escape from vulnerable size classes and reach a rooting depth sufficient for persistence through an average dry season
3. Adult maintenance; to keep the phreatic zone near roots of sensitive species.

In-stream Flow Requirements for riparian species at Pafuri were developed over a series of workshops from 1994-1996. Serious concerns were voiced by ecologists at the refinement of certain hydraulic parameters that significantly reduced the required flows (Louw 1995, Louw 1996). The summary of refined IFRs are presented in **Table 1**, (see Louw 1996) for a full explanation).

Table 1: Final refined IFR requirements for the Luvhuvhu River for maintenance and drought years. Reproduced from Louw 1996. All values are in $m^3.s^{-1}$. Flood duration is given in (days), all annotations in *Italics*.

IFR req.	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep
Low Flows	0.18	0.3	0.39	0.53	0.63	0.63	0.46	0.39	0.3	0.23	0.18	0.18
Floods (duration)		0.46 X2	1.3 (3)		8.9 (5)	0.82 (3)						
Drought Low flows	0.02	0.1	0.1	0.12	0.14	0.15	0.14	0.1	0.02	0.02	0.02	0.02
Drought Floods		0.18 (2)			1.4 *for forest*							

The current IFRs have been set for instream biota and guessed at for riparian trees (Louw 1995). These IFRs are seen as insufficient for maintaining the forest communities for 3 reasons:

1- Intermediate flood frequencies (and flood height) for juvenile establishment will be severely affected by the proposed catchment development, and this is not specifically catered for in release programs.

2- Geomorphological effects have not been taken into account. This will result in changing landform configurations on the floodplain. For example, very low flows will lead to a stabilisation of certain features, a lack of sediment supply (sand or fresh silt), and insufficient flooding of channels and terraces.

3- Minimum low flow levels may be insufficient to keep bank aquifer and flood water table recharged in an average season. The 1997 hydrological data (Oct 97-Sept 98, representative of an average for the last decade) illustrates this. In that year the floodplain water table was only marginally above the drought years of 1991/2, despite a large flood and above average rainfall of 1996. Only with the arrival of year-round flow and several small freshets (20-30 $m^3.s^{-1}$) in the 1998 hydrological year, did levels rise significantly, both in the bank aquifer and floodplain water table.

This thesis shows, repeatedly, that flood events are crucial determinants of floodplain vegetation, and need to be of sufficiently large magnitude and *frequency. Further, it appears that the ground water table and bank aquifer are* very closely linked to river flow, and need to be maintained as a precautionary measure.

<u>Recommendations:</u>

1: I suggest an initial minimum basal flow rate of 0.4 cumecs for at least 9 months of the year be implemented, and that this should only be reduced when borehole levels indicate that the water table and bank aquifer are not reduced by more than 1m after three months of low flow. However, the contribution of intermediate and large floods, and significant rainfall events, to soil aquifers must be quantified before any flow regulations can be accepted.

2: Floods that deposit sediment and initiate seedling growth must not be removed from the system. Every third or fourth year, a small flood should be released in December, to result in a flood of maximum 100 cumecs or under bank full. This will maximise the recharge of sandy terraces, and flood channels and permit initial seedling establishment. It is suggested that flood magnitude must be sufficient to activate all channel features, but it is not necessary to submerge the edges of the floodplain or overtop the banks of the highest levees.

3: Every five years or so, a large flood in February or early March, up to 400 cumecs or as great as dam construction will allow. Actual timing will be dependent on local catchment floods, the Mutale and Limpopo Rivers and previous years' cyclonic flooding. Synchronisation with the Mutale, or high levels of the Limpopo, may be important to maximise flood peak, and the hydrological parameters of this should be determined wherever possible. This flood level is just over bank full and will activate most levees, terraces and much of the floodplain. This is important for recharging soil and bank aquifers and permitting "drought-safe" seedling establishment, particularly of *Ficus sycomorus*. This seasonality is important to take advantage of peaks in seed availability.

EVALUATION OF THE STUDY:

This thesis has several useful outcomes. Predictably, it has also pointed the way to further research or altered sampling strategies to better understand important ecological factors in floodplain functioning.

Useful Outcomes

1- The tree demographic studies are useful, and simple, tools to identify limiting factors. They can also provide functional groups for analysis of community dynamics.

2- Potentially useful hypotheses concerning tree distribution, and flow management, have been suggested. Some of these are counter-intuitive, such as the lack of influence of Water Use Efficiency on adult persistence.

3- A putative explanation for the intriguing reverse phenology of *Faidherbia* (poor stress tolerance) is proposed, and corroborated with several autoecological observations.

4- Seedling flood tolerance appears to be less important than previously thought, but magnitude and season might be crucial for permitting establishment.

Weaknesses

1- Fine scale differences in landform elevation were not discerned and accurate height:discharge curves for several cross sections of the floodplain would have provided a more accurate investigation of the effect of flood frequency on seedling distribution patterns.

2- More accurate flow frequencies would have allowed better correlation with landform inundation, aquifer recharge and flow recommendations.

3- An early objective of the project was to quantify the dependence of "indicator" bird species on "keystone" resources (*Ficus*) in the landscape, and predict likely consequences of a loss or decline in *Ficus* communities on both floodplains resulting from poor flow management. This had to be abandoned at a late stage due to a sampling season being missed, but would have provided a far more appropriate context for much of the initial sampling.

4- Experimental flooding should have been replicated on different sized individuals, on different sediment types, and should have included total plant submergence. This would have provided a more complete idea of the ecological role of floods in seedling distribution, and provided an estimate of minimum flood return periods.

Further research and monitoring required

Each floodplain forest is an integrated expression of tree life histories and climatic cycles, which operate in the scale of centuries, and each is modified by river flow regimes, geomorphology, herbivory and rainfall which interact seasonally. Although an immediate tree response to some events can be observed, long-term community changes will only be noticeable after decades or centuries. Thus not only is research required in some areas, but so are long term monitoring studies within the correct management context.

1. The importance of groundwater depth was not directly determined, nor the exact nature of the relationship between it and river flow. All boreholes on the floodplain need to be accurately surveyed, and their depths monitored at least bi-monthly, to provide a more complete picture of water table fluctuations with river flow, and determine any correlation between depth to the water table and tree community.

2. A more thorough investigation of plant moisture stress across species and different size classes would permit more accurate determination of population limiting stages. It may be useful to corroborate this using reciprocal transplant experiments in different landforms.
3. It may be impossible to determine water source using isotopes, unless a more precise method is readily available, or further studies show strong signature differences after a particular event. This would be a critical component of a water budget for each community type, as well as indicating how these depend on relative access to soil or ground water.
4. The interplay of other, especially biotic, factors is a crucial component of any further demographic studies. Biotic processes that promote or inhibit regeneration (mutualisms, dispersal and herbivory) will have to be monitored at a tree population level and at a river reach scale to ascertain their effects.
5. The importance of stem photosynthesis to *Acacia xanthophloea* would be an interesting addendum to further studies.

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Appendix Table A: Two-way ordered table of all Mkuze transects, with grouped pseudo-species and the communities constructed.

Transect	2					1	2	2				1	1	1	1		1		2	1	1	1	1	2	2	2		
	5	3	4	5	6	2	3	2	1	2	9	0	3	4	5	7	6	8	4	1	7	8	9	0	1	4		
Species																												
4 BLIcan	-	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
7 CELcan	1	1	1	1	1	1	1	-	-	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	0	0
13 RAUcan	-	1	1	1	-	1	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	0	0
16 TRIcan	1	1	1	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
5 BLIreg	2	2	2	1	3	1	2	1	1	1	2	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	0	1
6 BLIund	-	1	1	1	2	-	1	1	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	0	1
8 CELreg	3	2	2	2	1	2	-	1	2	1	2	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	0	1
9 CELund	3	2	2	1	1	2	1	1	1	1	2	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	0	1
17 TRIreg	1	2	1	1	1	1	1	-	1	1	1	-	1	1	1	1	1	-	-	-	-	-	-	-	-	-	0	1
18 TRIund	1	1	1	1	-	1	1	-	1	1	1	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	0	1
14 RAUreg	-	1	1	1	1	1	-	-	2	1	1	1	-	1	-	2	-	-	-	-	-	-	1	1	-	-	1	
10 FICcan	1	1	1	1	1	1	-	-	1	1	2	1	1	1	2	1	1	1	-	1	-	-	-	1	1	-	10	0
15 RAUund	-	1	1	1	1	1	1	-	1	1	2	1	1	1	-	1	1	-	-	-	1	-	1	1	1	-	10	0
12 FICund	1	1	1	-	1	1	-	-	1	1	2	2	-	-	2	1	1	3	2	2	1	1	2	2	1	2	10	1
1 ACAcan	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	1	1	-	1	1	1	1	1	1	1	1	11	0
3 ACAund	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	1	1	-	-	1	11	0
11 FICreg	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-	1	1	1	-	1	-	-	11	0
2 ACAreg	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	11	1
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1		
	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1		
	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1			0	0	0	0	0	0	0	0	1		
	Broadleaf Evergreen						Mature *Ficus*								Young *Ficus*				*Acacia xanthophloea* woodland									

Appendix Table B: The Mkuze transect data in demographic groups and environmental correlates

Sum of index	Transect																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	15	16	17	18	19	20	21	22	23	24	25	26	27
ACAcan	3	0	0	0	0	0	3	0	0	0	3	1	0	0	0	8	9	6	6	4	1	0	0	2	0
ACAreg	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ACAund	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	9	1	2	0	0	0	0	4	0
BLIcan	0	0	2	1	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
BLIreg	12	2	24	34	19	300	0	0	22	1	0	13	3	3	12	0	0	0	0	0	0	13	23	0	34
BLIund	0	0	1	9	5	26	0	0	5	0	0	0	0	2	2	0	0	0	0	0	0	10	4	0	0
CELcan	0	7	2	7	8	19	0	0	2	0	0	4	4	7	0	0	0	0	0	0	0	0	6	0	5
CELreg	31	11	68	41	21	14	5	0	72	4	0	27	1	1	16	2	0	0	0	0	0	2	0	0	110
CELund	2	10	33	26	9	16	0	0	50	0	0	27	11	8	1	4	0	0	0	0	0	18	15	0	133
FICcan	16	1	5	1	3	3	6	1	0	3	4	16	1	2	0	3	0	0	0	2	3	0	0	0	6
FICreg	0	0	6	0	0	0	31	0	0	0	7	0	0	0	0	0	2	1	0	1	0	0	0	0	0
FICund	6	3	4	15	0	2	19	122	32	69	45	1	0	0	40	2	10	7	49	65	17	0	0	39	1
RAUcan	0	7	8	4	2	0	1	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	2	0	0
RAUreg	48	3	9	5	3	6	23	0	6	3	0	9	0	2	0	0	0	0	3	5	0	0	0	0	0
RAUund	5	8	4	7	2	1	9	0	38	3	0	5	2	5	0	4	1	0	2	1	7	0	1	0	0
TRIcan	0	0	1	6	10	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
TRIreg	8	3	22	6	9	3	1	0	2	0	0	6	5	8	1	1	0	0	0	0	0	0	2	0	5
TRIund	1	2	2	3	7	0	0	0	4	0	0	2	1	2	2	0	0	0	0	0	0	0	11	0	3
Grand Total	132	57	191	165	98	398	99	123	233	83	59	119	28	40	74	26	31	15	62	78	28	44	64	45	298
Community	f	e	f	f	e	e	y	y	y	y	y	f	e	e	y	a	a	a	a	y	f	e	e	y	f
EnvVar																									
Transect	1	2	3	4	5	6	7	8	9	10	11	12	15	16	17	18	19	20	21	22	23	24	25	26	27
sediment	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
htabove	2	2.5	2.5	2	3	2	1.2	2	2	2	2	2.5	3	3	2	2	1.5	1.5	1.5	1.5	1.5	3	3	1.5	2.5
distaway	140	200	300	340	400	150	10	30	250	30	60	200	160	200	40	60	30	20	40	180	300	400	450	500	150
canhgt	22	24	25	18	22	16	22	10	18	14	16	28	12	20	14	26	15	15	18	12	14	12	15	11	28
cover	95	40	60	80	30	20	70	0	80	50	10	90	100	70	70	100	100	100	100	100	30	30	60	100	10
midstr	40	30	80	20	30	60	40	0	80	0	0	80	80	80	10	40	60	40	40	80	10	20	20	20	80
subcan	60	90	100	60	80	70	20	60	60	40	40	50	80	60	60	0	0	0	60	20	10	80	80	0	40
cancov	100	40	40	100	80	90	60	95	60	85	70	90	100	90	80	70	60	40	40	40	100	100	100	90	100
sed	C	CSI	C	C	C	C	C	C	C	CSI	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C

Appendix Table C: The Pafuri transect data in demographic groups with environmental correlates

DCA DATA 1 20 80 + CATEGORIES

Spp.	Transect A	B	C	13	15	D	E	F	G	H	3	5	6	7	17	18	20	21	22	26	1	11	2	4	8	16	10	12	9	14	19	23	24	25
FICREG	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FICSUB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	0	0	0	0
FICCAN	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	2	0	0	18	3	8	5	5	13	0	0	4	0	0	0	0	0
FAIREG	0	0	0	3	0	0	0	0	0	0	0	3	40	0	2	0	2	0	200	0	13	0	9	0	0	0	0	0	0	0	0	0	0	0
FAISUB	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
FAICAN	0	0	0	0	1	0	0	0	0	0	28	14	12	16	4	17	26	16	19	18	12	0	34	1	6	0	0	0	0	0	0	0	0	0
A. XREG	0	0	0	0	51	0	0	77	79	40	0	0	0	0	0	0	0	0	0	7	3	0	1	0	107	3	0	0	0	0	0	0	0	0
A.XSUB	0	0	0	0	0	41	30	17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
A.XCAN	0	0	1	11	11	4	11	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
XANREG	0	0	0	0	0	0	0	0	0	0	35	0	0	50	0	6	200	0	0	0	230	45	0	9	0	21	100	50	36	2	14	33	8	0
XANSUB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
XANCAN	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	6	2	3	0	0	4	1	3	1	0	2	0	0
DIOREG	0	0	0	35	0	0	0	0	0	0	4	1	0	2	0	0	0	0	0	27	49	37	11	82	59	9	5	10	27	2	0	1	2	0
DIOSUB	0	0	0	15	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	9	1
DIOCAN	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	1	0	0	0	3	7	12	3	2	8	12	9
A. RREG	0	0	0	0	0	0	0	0	0	0	102	0	0	6	31	24	300	26	3	335	6	23	63	164	106	21	3	2	34	6	47	25	113	34
A.RSUB	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	10	0	0	0	0	0	0	1	1	1	0	3	18	6	3
A.RCAN	0	0	0	0	0	0	0	0	0	0	4	0	1	0	5	2	1	1	0	5	1	7	1	3	1	1	3	2	6	1	15	7	5	8
A.TREG	29	16	28	0	0	34	5	0	0	0	0	0	0	0	4	23	0	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A.TSUB	10	21	6	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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CROREG	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	6	5	28	60	19	13	0	1	65	0	44	0	0	0	0	27	0	7	5
CROSUB	0	0	0	0	0	0	0	0	0	0	1	0	0	0	6	9	4	41	30	0	4	1	0	4	0	3	0	0	0	0	3	3	2	0
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HABITAT	T	T	T	X	X	X	X	X	X	X	FA	FA	FA	FA	FA	FA	FA	FA	FA	FA	FA	F	F/FA	F	F	F	E	E	E	E	E	E	E	E
ENVVAR																																		
	A	B	C	13	15	D	E	F	G	H	3	5	6	7	17	18	20	21	22	26	1	11	2	4	8	16	10	12	9	14	19	23	24	25
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canhgt	6	5.5	5.5	12	16	12	14	18	3	2	20	10	20	22	20	18	20	15	16	20	20	20	22	22	20	19	22	25	25	14	16	20	20	18
cover	0	0	0	30	0	50	30	5	10	15	0	10	20	20	90	20	10	80	10	10	10	60	5	10	40	20	10	80	10	30	90	80	20	20
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subcan	40	40	50	80	10	40	10	0	40	0	30	80	0	10	20	10	0	60	30	10	10	20	10	30	30	0	40	40	60	40	10	40	10	10
cancov	0	0	0	60	40	60	60	80	0	0	100	30	85	100	20	40	80	80	90	60	80	80	90	60	30	80	95	100	80	50	60	60	95	95
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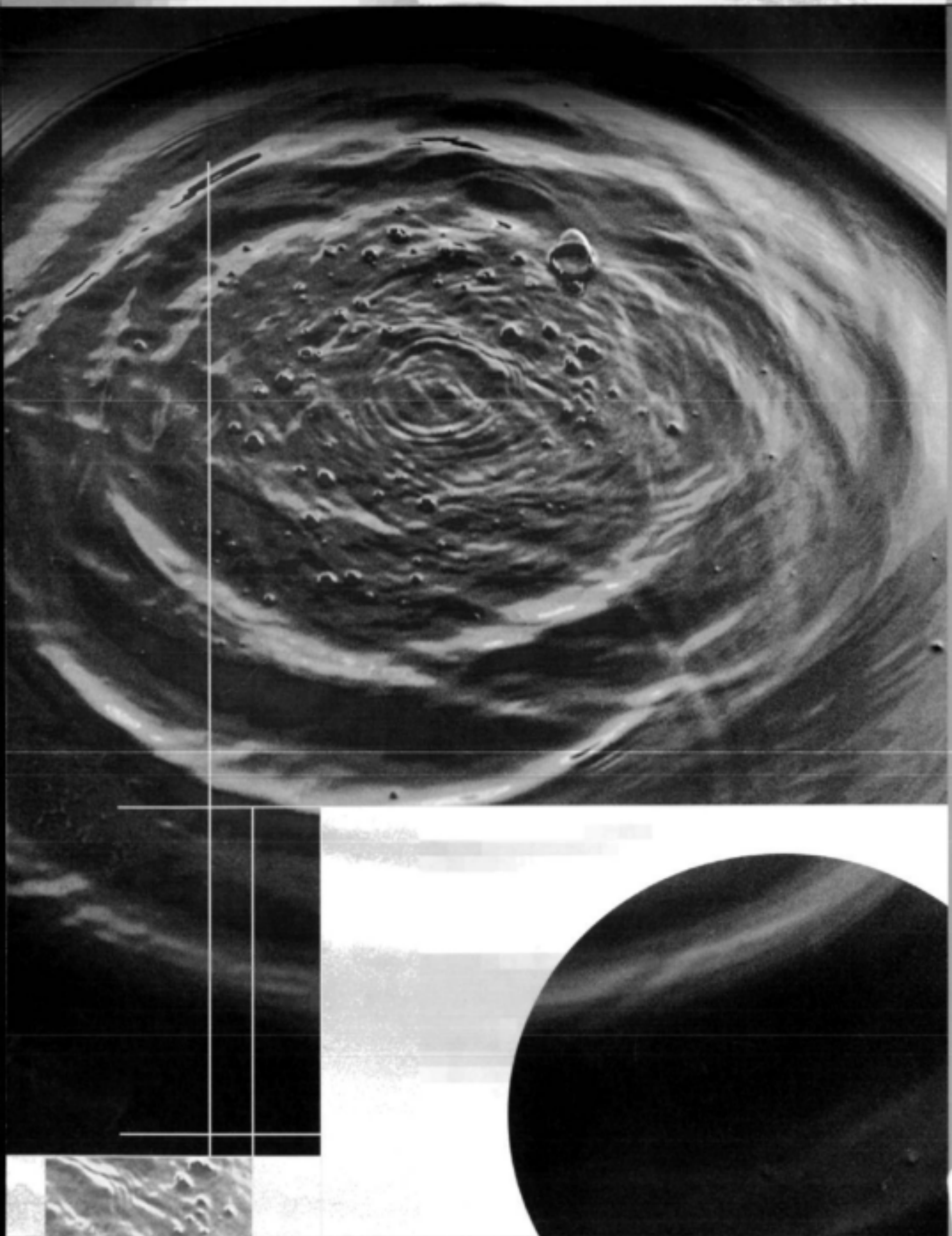
Sed	C	C	C	C	C	C	C	C	C	CSI	SI	SA	SA	SASI	SI	CSI	CSI	CSI	SA	SI	SASI	C	SI	CSI	CSI	SA	CSI	C	CSI	C	CSI	C	CSI	C



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