HOW SEASONAL PATTERNS OF LEAF DISPLAY IMPACT LIFE HISTORIES OF SAVANNA TREES

Nthambeleni Dalton Masia

Supervisor: Prof. Sally Archibald
Co-Supervisor: Dr. Nicola Stevens

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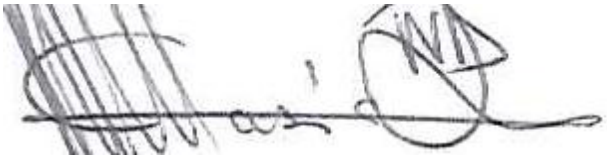
DECLARATION

I declare that this Thesis is my own, unaided work. It is being submitted for the Degree of Master of Science (Dissertation) at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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ABSTRACT

Global changes are likely to have negative impacts on many ecosystems including savannas. Semi-arid environments are notable for the wide range of seasonal patterns of leaf display in the tree communities. The environmental cues of leaf out and leaf drop are not consistent across species, and are not always directly linked to water availability, indicating that some species might be particularly sensitive to changes in climate. Strategies employed by trees which leaf early or drop their leaves late are likely to impact other aspects of their life-history and functioning so I expect particular plant functional types to be associated with particular vegetation functional traits. I assessed how variable savanna leafing strategies are among 28 species at a semi-arid savanna site at Nylsvley, and used this information to group species into plant functional types (PFTs). These PFTs were then assessed in terms of key vegetative traits to explore the life history consequences of different leafing strategies. Leaf phenology was monitored throughout one growing season and quantified using 8 key phenological metrics. The timing of leaf display tracks the timing of seasonal rainfall but with wide variation, with some species retaining their leaves throughout dry season. Other species loss some leaves throughout the growing season, some species only flushed their leaves after the first rains, and other flush before the first rains. I identified 4 clear PFTs using the MClust clustering integrated with subjective procedure. Four vegetative traits were measured: specific leaf area, leaf nitrogen, maximum stomatal conductance and wood density. I identified some clear trade-offs between vegetative traits and phenological strategies. There was also a positive relationship between degree of rain stimulated flushing metric and wood density. Using objective clustering methods to determine plant functional types has some clear advantages over more subjective methods but depends on good input data. Identifying plant functional types at Nylsvley has led to some insights into functioning of these savannas, but as there appear to be strong links between plant traits and particular leafing strategies it might be more appropriate to explore syndromes of vegetation functional traits when modelling responses to global change.

DEDICATION

I would like to dedicate this thesis work to my parents, my father Mr Samuel Masia and Mom Mrs Irene Munyai for their courage and support, and the time they spent supporting my daughter during my studies and the rest of my family. Most importantly I would also like to thank my wife Vanessa Matukana and my daughter Zwavhudi Masia for their love, support and courage they gave me during this time, as I spent little time with them.

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LIST OF ABBREVIATIONS

PFTs	-	Plant Functional types
PCA	-	Principal Component Analysis
MClust	-	Model-Based Clustering
BIC	-	Bayesian Information Criterion
DGVMs	-	Dynamic Global Vegetation Models
SLA	-	Specific Leaf Area
Gs_{max}	-	Maximum stomatal conductance
leafN	-	Leaf nitrogen
HCL	-	Hydrogen Chlorine
%	-	Percentages
mm	-	milli meters
m	-	Mean
sd	-	Standard Deviation
^{o}C	-	Degrees Celsius

CHAPTER 1.0
INTRODUCTION

1.1 GLOBAL CHANGE AND THE CONCEPT OF PLANT FUNCTIONAL TYPES (PFTs)

Global change and land-use changes are likely to drive changes in ecosystems, their functioning and the ecosystem services they provide (Loreau et al., 2001; Vitousek et al., 1997). To improve our ability to predict and manage vegetation responses to these environmental changes we need to understand what drives current and future vegetation dynamics (Box, 1996). PFTs are defined as groups of plant species with similar plant traits responding to similar environmental factors (Noble and Gitay, 1996). They are used widely in ecology as a method to simplify the huge diversity of plants on the planet: by grouping them to a limited set of functionally similar types. Identifying meaningful PFTs is an important research topic, as it is more efficient to work with a functional classification of plants than with species (Skarpe, 1996), especially when modelling at global scales.

However, someone interested in herbivory would classify vegetation in a totally different way from someone interested in modelling carbon gain, or vegetation response to fire (Bond et al., 2005; Owen-smith and Cooper, 1987), so PFTs are only defined with reference to particular research questions (Noble and Gitay, 1996; Skarpe, 1996). For this reason it has been difficult to come up with global PFTs that can satisfactorily be used in vegetation modelling at a global scale (Box, 1996; Prentice et al., 1992). One context in which plant ecologist often used PFTs is when describing vegetation phenology.

Grouping plants according to PFTs allows us to understand the response of several plants with similar properties. This has the potential to provide a meaningful tool for generalising vegetation response to different environmental drivers (Louault et al., 2005). Key to the importance of PFTs is the idea that plant

traits are associated with differences in function – such as the ability to compete, survive and re-grow under different environmental constraints. Therefore, it is often assumed that PFTs share similar quantitative traits, such as leaf specific area (SLA), leaf nitrogen concentrations, wood density, and maximum stomatal conductance (Gs_{max}) (Cornelissen et al., 2003). This concept has been commonly used in the global change research in order to generalize classification of plant phenology.

To understand the vegetation dynamics of many species, it is useful to identify easily measured plant traits which can be applicable worldwide and give meaningful ecological characteristics of a plant community (Díaz et al., 2001; Hodgson et al., 1999; Westoby, 1998; Weiher et al., 1999).Plant traits have been used in assessing adaptive strategies of plant community functioning (Westoby, 1998; Westoby et al., 2002). Plant traits are also often used to group plant species into meaningful ecological groups: plant functional types (PFTs) (Lavorel et al., 1997).

Phenology is one very important aspect of plant and ecosystem functioning as it influences the exchange of energy and carbon dioxide that is the timing of the onset and offset of leaves (Arora and Boer, 2005). It has been demonstrated to be very sensitive to climate change and thus understanding different factors that drive phenology in savanna systems is crucial. There had been a lack of phenology data in savannas especially for woody plant species (Cleland et al., 2007). Phenology patterns of savanna species are dominant by PFTs which follow the rainfall patterns – deciduousness and it is important to understand what influence these environmental cues.

1.2 VEGETATION PHENOLOGY

Phenology refers to any aspect of biological functioning that varies seasonally – flowering, seed set, fruiting, leaf onset and offset, nesting, migration (Cornelissen et al., 2003) – but leaf phenology refers particularly to seasonal patterns of leaf

display (Kikuzawa, 1995). Green leaves provide important food source for herbivores (Owen-smith and Cooper, 1987). Seasonal patterns of changes in green leaves set the time available for resource capture in plants (Kikuzawa, 1995; Chuine, 2010). Therefore, it is an important aspect to represent correctly in plant phenology models. Changes in vegetation phenology of trees indicate that trees are responding to local and global environmental changes (Myneni et al., 1997; White et al., 1999).

One key constraint to predicting leaf phenology in models is the lack of understanding of the environmental processes that govern the phenology of the leaves (Arora and Boer, 2005). The drivers of leaf display are unlikely to be the same across the world. For example patterns of leaf display in most temperate systems are driven by temperature and day-length (Chuine and Cour, 1999; Seiwa, 1999; Nizinsiki and Saugier, 1988), as would be expected as they are the main limiting factor for plant growth. Several phenological studies from temperate system have shown evidence of a shift in leaf onset and offset, and leaf colouring in response to temperature in recent years (Menzel et al., 2006).

In tropical systems, the drivers of phenology are likely to differ as the major constraint on plant growth is water availability not temperature (Scholes and Walker, 1993). Although plants in seasonally-dry systems should have leaf display patterns that follow the seasonal pattern of wetting and drying. Many savanna tree species green-up before the first rains of the season (Do et al., 2005), when the soil moisture is at a minimum, and some species also keep their leaves well into the dormant dry season (Reich and Borchert, 1984), and also flush new leaves during dry season (Rivera et al., 2002).

Furthermore watering experiments in seasonally dry systems have also indicated that leaf drop is not always driven by water availability (Gebauer et al., 2002). Unlike heat, water can be stored, and plants in sub-tropical and tropical areas have the potential to access deep water reserves or to store their own water supplies (Eamus, 1999), and therefore, to become independent of the seasonal rainfall

signal (Meinzer et al., 2001). However, the savanna leaf drop can be responding to water availability, but leaf drop response manifests itself differently in different species. This might be due to different access water mechanisms or only some species may be responding to water stress, while other have leaf drop cues which are controlled by different environmental cues (Shackleton, 1999; Singh and Kushwaha, 2005).

The complexity of leaf phenological patterns in semi-arid ecosystems both in terms of their variety and in terms of their environmental cues, means it has been difficult to represent these vegetation types in DGVMs (Higgins et al., 2010; Scheiter et al., 2013). In particular, there does not seem to be agreement between different tropical and sub-tropical systems in terms of identifying basic plant functional types (Banin et al., 2012). However, this study focused on semi-arid savanna where water is always a limiting factor, and leaf phenology of tree species in the areas can be relevant to the rest of the world.

Having a better understanding of the range of phenological adaptive strategies in savanna systems can be an important first step in identifying whether all tropical savannas exhibit the same PFTs or have the same life-history strategies. There is a large amount of information on the functional differences between deciduous and evergreen species. For example, with evergreen species being shown to have longer-lived leaves, consequently a suite of other associated vegetation functional traits - lower leaf N-content, and a lower specific leaf area. I should expect similar suites of traits to be associated with plants with other phenological patterns in savannas as well. These depend on different morphological of the trees and environmental factors (Singh and Kushwaha, 2005). The diversity of PFTs in tropical is influenced by water stress during seasonal drought which is a major cause of leaf fall.

However, the debate between evergreen and deciduous physiological adaptation to tropical areas has long been in ecological research. It has also been generally agreed that evergreen leaves offer a potentially longer photosynthetic season than

deciduous leaves. Deciduous tree species tend to short-lived leaves as a strategy to reduced transpiration and respiration during seasonal drought and often having higher photosynthetic rates (Givnish, 2002). Nevertheless, leaf phenology can be viewed as a central element in plant strategies for carbon gain, which include leaf habit, leaf initiation and longevity. Plant species tend to produce many leaves at the same time might face leaf shedding and reduce energy gain (Kikuzawa, 1995).

Variation in the leaf phenology of woody plants is thought to be affected by wood density, as it determines water storage (Bucci et al., 2004). Low density wood increases the ability of a plant to store water in its stems or branches however trees are then more susceptible to pathogens and less structurally sound (potentially resulting in shorter life-spans). The variation in wood density and water storage capacity in tropical trees is high in comparison to temperate trees (Bucci et al., 2004). It has been speculated that low wood density allows these savanna trees to successfully survive long dry seasons. One would therefore predict that plants with phenology that is independent of rainfall will have low wood density and may be able to flush during dry seasons when the environmental water is low (Reich and Borchert, 1984). However, the rehydration of stem cause the bud break (Rivera et al., 2002).

Low wood density also correlates with high photosynthetic rates; because the xylem vessels are larger, and are able to transport more water allowing the plant to open their stomata wider, thus allowing high photosynthetic rates (Santiago et al., 2004). Low wood density in trees of Cerrado Savanna in Brazil have exhibited high daily transpiration rates and high stomatal conductance (Bucci et al., 2004). These traits are usually associated with short-lived leaves with high leaf nitrogen content and high SLA, so it would be important to test whether these traits are also associated with particular phenologies. There have also been observations that early-greening plants tend to have high nitrogen leaves (Prior et al., 2003).
There is a great deal of research on the different life-history characteristics and vegetation functional traits associated with evergreen and deciduous species in general. Given that savanna trees are known to display a variety of phenological

strategies that go beyond these classic functional type's definitions it is necessary to investigate which particular suites of traits are associated with these novel savanna functional types. Understanding this will improve our understanding of the ecological significance of these phenological strategies. It will also enable us to generalise the responses of these different trees to predicted global change.

1.3 IMPORTANCE OF PLANT FUNCTIONAL TYPES (PFTs)

1.3.1 Using PFTs in models (Modelling)

Environmental models are used to assess and predict the impact of different environmental constraints on plants and ecosystems (Hickler et al., 2012). Process-based models termed Dynamic Global Vegetation Models (DGVMs) are increasingly used. Before DGVMs emerged, scientists used equilibrium biogeography models, terrestrial biogeochemistry models, and forest gap models. Equilibrium biogeography models could simulate equilibrium vegetation given a certain climate (Prentice et al. 1992). Terrestrial biogeochemistry models focused on the simulation of biogeochemical cycles through plant ecosystems (Parton et al. 1987). The DGVMs are bottom-up description of plant communities based on physiological and population processes (McMahon et al., 2011; Díaz et al., 2001; Prentice et al., 2007; Hartig et al., 2012).

Equilibrium biogeography models do not represent transient responses of vegetation to climate change because the ecological time scales of vegetation dynamics are neglected. Hence, such models are used in iterative climate-vegetation coupling. This model involves net primary production, which comprises of parameters which link processes across time scales. Net Primary Production (NPP) is the main input required by the slow dynamic vegetation processes, which occur in the following order: reproduction, turnover, mortality due to negative NPP, allocation, competition for light, background and stress mortality, mortality due to fire, establishment (Oleson et al. 2004; Bonan et al.,2003).

However, important shortcomings became apparent with these model families with respect to 1 their coupling to Global Climate Models. The weakness of DGVMs is that in order to work at global scales they need to simplify much of the diversity in the composition and functioning of ecosystems (Guisan and Thuiller, 2005). PFTs are an essential tool for DGVMs, but the degree to which these should be simplified is a matter of much debate. This group of models (DGVMs) was designed to fit in the framework of existing land models, such as the Community Land Models (CLM), to facilitate the coupling to global climate models. The coupling design allows for internal consistency in the representation of simulated processes and ensures conservation of energy and mass in the modeled system, which is referred to as climate vegetation coupling (Foley et al. 1998).

1.3.2 Why is it useful to understand PFTs in the face of change?

Paleoecology studies demonstrate that vegetation has changed with climate in semi-arid savannas (Skarpe, 1996). Understanding PFTs in southern African savannas is of great importance; as is predicted to be affected by global change due to increase in temperatures. Changes have been observed at global or regional scale, and understanding the interaction between environments and plants is vital (Vitousek, 1994). For such reason it is important to work with functional classification of plants (Boutin and Keddy, 1993). It is also important to understand the vegetation characteristics, as it influences globe climate through carbon exchange and accumulation, water balance and evapotranspiration (Bonan, 2008). These changes are more likely to change the patterns of vegetation phenology response to current and future climatic conditions.

1.4 Study site

I selected a semi-arid savanna ecosystem in Nylsvley Nature Reserve, Limpopo Province, South Africa (24°39′S 28°42′E) (Figure 2.1). Nylsvley has been the

focus of several long-term research campaigns and therefore provides good baseline soil and climate (Frost 1987; Owen-smith and Cooper 1987). Nylsvley has a mean annual rainfall 623 mm and mean annual temperature of 19 °C (Scholes and Walker, 1993; Frost, 1987). During the study period rainfall started very early in 2012 and by the 7th September the site had already received 103.9 mm of rains. 2013 was a normal rainfall year, where the first rains occurred on 7 October. Data collection took place near Marulakop in the South East of the reserve (Figure 2.1). The site is characterised by low nutrient sandy soils (Frost, 1987) interspersed with patches of higher-nutrient clay soils thought to be derived from Waterberg sandstones (Scholes and Walker, 1993). The vegetation at the study site is described as bushveld, dominated by *Burkea africana* and *Terminalia sericea* tree species with *Eragrostis pallens* in the grass layer (Blackmore et al., 1990; Frost, 1987).

Figure 1.1 *Map of the study site at Nylsvley, located in South Africa; with site I and II indicating sites close to Marulakop – which is South-East of the two Red stars.*

1.5 AIMS

This study aims to investigate the seasonal patterns of leaf display in a semi-arid savanna site in South Africa, Nylsvley, to improve our understanding of the range of phenological strategies used by savanna trees, and the life history consequences of these strategies. It aims to determine the relationships between different PFTs and vegetative traits in savanna, and trade-offs in response to seasonal drought. It also aims to demonstrate a data-driven approach to identifying phenological functional types as a step towards integrating information across a range of different savanna ecosystems on the globe. Ultimately this work hopes to contribute towards a better characterisation of semi-arid savanna vegetation in DGVMs.

1.6 OBJECTIVES AND HYPOTHESES

1.6.1 Objectives

1. To use defensible, repeatable methods to identify/define the plant phenological functional types in a semi-arid savanna in South Africa.
2. To test how phenological strategies are related to other vegetative traits that impact plant life history; and
3. To determine the environmental trade-offs associated with these functional types and their response to seasonal drought.

1.6.2 Hypotheses

1. Hypothesis 1: To assess if multiple leaf phenology strategies in savanna trees exist.

2. Hypothesis 2: Trees which display their leaves during the dry season must have access to a stored water source and will have low wood density.
3. Hypothesis 3: Trees species in the same family will fall into the same phenological functional types (PFTs) (i.e. phenology is phylogenetically conserved).
4. Hypothesis 4: Trees with the same phenological grouping will have the same vegetative traits (leaf, wood and physiological) and display similar trade-offs between traits.

1.7 STRUCTURE OF THE THESIS

This chapter is the general introduction of the thesis clarifying detailed background of plant functional types (PFTs) research and results. Each chapter addresses different topics on vegetation dynamics. Chapter 2 focuses on defining phenological functional types in the semi-arid savanna addressing hypothesis 1 and 2. Chapter 3 focuses on linking PFTs identified in chapter 2, to different vegetative traits and identify trade-offs between them, while answering hypotheses 2, 3 and 4. The study site of the thesis is explained in Chapter 1, and methods of chapters are explained in detail on each chapter. Chapter 4 has the overall conclusion of the whole thesis, which draws out the key findings from all the chapters and discusses what has been achieved, and how it contributes to improving our understanding of semi-arid savanna PFTs in southern Africa, but each chapter has its own conclusion. References are at the end in a section titles: references.

CHAPTER 2.0
DEFINING PLANT FUNCTIONAL TYPES OF SEMI-ARID SAVANNA TREES

2.1. LEAF PHENOLOGY – BRIEF DEFINITION

Leaf phenology describes the timing of leaf display and fall (Kikuzawa, 1995), and is a major driver of seasonal patterns of heat, energy, and water exchange in ecosystems (Hogg et al., 2000). Annual plant carbon gain is therefore dependent on leaf phenology (Kikuzawa, 1995). Understanding leaf phenology both at an individual and a community level can give insight in the understanding of plant and ecosystem functioning. Leaf phenology is often responsive to environmental conditions (Badeck et al., 2004). Therefore, variation in leaf phenology has been considered as a major variable in differentiating plant functional types (Chave, 1999). The deciduousness of species indicates the adaptation to severe drought and it also show the period of annual resource cycle (light, water, carbon, nutrients etc.) are not being utilised (Singh and Kushwaha, 2005).

Maintaining green leaves costs water and carbon to the plant in terms of transpiration and carbon, so plants are only likely to display leaves when the environmental conditions are suitable for growth. Alternately, building leaves may be so costly, in terms of carbon and nitrogen; there may be a selective pressure to retain existing leaves as long as possible. The degree to which plants show seasonal patterns of leaf display can therefore reflect environmental stresses in a particular ecosystem. African savanna ecosystems tend to be dominated by deciduous species (Reich, 1995). This is due to the predictable and lengthy seasonal drought which is distinctive of this biome (Lehmann et al., 2011). The evergreen component in savannas is usually quite low – as evergreen species are usually predicted to occur when favourable conditions for photosynthesis are shorter (Kikuzawa, 1991).

One of the key climatic changes predicted by global models is a change in the length and timing of growing season – either due to warming or changes in the patterns of rainfall (Rivera et al., 2002; Rivera and Borchert, 2001). Describing the different phenological strategies and the life-history trade-offs associated with these strategies, might help us to predict which strategies are at risk under changing environments. Semi-arid savanna systems are one of the most vulnerable systems to be affected by global change impacts (IPCC, 2007).

2.2 WHAT IS KNOWN ABOUT LEAF PHENOLOGY IN SAVANNA ECOSYSTEMS?

Phenological studies from tropical systems in across the world have shown that tree leaf phenology does not always follow seasonal patterns of soil moisture availability nor do they always follow temperature like those in temperate regions (Chidumayo, 1990; Williams et al., 1997). Some trees put on leaves before the start of the rainy season, and many trees maintain their leaves after the end of rainy season (Owen-smith and Cooper, 1987; Sarmiento and Monasterio, 1983). Some trees also appear to drop a certain percentage, but not all, of their leaves (Williams et al., 1997) in North Territory Australia.

The strategy of early-greening leafing out before the first rains of the season (Archibald and Scholes, 2007; Borchert, 1994), implies that these savanna trees have access deep water or to stored water (Eamus, 1999). They can therefore disconnect their seasonal patterns of leaf display from seasonal water limitation, unlike grasses (the other dominant life form in savannas) that are dependent on soil moisture. The relative dominance of trees with this "early-greening" strategy in different savanna environments, and the potential ecological benefits of this strategy have never been well quantified. Moreover, there are also many savanna tree species that drop their leaves early – before the end of the rains, as well as those that maintain a canopy well into the dry season before dropping their leaves. In an attempt to make sense of the variety of leaf display patterns in tropical or sub-tropical savanna environments, several authors have classified them into

phenological strategies. However, the methods used are often subjective and definitions are not always comparable across environments.

For example, Borchert, (1994), classified trees in South America into three functional types, based on tree wood density. Elliott et al., (2006), in south East Asia defined five functional types in savanna woodlands based on their timing of leaf flush: rain-induced deciduous, spring flushing deciduous, irregularly leaf-exchanging, leaf exchanging and evergreen. Furthermore, Williams et al., (1997), in Northern Australia used a quantitative classification based on how many leaves were lost at the peak of the dry season: evergreen, brevi-deciduous, semi-deciduous and deciduous. Similarly, in the West African savannas: In Mali and Burkina Faso, three PFTs were identified based on the presence of green leaves and timing of leaf displays (De Bie et al., 1998).

Integrating understanding about savanna structure and function across different savanna ecosystems is a current research priority (Lehmann et al., 2011). There is a need to derive less subjective methods for assessing tree plant functional types that can be used to compare life-history strategies between savanna environments, draw conclusions about the relative importance of soil moisture and temperature, and implement DGVMs. In systems with seasonal temperature limitation, like temperate systems - accurate leaf phenology models can be derived from simple temperature and day length cues (Chuine and Cour 1999; Seiwa, 1999; Nizinsiki and Saugier, 1988). In contrast, the timing of leaf onset and leaf drop, as well as the length of the dormant period are very variable in seasonally-dry regions, and models which predict vegetation greenness from soil moisture alone have been shown to be inadequate for savanna ecosystems (Jolly and Running, 2004; van Wijk and Rodriguez-Iturbe, 2002).

2.3 AIMS OF THIS CHAPTER

This chapter aims to compare a data-driven approach (ordination and clustering methods) with a subjective approach, to assess the variety of phenological strategies shown by savanna trees in a semi-arid savanna ecosystem, and to

identify clear plant functional types. This will set the context for my next chapter which will explore the life history strategies and vegetative traits associated with the functional types identified.

2.4 MATERIALS AND METHODS

2.4.1 Data collection and analysis

2.4.1.1 Phenology and rainfall data

The vegetative phenology of 28 tree and shrub species representing, 18 genera and 12 families were collected from July 2012 - September 2013. The number of replicates varied from 1 to 10 individual species and were marked using GPS (Garmin, 3 meter accuracy). Leaf phenology was monitored for a total of 174 trees. To describe the phenology I used methodology from Pérez-Harguindeguy et al., (2013). Canopy fullness was visually assessed monthly for each individual tree. Canopy greenness index was categorised on a scale of 1:5 where: 1<10%; 2>10%; 3>25% but less than 50%, 4>50% but less than 75%; 5>75% full leaf canopy.

In 1982/83 leaf biomass were monitored at Nylsvley monthly over a full growing season for the purposes of assessing available forage (Owen-smith and Cooper, 1987). The leaf longevity in this study include all leaves attached to the tree, therefore this data was not used for further analysis. The weight of leaf material present on the tree was assessed monthly. As data collection methodologies differed from this study I transformed both measures to scale from 0 to 1 where 0 = no leaves on the trees, and 1 = a full canopy, to make the data comparable. I collected rainfall data using a tipping bucket rain gauge, which was installed in 2011 at a weather station at the Nylsvley office, and data found from Nylsvley data records (Scholes and Walker, 1993), and summarised to monthly totals. I put Owen-Smith data to give some sense of variability between years, and was not used for further analysis.

2.4.1.2 Calculating phenological metrics

There have been metrics which have already been identified using time-set (Jonsson and Eklundh, 2004). To facilitate comparison of phenological characteristics between tree species, I identified 8 phenological metrics and all were quantified from this study dataset:

1. Length of dormant season (LDS) defined as the number of months where the greenness index was less than or equal to 1.
2. Length of growing season (LGS) defined as the number of months which had greenness index greater than 3.
3. Green-Up Date (GUD) defined as the date when the greenness first goes above the minimum value for the year. Therefore even evergreen species can have a green-up date if they show some variation in leaf area during the season.
4. Length of green-up period (LGUP) defined as the number of months between green-up date, and the date it first reaches its maximum greenness.
5. Date of first leaf drop (DFLD): the date where the greenness value drops below its maximum (*i.e.* the first month where the greenness index goes below its maximum greenness index).
6. Length of dry down period (LDDP) defined as the number of months from the date of first leaf drop to the date it first reaches its minimum value.
7. Degree of rain-stimulated flushing (DRSF**)**: the difference between greenness in September 2012 and September 2013. Because of the early September rains in 2012 I expect that trees that wait for the rains before they flush would therefore have big difference between those two years, whereas trees that green early would have a smaller difference (Table. 2.2).
8. Difference between maximum and minimum mean value (DIFFMax/Min) defined as the difference between the maximum and minimum greenness of the species. DIFFMax/Min was only used to distinguish evegreen species in the analysis, and not selected for other analysis in this chapter.

2.4.1.3 Methods of identifying plant functional types

I used two methods to identify PFTs: a) a subjective approach, where the seasonal patterns of greening were used in grouping species into categories that made ecological sense to me (the approach used in most phenological studies up to now). b) The data-defined approach, where the phenological metrics quantified from the data were interrogated using ordination techniques and clustering analysis to identify clusters of species with similar combinations of phenological traits (Skarpe, 1996).

2.4.1.4 Principal Component Analysis (PCA)

A principal component analysis (PCA) was used to explore the distribution of tree species in phenological trait-space, and to determine the major axes of variation. The relationships amongst phenological metrics and tree species were performed using a clustering approach to define phenological functional types (PFT). It is a simple and easy analytical tool for data analysis and processing (Hotelling, 1933). This technique is a way of summarising multivariate data into two or three "components" which account for most of the variation in the dataset. Different variables contribute differently to each component, and by exploring this one can understand which variables, or combination of variables, drive most of the variability in the data (Jackson, 1997). Usually the first 2 or 3 components account for most of the variability.

PCA is sensitive to the relative scaling of the original variables, for example if one variable ranges from 0-100 and the other from 0-10 then the contribution of the first variable will be overestimated. For this reason, it is important to re-scale and normalise the data before running a PCA. A PCA was run using the prcomp package in the R statistical package (www.r-project.org). Non-normal data (LDS, LGS, GUD, LGUP, DFLD, LDDP, and DRSF) were logged except DIFFMax/Min. The prcomp package automatically centred and scaled the data.

2.4.1.5 Clustering methods

Cluster analysis means the manipulation of observation data into meaningful groups, and clustering analyses requires that the number of groups are known beforehand. Clustering methods range from those that largely depend on the experience of the observer (ecologists) to more formal procedures based on statistical models (Fraley and Raftery, 1998). Various clustering methods have been developed for a variety of applications – ranging from information theory to social science.

The Model-Based clustering uses expectation maximisation to identify clusters (Fraley and Raftery, 2007). This method also uses maximum-likelihood criterion to rotate the characteristics along the axes to get the best groups (Banfield and Raftery, 1993). Importantly, this method can be used to determine the most appropriate number of clusters: in this case MClust is run performed increasing numbers of clusters (e.g. from 1:9) and assigning a Bayesian Information Criterion (BIC) to the results of each run. The most likely number of clusters is considered to be that where the BIC in minimised (Dasgupta and Raftery, 1998; Campbell et al., 1997). Similarly, this method can be used to test assumptions about the shape and size of the clusters. Finally, model-based clustering also estimate the uncertainty around grouping by using expectation maximisation methods (Fraley and Raftery, 2007), and for predicting the grouping of points not used in the original analysis based on their attributes.

2.4.1.6 Statistical analysis

The R statistical package was used to analyse the dataset. All the data were cleaned in the spreadsheet in input into R package. The ANOVA was use to test statistical significance of differences between species and groups. The MClust prcomp was used to group species into similar PFTs. The MClust promp enable to normalise and centred the phenological metric data. The data was then run on MClust algorithm for a range of cluster sizes from one to ten and cluster volumes

and shapes (equal/equal, Variable/equal and variable/variable). I then used standard model selection methods (minimising the BIC value) to ascertain which was the appropriate formulation for the data. This model was then used to identify the phenological functional types at the study site. The more automated method (MClust) was then compared with ecological understanding "subjective" classification, where the phenological metrics (patterns) were used to derive "ecologically meaningful" grouping of species in terms of leaf phenology (July 2012 – June 2013). The subjective classification was assessed based on the raw greenness values of each species looking at the timing of greening. Most authors have used this "subjective" approach in the past which is possibly why there is so much disagreement between studies. These classifications were run on my dataset and not on the Owen-Smith dataset.

2.5 RESULTS

2.5.1 Rainfall

The site shows strongly seasonal rainfall with the rainy season starting in October/November and ending in April (Table 2.1). However, there is a great deal of variability from year to year. Annual total rainfall during each of the complete seasons (July 2012 – June 2013 and July 1982 – June 1983) was ~634.9 mm and ~497.3 mm respectively (Table 2.1). The annual long-term average rainfall for this location is 623 mm (Frost, 1987); therefore the rainfall of 497.3 mm in 82/83 was below average mean and was a drought year. In 82/83, the first significant rains (>20 mm) arrived in October (46.6 mm) and the rains only really set in by December (92.7 mm). In the 2012/13, the annual total rainfall was (634.6 mm), which shows that it was a normal rainy year, representative of the average annual rainfall for the area. In 2012 the first significant rains arrived on 7 September (103.9 mm), which can be regarded as early. This was an unfortunate event for my project, as it made it difficult for me to identify "early greeners"- most tree species started greening in September. In comparison, 2013 first rains

arrived on 7 October (69.9 mm). As I had greenness data for September 2012 and 2013 it was possible to assess early-greening by comparing greenness values in September between years (See section 2.4.2.2 (DRSF). The highest monthly rains reached (131.1 mm) in January 2013 (Table 2.1).

Table 2.1 *The rainfall (mm) at Nylsvley during two growing season when phenology was assessed. The total represents the seasonal pattern of rainfall from July 2012 to June 2013 (twelve months period), with bold > 50 mm representing significant rainfall. The third column shows the monthly average rainfall from (Scholes and Walker 1993).*

Month	Rainfall (mm)		
	2012/13	1982/83	1975-1984
July	0	4.6	0.08
August	0	0	8.6
September	103.9	4	21.6
October	69.9	46.6	53.1
November	62	39.9	106.9
December	77.7	92.7	81.3
January	131.1	87.9	150.6
February	45.7	47	87.2
March	66.6	105.5	69
April	78	53.1	27.8
May	0	2.6	6
June	0	13.4	0.8
Total	634.9	497.3	612.94
July	0	0.3	
August	1.3	15.7	
September	0	0	

2.5.2 Seasonal patterns of leaf display

The timing of leaf display at the site generally shows the timing of seasonal rainfall but with wide variation. Most of the species reached their full canopy leaf greenness in November and started to lose leaves in February (Figure 2.2 top panel). The timing of initiation of leaf display ranged from during the dry season to the beginning of season, and leaf drop could start as early as February or as late as June (Figure 2.2 top panel). Some species never dropped their leaves, and other only dropped some of their leaves. Differences in the patterns shown between 2012/2013 and 1982/83 could represent differences in data collection (no data were collected between December and April in the Owen-smith dataset (pers comm), (Figure 2.2 bottom panel). The differences in the timing of rainfall (rains arrived very early in 2012 so many species greened early).

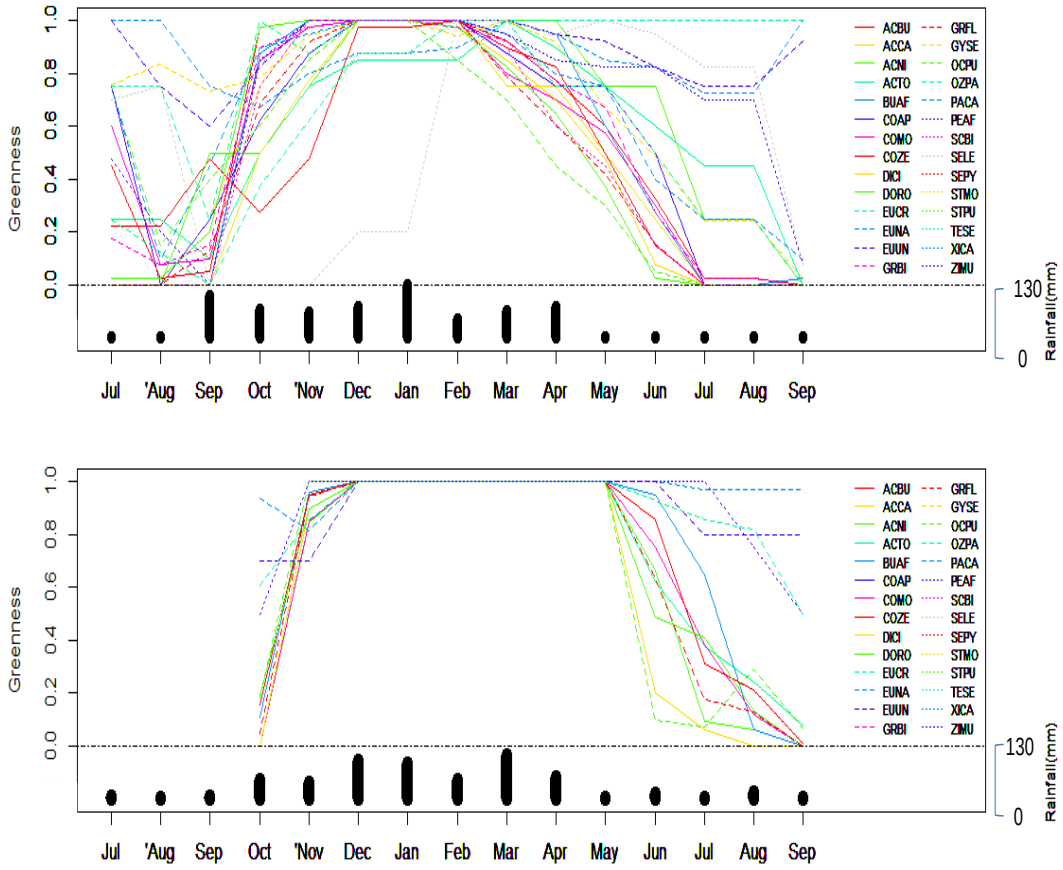

Figure 2.1 *Seasonal patterns of leaf display of the 28 tree species at Nylsvley Nature Reserve during 2012/13 (top panel) and 1982/83 (bottom panel). The black bars show monthly rainfall (mm). See Table 1 for the full species names. Only the species in common with this study's data are shown in the bottom panel*

Table 2.2 *Variability in phenological metrics (mean) and standard deviation in brackets across the sampled species. Variation in phonological metrics within species was generally quite low, indicating that it should be acceptable to use the mean values in my analysis.*

Family	Species	Abbr	No. of trees	LDS	LGS	GUD	LGUP	DFLD	LDDP	DRSF	DIFFMax/Min	MClust PFT	Subjectiv PFT
Fabaceae	*Acacia burkei*	ACBU	7	2.4(1.9)	5.7(1.9)	9.3(0.75)	2.2(1.6)	3	4	1.8(1.21)	4(0)	BDS	d
Fabaceae	*Acacia nilotica*	ACNI	1	2	8	9	3	5	3	2	4	BDS	c
Fabaceae	*Acacia tortillis*	ACTO	5	0.6(0.55)	7.8(0.84)	10(0)	3(1.87)	4	3	0.4(0.55)	4(0)	BDS	e
Celestraceae	*Gymnosporia senegalensis*	GYSE	10	0.1(0.32)	9.2(1.48)	8.7(3.23)	2.4(0.55)	4	3	2.6	3.9(0.31)	BDS	e
Anacardiaceae	*Ozoroa paniculosa*	OZPA	2	2(1.41)	6(0)	10.5(0.71)	1.4	1.4(0.55)	3	0	4(0)	BDS	e
Fabaceae	*Peltophorum africanum*	PEAF	8	2.1(0.83)	9.5(0.93)	10(0)	1	3	4	-0.3	3.8(0.46)	BDS	d
Anacardiaceae	*Searsia leptodicta*	SELE	4	3.8(0.5)	7.5(0.58)	3.8(5.5)	2	6	1	-0.3	4(0)	BDS	e
Anacardiaceae	*Searsia pyroides*	SEPY	5	0.8(0.45)	9.2(0.45)	9.2(0.45)	2	5	2	0.7	3.7(0.45)	BDS	c
Strychnaceae	*Strychnos pungens*	STPU	1	0	9	8	3	4	3	0	4	BDS	e
Ebenaceae	*Euclea crispa*	EUCR	3	0(0)	9.7(1.88)	10(0)	0(0)	0	0	-3	0.3(0.47)	EVG	a
Ebenaceae	*Euclea natalesis*	EUNA	10	0(0)	10.5(1.58)	9.9(2.56)	-2.9	4	4	-1	1.7(0.48)	EVG	a
Ebenaceae	*Euclea undulata*	EUUN	10	0(0)	11.2(0.42)	9.7(0.48)	-2.9	4	3	-1.3	1.4(0.92)	EVG	a
Strychnaceae	*Strychnos madagascariensis*	STMO	5	0.2(0.45)	9(1)	9(1)	1	2	3	-0.1	2	EVR	a
Olacaceae	*Ximenia caffra*	XICA	1	1	5	9	3	6	1	-1	2	EVR	c
Leguminosae	*Burkea africana*	BUAF	10	3.1(0.3)	7.2(0.6)	10(0)	0.5(0.5)	4	3	-0.1	4(0)	LDS	e
Fabaceae	*Dichrostachys cinerea*	DICI	10	3.7(0.46)	6.1(1.04)	10(0)	1.8(0.4)	2	5	0	4(0)	LDS	d
Malvaceae	*Grewia flavescens*	GRFL	10	3(0.67)	5.8(1.13)	9.5(0.53)	2.7(4.95)	3	4	0.5	3.9(0.31)	LDS	b
Anacardiaceae	*Sclerocarya birrea*	SCBI	5	3.4(0.55)	6.8(1.3)	10(0)	1	3	5	0	4(0)	LDS	d

Combretaceae	*Terminalia sericea*	TESE	10	3.3(0.82)	5.8(1.69)	10(0)	2	3	4	0	3.9(0.32)	LDS	d
Fabaceae	*Acacia caffra*	ACCA	1	1	6	9	2	3	4	1	4	RS	b
Combretaceae	*Combretum apiculatum*	COAP	2	1(0)	8.5(0.35)	9(0)	2.5(0.35)	3	4	1	4(0)	RS	b
Combretaceae	*Combretum molle*	COMO	10	1.7(1.06)	7.4(1.07)	9.8(0.42)	0.8(0.63)	3	4	0.4	4(0)	RS	b
Combretaceae	*Combretum zeyheri*	COZE	10	2.6(0.84)	8(0.67)	9.9(0.32)	0.2(0.63)	3	4	0.2	4(0)	RS	b
Sterculiaceae	*Dombeya rotundifolia*	DORO	10	2.9(0.88)	6.2(0.63)	9.1(0.57)	1(0.67)	2	5	0.8	4(0)	RS	b
Malvaceae	*Grewia bicolor*	GRBI	9	2.1(0.93)	8(1.32)	9.6(0.53)	1.8(0.92)	2	6	0.6	4(0)	RS	b
Ochnaceae	*Ochna pulchra*	OCPU	5	1.4(0.55)	7.2(1.79)	9.2(0.45)	2.5(2.12)	2	5	1.6	4(0)	RS	b
Sapindaceae	*Pappea capensis*	PACA	5	0.4(0.55)	9.2(0.84)	9(0)	3	0.6(0.51)	4	1.4	3.6(0.55)	RS	b
Rhamnaceas	*Ziziphus mucronata*	ZIMU	5	1.4(0.89)	8.4(1.14)	9.6(0.54)	2.5	2	5	0.4	4(0)	RS	b

Table 2.3 *PCA correlation coefficients between phenological metrics. Values in brackets indicating statistical significance of these correlations (p values < 0.05).*

Phenological metrics	LDS	LGS	GUD	LGUP	DFLD	LDDP	DRSF
LDS	1						
LGS	-0.47 (0.012)	1					
GUD	0.3	-0.05	1				
LGUP	-0.33	-0.11	0.12	1			
DFLD	0.26	0.01	0.29	0.25	1		
LDDP	-0.03	-0.42(0.026)	-0.3	0.11	-0.41 (0.002)	1	
DRSF	-0.07	-0.4 (0.035)	-0.26	0.55 (0.002)	0.14	0.47 (0.012)	1

2.5.3 Identifying clusters of similar species

2.5.3.1 Principal Component Analysis

All seven phenological metrics contributed significantly to the principal components. The standard deviation (sd) of the first three components was 1.46, 1.32 and 1.23, respectively. All other components were smaller (eigenvalue <1.0) and explained a minor proportion of variance in phenological metrics. The overall PCA results show a wide variation among phenological metrics and tree species. Species were well dispersed throughout the multidimensional PCA space, but no obvious clusters emerge (Figure 2.2).

The first component was driven largely by variation in the length of the dry-down period, which were negatively related to the length of growing season ($r = -0.42$) and $p = 0.026$ (Table 2.3), and positively related to the degree of rain-stimulated flushing (i.e. plants that take a long time to dry down do not green up early and their leaf flush is stimulated by rains).

The second component largely describes trade-off between length of dormant season and length of growing season with the correlation coefficient of r = -0.47 and p = 0.012 (Table 2.3, Figure 2.2 b). However, it is interesting to note that species with a long dormant season also had a late green up date and a late date of first leaf drop (DFLD and GUD also contribute to PC2 – i.e. plants with long dormant season are not influenced by rainfall to flush or drop leaves).

The third component represents variability in the date of first leaf drop – species with long dry down periods tend to have early dates of leaf drop (Figure 2.2 b). More interestingly, it appears that species that take a long time to dry down generally green up quickly, and vice versa. The degree of rain-stimulated flushing and length of green-up period were positively correlated (r= 0.55 and p = 0.002) (Table 2.3), and were largely negatively related to length of growing season (Figure 2.2 a). This means that species which flush after rains take a long time to reach full canopy and have short growing seasons.

There was also statistical significance between DRSF and LGS with r = -0.4 and p = 0.035, and between LDDP and DFLD with r = -0.41 and p = 0,003. Positive Statistical significance was also observed between DRSF and LDDP with p = 0.012.

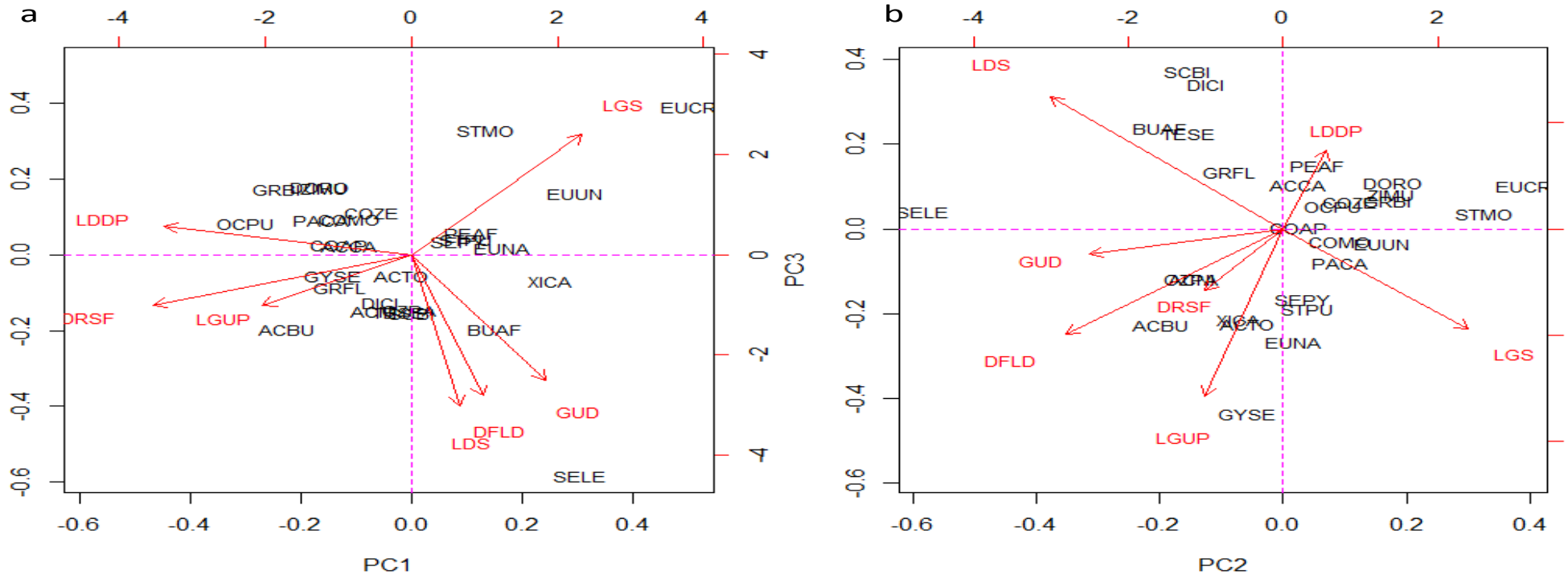

Figure 2.2 *Dimensions of variation in phenological strategies using principle component analysis of the mean values of 7 phenological metrics of 28 savanna trees, with a) representing PC1 vs. PC2 and b) representing PC2 vs. PC3. The phenological metrics represented by red lines with arrows, with species represented within each four quarters, divided by orange lines and black bold letters in two of the graphs.*

2.5.3.2 Subjective classifications

From subjectively assessing the variation in phenological patterns shown in (Figure 2.2), I identified 5 different functional types.

a. Evergreen species were species which had substantial canopies all year round, namely: *E. crispa*, *E. natalensis*, *E. undulata*, *G. senegalensis*, *S. madagascariesis*, *S. pungens*, and *X. caffra*.
b. Early greener, early dropper were species which had a green-up date occurred in September, and drop their leaves early between February and March, which includes: *C. apiculatum*, *C. molle*, *C. zeyheri*, *D. cinerea*, *D. rotundifolia, A. caffra*, *G. bicolor, G. flavescens, O. pulchra*, *P. capensis*, and *Z. mucronata*.
c. Early greener, later dropper species were which had flush out their leaves early in September and drop late between May and June. Namely: *A. burkei*, *A. nilotica*, *A. tortilis*, *B. africana*, *P. africanum*, and *S. pyroides.*
d. Late greener, early dropper species were species which green-up date occurred in October and start to loss leaves between February, this includes *T. sericea* and *S. birrea.*
e. Late greener, late dropper species were species which green-up late between October and December, and drop their leaves between April and May, which includes *O. paniculosa* and *S. leptodicta*.

Obviously the subjective classification was influenced by the early rains in September 2012, which meant that my identification of "early greeners" might also have included those that were stimulated to flush with the rains. Mostly the data from Owen-Smith dataset corroborated my data and were not used in the "subjective" classification.

2.5.3.3 Objective clustering procedure (MClust)

Applying MClust to the same 8 phenological metrics used in the PCA indicated that a spherical cluster with unequal volume was by far the best model to fit (Figure 2.4 BIC value -534.77, df = 26, log likelihood = -224.57). Using this model, the analysis identified three plant functional types (PFT's). Beyond three phenological types, the increase in BIC was negligible (Figure 2.4), and did not justify further splitting of the data. The number of plant species in each of the three PFTs varied from five to nine (Table 2.2), indicating that not all phenological strategies are equally common. As MClust, did not clearly distinguish evergreen species DIFFMax/Min metric was introduced in order to split these species. All species which had the DIFFMax/Min mean less than 3 were considered to be evergreen. This means that the total of four PFTs were identified using both objective (MClust) and subjective method.

The first PFT had the highest number of species 9. These species were trees with a longer length of growing season of approximately 5-9 months. These are "brevi-deciduous species" (BDS). These species keep their leaves throughout the year and they had a lowest degree of rain stimulated flushing DRSF (0.04) (Table 2.4). The second PFT had 9 species, and were rain-stimulated species (RS) which flush just after the first rains arrive and drop their leaves early as dry season approaches. In 2012, these trees started to flush in September and dropped their leaves early May. These species had the highest DRSF (0.82), indicating that rainfall stimulated their flushing. The third PFT had 4 species. These were "Longer dormant species" (LDS), and showed lengthy dormant season of approximately 3 months, with a shorter growing season of approximately 6 months. These species flush their leaves before the first rains. They also show shorter length of green up period of approximately 2 months, but start to green up approximately as early as September (Table 2.4).

The fourth PFT had 5 species, which were classified using DIFFMax/Min metric with less than 3 mean values which were *E. Crispa, E. natalesis E. Undulate, S.*

Pyroides and *X. Caffra*. These species were classified as evergreen species. However, these species also had longest growing season of approximately between 9 -11, except for *S. Pyroides* and *X. caffra* with 5 as they were represented by only 1 individual tree (Table 2.2).

Table 2.4 *The mean with standard deviation in brackets in each functional group. Clusters represented by: "brevi-deciduous" species (BDS), Evegreen species (EVR), Rain-stimulated species (RS), and Longer dormant season specie (LDS).*

Phenological metrics	Clusters			
	BDS	EVR	RS	LDS
LDS	1.46(1.3)	0.36(0.49)	1.61(0.8)	3.3(0.27)
LGS	7.9(5.63)	9.1(9.9)	7.7(4.12)	6.3(2.28)
GUD	8.7(1.98)	9.56(0.43)	9.36(0.36)	9.9(0.22)
LGUP	8.7(0.82)	9.56(2.28)	9.36(0.94)	9.9(0.86)
DFLD	3.6 (1.42)	3.8(2.28)	2.29(0.81)	3(0.71)
LDDP	3 (0.86)	2(1.58)	4.56(0.72)	4.2(0.83)
DRSF	0.67(1.13)	-1.12	0.82(0.45)	0.08(0.23)
DIFFMax/Min	3.74(0.65	1.82(1.23)	3.95(0.13)	3.96(0.05)

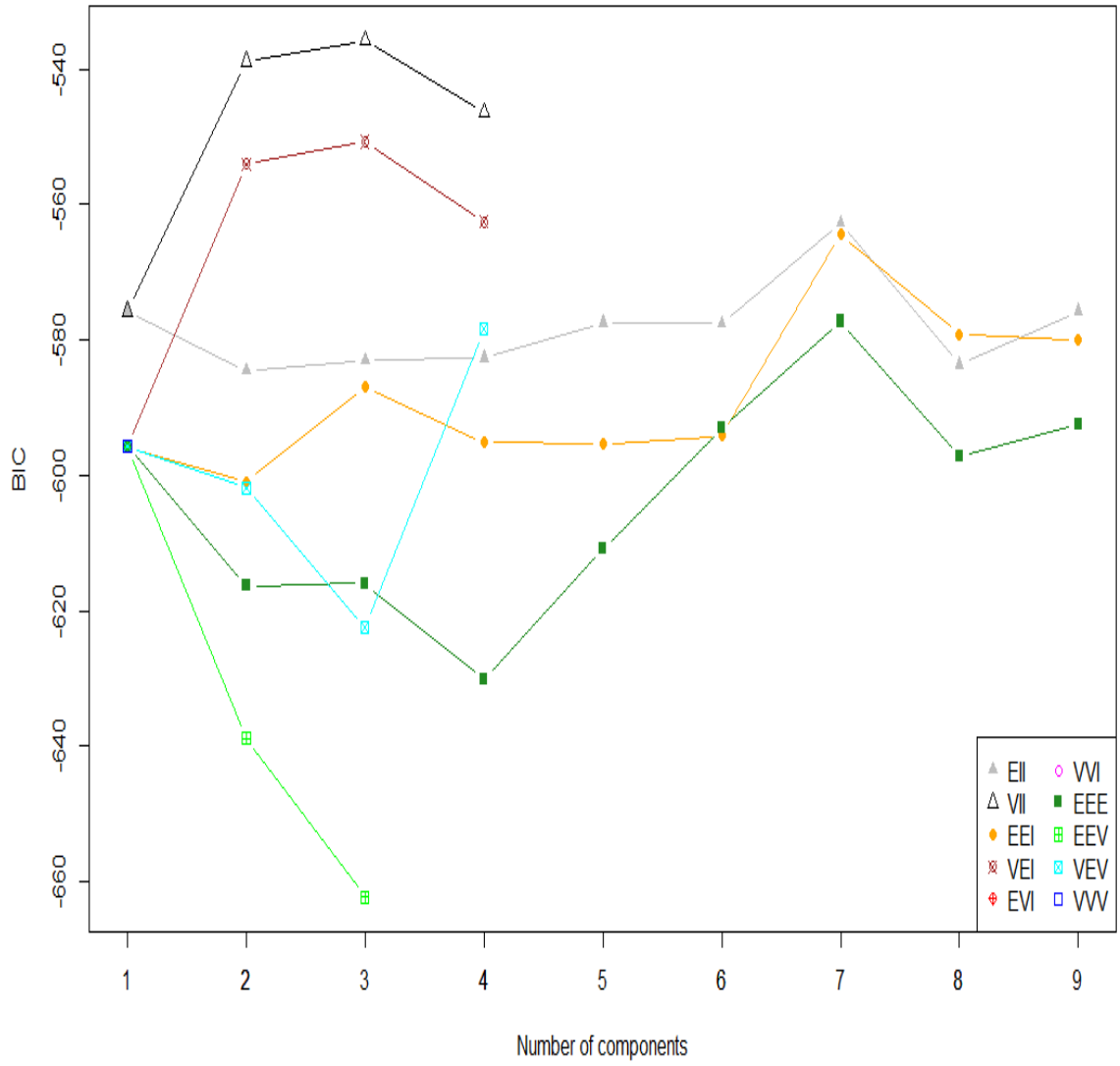

Figure 2.3 *The most likely number and shape of clusters of plant functional types using BIC and expectation-maximization. The different model shapes are represented by different colours as indicated on the legend, EII, VII, EEI, VEI, EVI, VVI, EEE, VVV, EEV, and VEV on the bottom right corner of the graph.*

2.5.4 MClust biplots between six phenological metrics and three PFTs

Biplots of the various phenological metrics give a visual assessment of the data in Table 2.4. There is very little overlap in the three PFTs within axes of length of dormant season and length of dry down period (Figure 2.4a, b). Figure 2.4c indicates that the rain-stimulated strategy is clearly differentiated from the other two using green up date, and that the other two functional types are distinguished by the length of the growing and length of dormant season. On the other hand, there is more overlap between functional types in the date of first leaf drop and length of the green up period (Figure 2.4 f).

2.5.5 Comparing the two approaches

Overall there was no agreement between the two clustering methods. All of the evergreen species, identified subjectively fall into brevi-deciduous species MClust group (Table 2.5), but this group also contains species that I classified at early greener late dropper, and late greener late dropper. On the other hand, all of the "rain-stimulated species" identified by MClust fell into early greener early dropper category, but this category also included a few other species. The subjective "Late greener early dropper category" coincided with the "longer dormant species" MClust category which is to be expected.

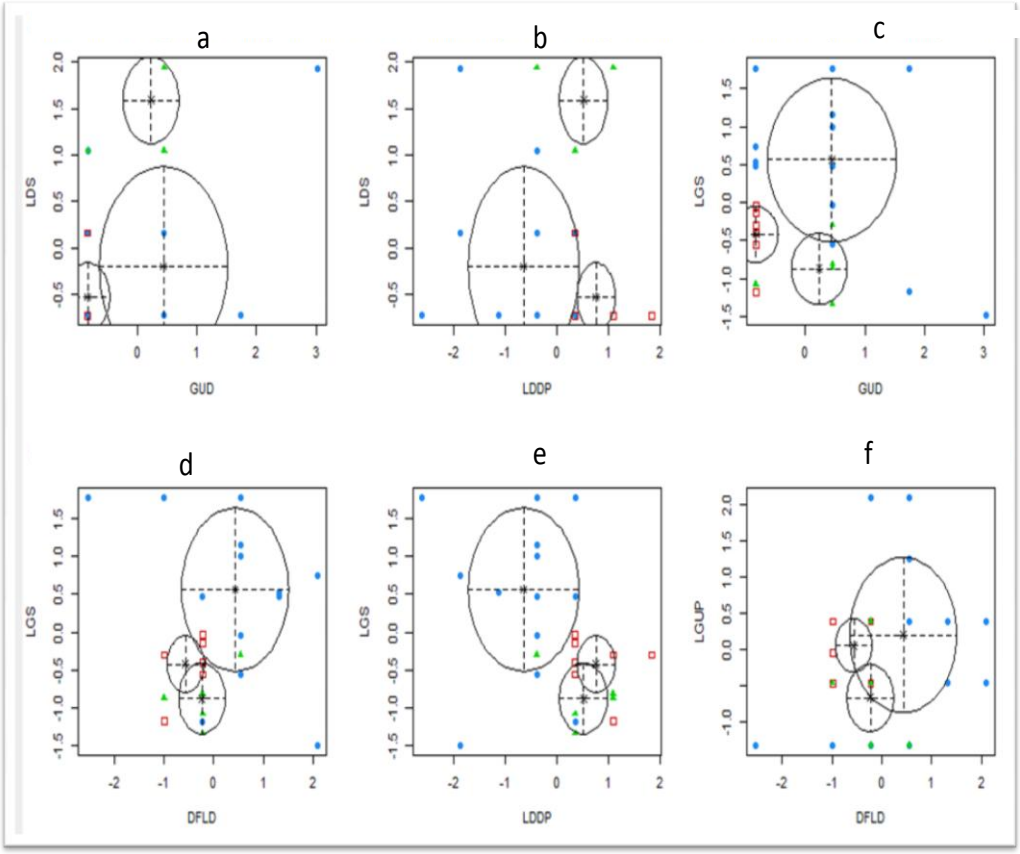

Figure 2.4 *Biplots of six phenological metrics and distribution of PFTs. a) LDS=length of dormant season and GUD=Green up data, b) LDS and LDDP=Length of dry down period, c) LGS=Length of growing season and GUD, d) LGS and DFLD=Degree of first leaf drop, e) LGS and LDDP and f) LGUP=Length of green up period and DFLD. Data have been centred and rescaled. The colours represent the three different clusters identified by expectation-maximisation clustering (Blue - longer growing species; Red - Rain stimulated species; and Green - longer dormant species. The volumes of these three clusters indicated with black stars (mean) and circles (sd).*

2.5.6 Comparing the subjective and objective approach

Table 2.5 *Testing for agreement between subjective and objective (MClust) approach of grouping species into functional types. Objective group BDS is very broad and includes species classified into three of the subjective groups. The clearest agreement seems to be in the rain-stimulated and early greener early dropper class.*

	Subjective approach				
MClust	A	B	C	D	E
	Evergreen	Early greener Early dropper	Early greener Late dropper	Late greener Early dropper	Late Greener late dropper
BDS	4	0	5	0	2
RS	0	9	0	0	0
LDS	0	2	1	2	0
EVG	3	0	0	0	0
Total	7	11	6	2	2

2.6 DISCUSSION AND CONCLUSION

2.6.1 Summary of the results

Trees in South African semi-arid savanna systems have a wide variation of seasonal leaf display. Using the subjective classification five PFTs were identified, whilst using the MClust 3 were identified and 1 include subjectively. Trees which were brevi-deciduous, rain stimulated, long dormant season species, and evergreen species. The groupings demonstrate some clear trade-offs, for example, trees that take a long time to dry down do not green up early. Trees that green up slowly tend to dry down quickly and vice versa. The results show that certain species in semi-arid flush their leaves before the first rains.

2.6.2 Identifying plant functional types (PFTs)

The subjective and objective classification (MClust) produced different results (Table 2.5), which were probably related to the particular metrics of interest that I used to make the classifications. The MClust classification used only the plant phenological metrics, with DIFFMax/Min used to classify evergreen species subjectively, while subjective approach focused mostly on the timing of green up and leaf drop.

The very large "brevi-deciduous" MClust group clearly contains all the evergreen species I identified. However, DIFFMax/Min was used to split this group further. In retrospect this may have occurred as I did have a good metric to distinguish evergreenness in my MClust algorithm. The introduction of a metric "difference between maximum and minimum greenness" allowed me to subjectively split the "long-growing season" functional type into "evergreen" and "brevi-deciduous" (only dropping some of their leaves). Therefore, the MClust algorithm separated out evergreen species – which are clearly very different from all the other three phenological strategies.

On the other hand, the methods tended to agree on the species that belonged to the "rain-stimulated greening" group: all of the species in MClust category 2 fell into subjective category b, and 9 out of the 11 species in subjective category b fell into MClust category 2. Tree species in semi-arid are mostly stimulated by rain to flush; this might be the reason why almost all rain-stimulated species from MClust were on the same category as early greener, early dropper (Table 2.5).

2.6.3 Ecological significance of subjective grouping

I categorised the species mostly on the timing of leaf on and leaf drop – as it had being very important for savanna functioning and tree life history strategy. On this approach I clearly separated out evergreen species which had green leaves throughout the year. *Euclea crispa*, *E. natalensis*, *E. undulata*, *G. senegalensis*, *S.*

madagascariesis, *S. pungens*, and *X. Caffra* were identified as evergreen. Leaf palatability study at the same site between 1982 and 1983 also identified *E. natalensis*, *E. undulata*, *S. pungens*, and *X. Caffra* as evergreen species (Owen-smith and Cooper, 1987).

"Early greener, early droppers" represent species which started to green up as early as September and start to drop their leaves in February the following year. As the rains in my study year continued until April, leaf drop started in February is notable and might be influenced by decrease soil moisture. They showed short length of growing season of about 4-5 months; include *C. apiculatum*, *C. molle*, *C. zeyheri*, *D. cinerea*, *D. rotundifolia*, *A. caffra*, *G. bicolor*, *G. flavescens*, *O. pulchra*, *P. capensis*, and *Z. mucronata*. This group appears to have a range of different plant types in it – from broad-leafed Combretaceae to fine-leaved *Dichrostachys cinerea*, which also represented many plant families.

The third classified category is "Early greener, late dropper" these were species which started to green up in September and drop their leaves early in the dry season in May or June. They have about 7 or 8 months length of growing season which enhance time for photosynthesis. The species in this category are: *A. burkei*, *A. nilotica*, *A. tortilis*, *B. africana*, *P. africanum*, and *S. pyroides*. Most of these species were savanna deciduous species (Owen-smith and Cooper, 1987).
"Late greener, early dropper" these are species which green up in late October or November and drop their leaves as early as February or March, with only 3-4 months of growing season, which were *T. sericea* and *S. birrea*, which are very common species in semi-arid savannas in southern Africa. *Sclerocarya birrea* has previously been identified as an early-greener (Archibald and Scholes, 2007), so it is possible that the strange rains in 2012 influenced this classification (i.e. that it green up at in October, but all the rain-stimulated species greened up in September with the rains).

The final group were "late greener, late dropper" which were two species *O. paniculosa* and *S. leptodicta*, nevertheless *S. leptodicta* was described as

evergreen species from previous study (Owen-smith and Cooper, 1987). Both of these species were severely impacted by insect herbivory in the year of study so this might have impacted their leaf canopy scores. Despite its limitation I chose to use the objective "MClust" classification for the rest of my research. While the metrics I chose were expanded to get better results, which the four PFTs grouping are clearly distinguished and relate to measured differences in the field.

2.6.4 Ecological significance of the MClust grouping

The "brevi-decuduous" functional type identified by MClust include trees with a longer growing season, but also drop some of their leaves, and flush their leaves after the first significant rains have occurred (>50 mm, ~ October). They have short a dormant season and if they do lose their leaves, they do it late, and quickly (Table 2.4). These species are *A. burkea, A. nilotica, A. tortilis, G. senegalensis, O. paniculum, P. africanum, S. leptodicta, S. modagascariensis,* and *S. Pungens*. I predict that this strategy distinguished by trees that are deep rooting and have access to more water, which enable them to maintain high transpiration rates during dry periods (Goldstein et al., 1989). I would also expect leaves on these species to have a low SLA, as they are likely to be long-lived (Wright et al., 2004).

The second MClust group was trees that had a large difference between greenness in September 2012 and September 2013 (DRSF = 0.82) and this functional group I termed "rain-stimulated species" – i.e. species whose leaf display is very sensitive to rainfall (Table 2.4). These species initiate leaf drop very early (end February on average) and have a very slow rate of dry down (Table 2.4). They therefore have the shortest period of total-dormancy. Species were: *A. caffa, C. apiculutum, C. molle, D. rotundifolia, G. bicolor, O. pulchra, P. capensis* and *Z. mucronata.* This functional type can therefore had species that were very responsive to soil moisture – whose phenology most closely tracks that of grasses. It is notable that *O. pulchra* and *D. rotundifolia* occurred in this category, as they

have been identified as “early-greeners” by previous studies (Owen-smith and Cooper, 1987; Childes et al., 1989).

The third leaf display category I termed “longer dormant species” which have a long dormant season (approximately 2-3 months), and a short growing season (6-7 months). These species green-up very quickly, reaching full leaf in less than 2 months (Table 2.4). Species were *B. africana, T. sericea, S. birrea, G. flavescence,* and *D. cineria*. They are also some of the most common species in southern African semi-arid systems. These species do not appear very responsive to soil moisture as the DRSF was low (0.8 – Table 2.4). Some of them represent species that have been identified as “early-greener” (e.g. *B. africana,* and *S. birrea*) (Archibald and Scholes, 2007).

The final category “evergreen species” were *E. crispa, E. natalensis, E. Undulata, S. pyroides,* and *X. Caffra* These tree species had a long growing season, but were mostly distinguished by DIFFMax/Min. They interchange their leaves, as they were showing flushing of new leaves throughout the year (evergreen strategy). This group had the fewest species.

It is important to construct a generalised approach in determining the impact of environmental change in different plant species, even though it is known that each species is ecologically different (Chapin III et al., 1995). Here I used two different methods to group species in Nylsvley into functional groups based on their phenology, both of which were very sensitive to metrics used to create the classification – for example, with the subjective classification I focused only on the timing of leaf display, and with the MClust classification I did not have a good metrics for amount of leaves kept in the canopy. Overall I selected the objective classification (MClust) as the preferred method. It is also easier to quantify the results. However, it is very important that the correct metrics go into the classification.

Using the MClust method the 28 savanna tree species in this study were easily divided into four distinct plant functional groups. The first PFT group was distinguished by growing season of about 5-9 months. The second group was identified by having a phenology that tracks the rainfall – only greening up after the rain has fallen, and drying down slowly as soil moisture declines at the end of the dry season. The third functional group was determined by a long dormant period, and not having a phenology that tracks rainfall. At my site, although LDS only had five species, they were all dominant species, and therefore at a landscape level this functional response is likely to dominate at Nylsvley. The fourth functional group also had five species which were mostly differentiated by DIFFMax/Min.

It will take more than one phenological study at one experimental site to resolve questions around the most appropriate and meaningful phenological functional types for semi-arid ecosystems. However, this research has been useful in a) renewing the focus on the timing of greening events, which is as important as assessing whether trees are evergreen or deciduous when looking at tree life history strategies and response to environmental change, b) developing objective methods for classifying phenological functional types that can be used on other datasets from other semi-arid ecosystems, so to test the generalisation of these results, c) enable modelling efforts to predict how semi-arid trees are shifting their leaf phenology in the changing environments.

Ideally this method could be expanded at a number of sites using a set of phenological metrics that represent all aspects of tree leaf phenolgoy. This would allow us to make comparisons between sites in terms of how similar their functional groupings are, what the functional types of the dominant species are, and whether some sites have more or less species in different classes. Using automated classification methods can be a way forward to identify and use PFTs in improving the understanding of phenological strategies of semi-arid trees and might be a great way to integrate ecological information across different savannas. Such groupings can also be used in the DGVMs. Rain-stimulated species will be

affected by decrease in rainfall in short term. However long growing season species will be least affected by rainfall, but may be most affected by change in temperature.

CHAPTER 3.0
USING PLANT FUNCTIONAL TRAIT DATA TO EXPLAIN LIFE-HISTORY TRADE-OFFS FOR DIFFERENT FUNCTIONAL TYPES - LINKING VEGETATIVE TRAITS WITH PHENOLOGICAL METRICS.

3.1 INTRODUCTION

Plant functional traits are simple and easily measured morphological or physiological characters, which enable plants to survive, compete and re-grow under different environmental conditions (Skarpe, 1996; Cornelissen et al., 2003). Plant traits impact ecosystem processes through their impacts on ecosystem structure (Westoby and Wright, 2006). Plants traits are useful in defining functional groups (see Chapter 2), in plant ecology to be grouped by their shared functional attributes. This allows ecologists to generalise how vegetation will respond to a current and changing environment. Analysing plant traits between and within environments gives insight into how vegetation characteristics vary across different environments (Westoby and Wright, 2006), and how and why plants with a certain suites of traits may respond to changing environments (Wright et al., 2004).

Different life history strategies can be successful in the same environment e.g. plants growing in water-limited environments can be annuals or long-lived (Chapin III et al., 1995). Although different strategies (groups of plants traits) can occur in the same environment it is likely that there will be some trade-offs between the different strategies. For example, leaves which have high nitrogen content are known to have high photosynthetic rates and specific leaf areas but this results in shorter leaf life-spans (Field and Mooney, 1983). It follows, at a global scale that plants in low nutrient systems will have lower photosynthetic rates and long-lived leaves, and in high nutrient systems plants will have higher photosynthetic rates, and a shorter leaf life span (Chapin III et al., 1995).

Deciduous species have higher water-use efficiency strategy because of the short life span of their leaves; while evergreen species usually have a more conservative strategy of water use (Lloyd and Farquhar, 1994). This in turn can affect the nutrient content (nitrogen) of the plant which in turn affects rates of photosynthesis. Deciduous trees have higher nitrogen concentrations than evergreen species and hence faster rates of photosynthesis (Eamus and Cole, 1997; Sobrado, 1994). There is already a substantial literature on the differences in vegetation functional traits between evergreen and deciduous species. Evergreen species can be considered drought tolerant as they retain their leaves throughout the dry season. The suites of traits which facilitate this include high stem density, and low specific leaf area (SLA) (Ackerly, 2004; Markesteijn et al., 2011). In contrast, deciduous species can be defined as drought avoiders, as they drop their leaves when soil moisture declines (Reich and Borchert, 1984). The traits that facilitate this promote a low building cost and leaves have a high SLA (thin leaves).

In Chapter 2, I demonstrated a wide variety of leaf phenological patterns in semi-arid savanna trees growing in the same environment. Four PFTs were identified based on leaf phenological patterns in woody trees. In this chapter I test whether these PFTs are associated with particular suites of vegetative traits – to gain an understanding of the constraints imposed by different phenological strategies on other aspects of a plants life history i.e. I aimed to expand on the already detailed theory around life history strategies of deciduous and evergreen species to include the novel functional types identified at Nylsvley. I measured four common plant traits that I considered would differ between the PFTs classified in chapter 2: specific leaf area (SLA), maximum stomatal conductance (Gs_{max}), leaf nitrogen (N) and wood density. These plant traits are all common vegetative traits that are measured using standardised methods across many different study environments (Skarpe, 1996; Noble and Gitay, 1996; Diaz and Cabido, 1997).

Specific leaf area (SLA) is a measure of leaf density and is defined as the one-sided area of a fresh leaf divided by its oven-dry weight (Cornelissen et al., 2003).

Plants that have a high SLA maximise photosynthetic area at the expense of having strong, structurally-sound leaves (Niinemets, 2001; Fonseca et al., 2000). These species are associated with low wood density which allows for rapid transport of water (Bucci et al., 2004). They are also generally associated with plants with short leaf lifespans and high leaf N-content.

Leaf nitrogen is the total amount of nitrogen, per unit of dry mass (Cornelissen et al., 2003). The amount of nitrogen in a leaf constrains its maximum photosynthetic rate as nitrogen is an element in the enzyme Rubisco, which facilitates photosynthesis. One would expect species with low nitrogen to have low photosynthesis (Meziane and Shipley, 2001). However, high nitrogen leaves are also more palatable and costly to build and maintain. For example, species in arid environments allocate resources in a way which provide optimal nitrogen use efficiency. This promotes a water conservative strategy in the system (Bucci et al., 2004).

Maximum stomatal conductance (Gs_{max}) is the measure of the rate of passage of carbon dioxide (CO_2) entering, or water vapour exiting through the stomata of a leaf (Cornelissen et al., 2003). The stomatal conductance constrains the maximum photosynthetic rate of a leaf, and so it is an indication of the degree to which a species is maximising carbon assimilation at the expense of water use efficiency.
Wood density is defined as the oven dry mass of a section of any plant main stem, divided by the volume (Cornelissen et al., 2003). It is expressed in $g.cm^{-3}$. It reflects the plant carbon investment and correlates with many key aspects of plant ecology (Chave et al., 2009). Wood density affects a) tree life span, b) Gs_{max}, c) water storage. Wood density is negatively correlated with growth rate, but positively associated with survival and lifespan. Fast growing, with short lifespan species have lower wood density than long-lived slow growing species (Muller-Landau, 2004).

The PFTs that were identified are more varied than the classical “evergreen” and “deciduous” classification, For example, trees putting on their leaves early before

the rains, compared to trees that wait for rain to leaf out will have different effect. I investigated these trade offs for the different functional groups identified by the MClust method in Chapter 2. Based upon the literature I expect to find relationships between vegetative traits. In particular I expect specific leaf area (SLA) to be positively correlated with leaf nitrogen (Wright et al., 2001), and Gs_{max} to be negatively correlated with wood density (Wright et al., 2001). I also have some expectations about what vegetation traits should be associated with different phenological functional types:

I expect long growing season species to have: low SLA (thicker leaves), as they invest in leaf structure. The literatures show that they should have similar strategies to evergreen species. I would therefore expect a suite of traits associated with low but predictable photosynthesis and water use: i.e. low nitrogen, low maximum stomatal conductance, and possibly low wood density. Rain-stimulated species: This is a unique semi-arid savanna functional type. I would predict that these species will have high maximum stomatal conductance because they photosynthesise very quickly when water is available. They do not appear to store water, as they drop their leaves slowly so low wood density. In that it would allow for high photosynthestic rates and water use. Based on the literature rain stimulated trees have lower leaf nitrogen than early greeners (Reich et al., 1991).
Longer dormant season species: I predict these species will have a low wood density and a high maximum stomatal conductance, as they have longer dormant period. I expect them to maximise the utilisation of resources when they are available. For the same reason I expect high leaf nitrogen and high SLA. Evergreen species: I predict similar characteristics with long growing species but with almost 12 months leaf longevity.

One of the problems with linking plant traits to PFTs across a range of species is that plant traits are an evolutionary processes. Therefore one would expect more closely related species to share similar vegetative traits. I was not able to account for this fully in my MSc project – to do so would require that I control for phylogeny by either comparing species within the same genus but with different

phenologies, or statistically by including the phylogenetic relationships between species in my analysis. However, I did want to explore whether there were any obvious phylogenetic patterns in my data.

3.2 AIMS OF THIS CHAPTER

This chapter aims to:
1: Identify trade-offs between the different plants vegetative traits, and identify trade-offs between vegetative traits and phenological metrics.
2: Determine whether the plant functional type groupings identified in chapter 2, (1, longer growing season species; 2, rain stimulated species, and 3, longer dormant season species) can be distinguished by their vegetation traits, and if so, whether this can associate particular stresses/life histories with each phenological type.
3: Test the null hypothesis that differences in leaf phenology and functional groupings are better explained by phylogenetic relationships.

3.3 MATERIALS AND METHODS

3.3.1 Ecological data collection

3.3.1.1 Specific leaf area (SLA)

Specific leaf area was measured on 24 species at the sites, with five individuals selected per species and ten leaves replicates on individual species. Sampling was done in December and January on fully-expanded leaves on mature adult plants without obvious symptoms of pathogen or herbivore attack. Leaves exposed to direct sunlight were selected and measured. Any petiole or rachis and all veins were considered part of the leaf for standardised specific leaf area measurement (Cornelissen et al., 2003). Instead of attempting to quantify fresh leaf area in the field I used plastic squares of different sizes to cut out a known area of leaf. These samples were then dried in an oven at 70 °C. The dry samples were weighed using a scale accurate to 0.001g. SLA was calculated by dividing the surface area of the

leaf by the oven dry mass. SLA measurements were expressed in m^2 kg^{-1}. Although I attempted to ensure that I had a complete set of SLA data I was not able to quantify this for some fine-leafed species. In these cases the mean SLA value was determined from the TRY database (http://www.try-db.org).

3.3.1.2 Leaf nitrogen content (LeafN).

I collected three to five bigger leaves and ten smaller leaves on every individual species. Leaves were collected on the outskirts of the tree canopies, which were always exposed to sunlight. The leaves were collected in September and December 2012 and were taken for further processing at the CSIR where they were in a drying oven at 70 °C until dry. Leaves were cut into small pieces using scissors and placed into a labelled glass test-tube. All leaves from the same individual were mixed together for the sampling to minimise costs, so I only had one nitrogen value per species.

The test tubes were filled with 1% hydrogen chlorine (HCL) solution to decontaminate all fungi or pathogen which might have developed, and then put in the ultra-sound bath for few seconds to mix the samples. Samples were left overnight in the HCL acid solution. Twelve hours later the HCL solution was poured off and the samples were rinsed with distilled water to ensure that the pH was neutral. pH was tested using pH-indicator strip. The washed samples were in the oven at 70 °C for approximately 48 hours or until dry. After the samples were dried they were ground into fine powder weighed ready for analysis in a mass spectrometer which recorded total nitrogen. Two capsules were run through a mass spectrometer for each species to avoid outliers.

3.3.1.3 Maximum stomatal conductance (Gs_{max}).

Maximum stomatal conductance was measured using a leaf porometer (Version 1.11, Decagon Devices, Inc). The porometer was calibrated before each measurement. New fully expanded leaves on the edge of the tree canopies receiving full sun exposure were measured. Measurements were taken in December when leaf surface areas were large, as small leaves would not be

measured accurately. Four to eight leaves were selected and measured on all individual trees of each species. Measurements were taken only on sunny days between 7am and 11am.

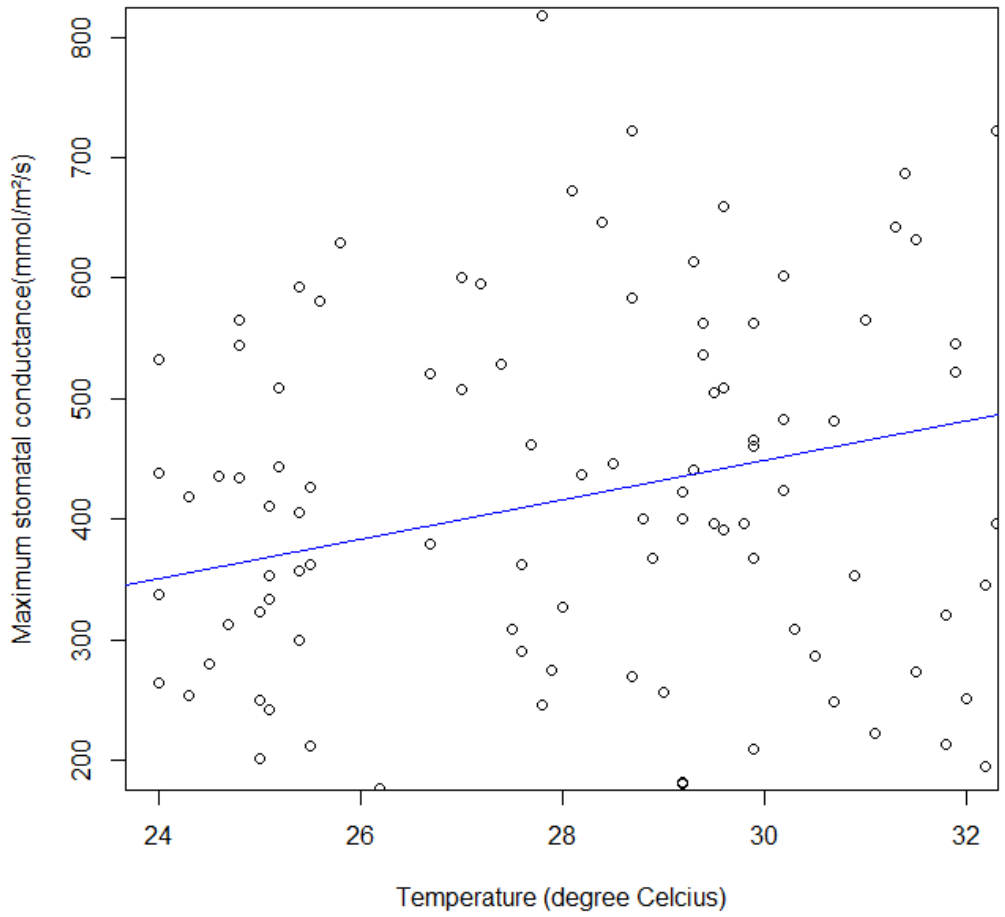

Figure 3.1 *Relationship between maximum stomatal conductance and leaf temperature.*

Stomatal conductance was very variable. I expected this as maximum stomatal conductance fluctuates hourly based on plant water status and atmospheric water demand. I expected that at high temperatures, stomatal conductance should level off due to closing of the stomates, to avoid water loss. To control for this I only took measurements before 11am. However, to test this assumption, and to ensure that I was indeed measuring the maximum stomatal conductance I plotted

maximum stomatal conductance data against leaf temperature (Figure 3.1). No clear levelling off was observed although there was a slight positive relationship with temperature and results were very variable within and between species. To ensure I was measuring the maximum stomatal conductance I took the 90 th percentile of my values for each species. This meant I avoided any outliers, but got an indication of the maximum rate of conductance possible for each plant's anatomy.

3.3.1.4 Wood density

Three individual stem cross-section samples per species were cut and collected. Trees were cut at approximately 1.3 meters height. Where stems were not available branches of 10 centimetres long were cut and collected. Samples were dried in a drying oven at 70 °C until completely dry. The displacement method was used to measure wood density in the laboratory. First the dry mass of each stem sample was determined. Then a volumetric flask was filled with tap water. Individual wood samples were submerged using a needle in order to reduce the weight. This was necessary to ensure that the sample do not touched sides and bottom of the flask. The dry mass then was divided by the volume of water displaced (representing the volume of the wood sample) to get the wood density in g/cm^3, and these values were averaged to get the wood density per species.

3.3.1.5 Try database

Try is a network of vegetation scientists headed by IGBP (International Geosphere-Biosphere Programme), and the Max Planck Institute for Biogeochemistry providing a global archive of curated plant traits. The database enables researchers to search the TRY dataset and provides information about the content of the traits with respect to traits, species, original datasets and regions (http://www.try-db.org). However, the Try dataset presented in Table 3.1 obtained in the database were not from the same study site as this study but in the southern Africa region.

3.3.1.6 Statistical analysis

Data were analysed in R (version 3.0.3) (http://cran.r-project.org). Some of my trait data were only available at a species level (e.g. leaf nitrogen, maximum stomatal conductance, and the values from the Try database). This meant I was limited in the types of analyses I could perform. Therefore, instead of performing nested analyses, with individual tree data nested within species nested within functional type, I performed more simple ANOVA-type analyses with species as my replicates and functional type as my grouping variable. The limited sample sizes and unbalanced sample design (n = 5, 9, and 13) meant that it was more appropriate to use non-parametric tests. I used a Krustal Wallis test to test for differences in the trait attributes between phenological traits. I performed linear regressions to look for relationships between plant traits and phenological traits.

Table 3.1 *Vegetative data for each species measured at Nylsvley, as well as the functional group they were classified in Chapter 2. Three MClust groups (PFT1, longer growing season species, PFT2, rain-stimulated species and PFT3, longer dormant season species) and four vegetative traits: (SLA) specific leaf area ($m^2.kg^{-1}$), wood density ($g.cm^{-3}$), leaf nitrogen (%), difference between September and December nitrogen (%) and maximum stomatal conductance ($mmol/m^2.s^{-1}$). All data from TRY database are in italics.*

Species	MClust FT	SLA ($m^{-2}kg^{-1}$)	Wood density ($g.cm^{-3}$)	Leaf N (%)	Gs_{max} ($mmol/m^2.s$)
Acacia burkei	BDS	*0.0052*	0.202	3.55	393.6
Acacia nilotica	BDS	*0.0063*	0.026	2.3	107.2
Acacia tortillis	BDS	*0.0247*	0.013	1.9	168.62
Gymnosporia senegalensis	BDS	0.0019	0.017	3	386.35
Ozoroa paniculosa	BDS	0.0028	0.002	2.2	626.27
Peltophorum africanum	BDS	*0.0052*	0.222	2.25	468.88
Searsia leptodicta	BDS	0.0007	0.012	2.3	522.14
Strychnos madagascariensis	BDS	0.0161	0.109	2.9	826.14
Strychnos pungens	BDS	0.0143	0.109	2.6	642.94
Euclea crispa	EVR	0.0153	0.01	1.8	337.16
Euclea natalesis	EVR	0.0169	0.004	1.8	756.05
Euclea undulata	EVR	0.0012	0.019	1.75	522.68
Searsia pyroides	EVR	0.0016	0.007	2.7	346.32
Ximenia caffra	EVR	0.0121	0.002	2.5	551.74
Acacia caffra	LDS	*0.0063*	0.005	2.1	256.9
Combretum apiculatum	LDS	0.0009	0.145	2.8	317.49
Combretum molle	LDS	0.0013	0.181	2.6	595.34
Combretum zeyheri	LDS	0.0009	0.206	2.8	419.07
Dombeya rotundifolia	LDS	0.0009	0.029	2.65	675.6
Grewia bicolor	LDS	0.0009	0.019	2.75	1002.58
Ochna pulchra	LDS	0.0014	0.035	2	602
Pappea capensis	LDS	0.0009	0.019	1.7	666.94
Ziziphus mucronata	LDS	0.0013	0.016	2.5	341.54
Burkea africana	RS	0.0011	0.024	2.2	726.88
Dichrostachys cinerea	RS	*0.0078*	0.216	2	575.95
Grewia flavescens	RS	0.0009	0.012	3.85	632.08
Sclerocarya birrea	RS	0.0071	0.209	1.4	59.8
Terminali sericea	RS	0.0017	0.145	1.75	507.82

3.4 RESULTS

3.4.1 The trade-offs between vegetative traits

Table 3.2 *Correlation coefficients between vegetative traits.*

Vegetative traits	SLA	WD	Leaf N	Gs_{max}
Specific leaf area (SLA)	1	-0.06	-0.24	-0.13
Wood density (WD)		1	0.07	-0.15
Leaf nitrogen (%)			1	0.20
Maximum stomatal conductance (Gs_{max})				1

As would be expected there were relationships between the four traits that were measured. Trade-offs was observed between the four traits that we measured. The strongest negative correlation occurred between SLA and leaf nitrogen (R = -0.24), and Gs_{max} (R = -0.13), which was surprising. There was a negative relationship as expected between Gs_{max} and wood density (R = -0.15). Positive correlations were expected and observed between Gs_{max} and leaf nitrogen (R = 0.20) (Table 3.2). Specific leaf area was negatively related to all other three vegetative traits, indicating that at my study site the species which maximise surface area are not necessarily maximising photosynthetic capacity. However, it is very clear that there is a lot of scatter in the data (Table 3.2).

3.4.2 The trade-offs between vegetative traits and phenological metrics

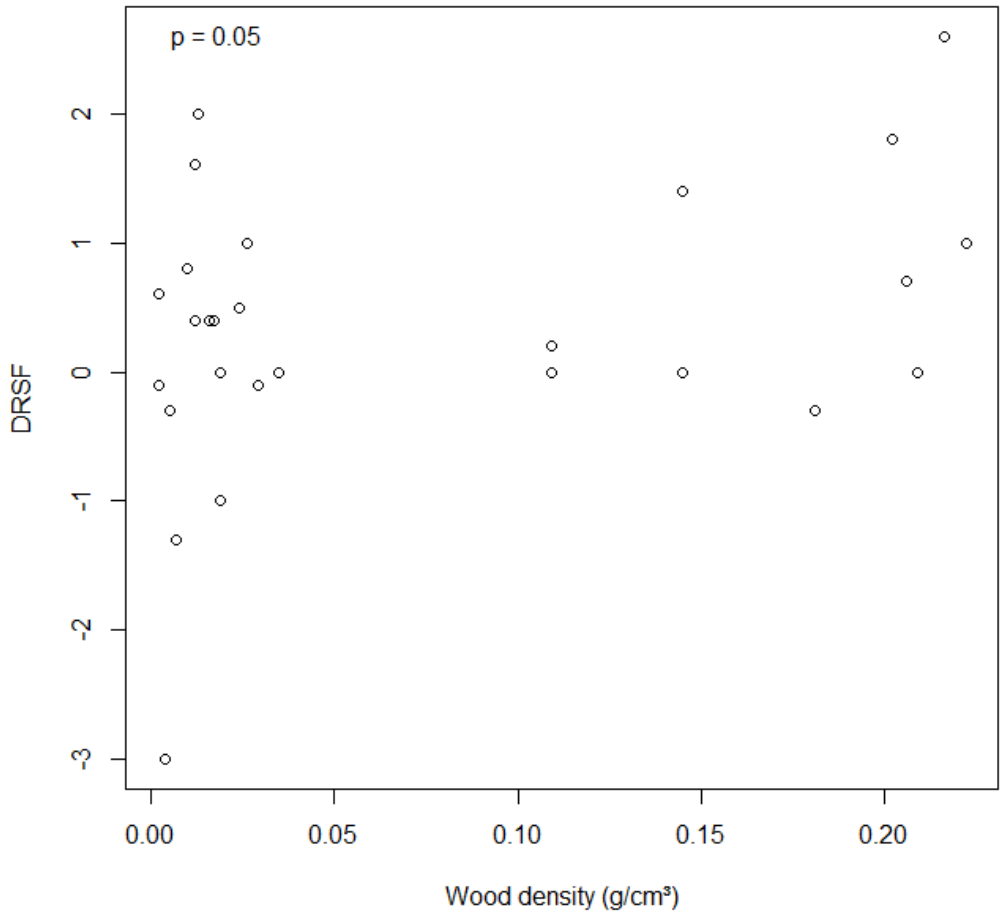

Figure 3.2 *Relationships between vegetative traits: wood density to phenological metrics defined in chapter 2: Degree of rain stimulated flushing (DRSF). These graphs represent the trade-offs between vegetative traits and phenological metrics.*

To assess how the basic traits changed with changing phenological strategy (leaf stages) we plotted the traits against phenological metrics. The relationship between vegetative traits and phenological metrics did not show good trends. However, wood density was significantly different to DRSF species p = 0.05

(Figure 3.1). This relationship shows that species with high wood density are more likely to be stimulated by rain.

3.4.3 The relationship between vegetative traits and PFTs

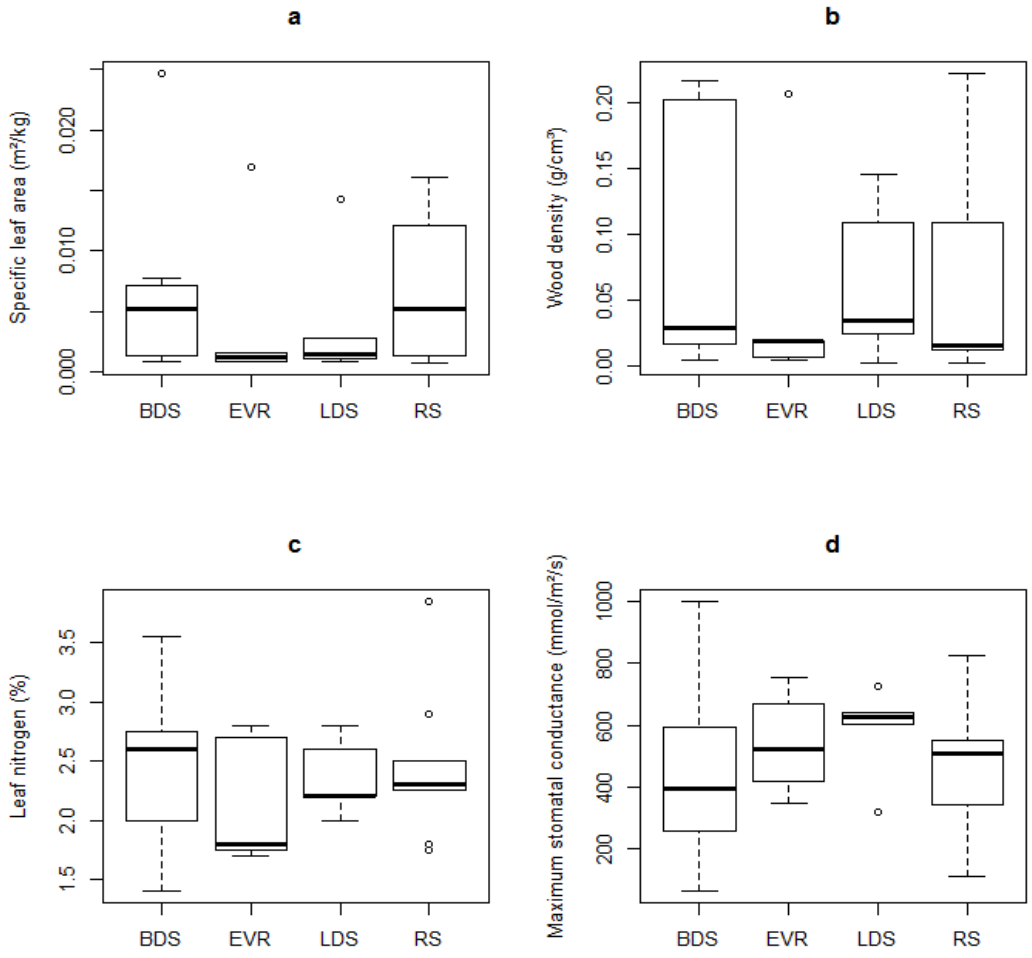

Figure 3.3 *Boxplot showing variation between a) specific leaf area ($m^2.kg^{-1}$), c) wood density ($g.cm^{-3}$) c), leaf nitrogen (%), d) maximum stomatal conductance (mmol. s^{-1}) and the four PFTs identified in Chapter 2: BDS (brevi-deciduous species), EVR (evergreen species), LDS (longer dormant season species), and RS (rain-stimulated species).*

There was no statistical significantly between all vegetative traits and PFTs. However, there are good trends which, can be presented from this graph. It is

shown that evergreen green species have low SLA, wood density, leaf nitrogen and high Gs_{max} (Figure 3.2a-d). Brevi-deciduous species showed higher leaf nitrogen than other PFTs, but with lowest Gs_{max} (Figure 3.2 c,d).

3.4.4 How species are distributed within PFTs at family level

Table 3.3 *Table testing if species of the same family belong to the same plant functional types (PFTs). The table shows the number of species per plant family in all four PFTs described in chapter 2.*

Family	BDS	RS	LDS	EVR	Total
Fabaceae	4	1	2	0	7
Anacardiaceae	3	0	1	0	4
Combretaceae	0	3	1	0	4
Ebenaceae	0	0	0	3	3
Malvaceae	0	1	1	0	2
Strychnaceae	2	0	0	0	2
Celestraceae	1	0	0	0	1
Ochnaceae	0	1	0	0	1
Olacaceae	0	0	0	1	1
Rhamnaceas	0	1	0	1	2
Sapindaceae	0	1	0	0	1
Sterculiaceae	0	1	0	0	1

Species belonging to the same family did not always fall into the same plant functional group (PFTs), except plants belonging to the Strychnaceae and Ebenacae families which all belonged to the same functional groups. Most species in Combretaceae fell into the rain-stimulated group with only one species found in longer dormant season group. Species in very common family Fabaceae were distributed across three PFTs, with 4 species in BDS, 1 in RS group, 2 in LDS and 0 for EVR group (Table 3.3). This suggests that phenology is phylogenetically conserved in some clades but not in others.

3.4.5 How species are distributed within PFTs at genus level

Table 3.4 *Table testing if species of the same genus belong to the same PFTs. The table shows the number of species per plant genus in all four PFTs described in chapter 2. This was represented at genus level only with more than one species.*

Genus	BDS	LDS	RS	EVR	Total
Acacias	3	0	1	0	4
Combretum	0	0	3	0	3
Euclea	0	0	0	3	3
Grewia	1	1	0	0	2
Searsia	1	0	0	1	2
Strychnos	2	0	0	0	2

Acacia species were distributed within two PFTs BDS and RS, but only two genus had species distributed in one group: Euclea and Strychnos, in BDS and EVR respectively.

3.5 DISCUSSION AND CONCLUSION

3.5.1 Summary of the results.

The data for this study were very variable, and it was difficult to draw strong conclusions. However, trade-offs were present between plant traits of different functional groups (PFTs). Unexpectedly, and contrary to prediction from the literature, there was no strong significant relationship between four vegetative traits: SLA, leaf nitrogen, Gs_{max} and wood density. Relationships between vegetative traits and phenological metrics showed many non-significant trends, with a slightly significant positive relationship between wood density and DRSF. There was also no significant relationship between each of the four PFTs and vegetative traits. Lastly I demonstrated that phylogenetic relatatedness is not always a good predictor of which PFTs a plant will belong to both at family and genus level.

3.5.2 Important trade-offs between vegetative traits

Although my relationships were not very strong, and seldom significant, they also did not always corroborate what I would have expected from the literature. I did find that species with lower wood densities had higher Gs_{max} values, as expected (Santiago et al., 2004), but the relationship between SLA and leaf nitrogen was negative despite the strong theoretical and empirical evidence for positive relationships between these variables (Eamus, 1999; Wright et al., 2004; Poorter and Evans, 1998; Meziane and Shipley, 2001; Eamus, 1999; Hoffmann et al., 2005). This positive relationship between SLA and leaf nitrogen occurs because plants with high nitrogen are generally have maximising growth rates, and having a large surface area per unit mass enables optimal light capture (Westoby, 1998; Meziane and Shipley 1999).

However, these results are also possible in savannas as the positive relationship can be substantially altered by water availability and herbivory (Wright et al.,

2001). As savanna are notorious for their high herbivory it could be that defence against herbivory is driving the correlation between SLA and leaf nitrogen rather than photosynthetic rates. Herbivory attack was found to enhance the allocation of resources through increase in leaf nitrogen after attack, but frequent attack affecting survival of the plant (Mundim et al., 2012). However, as most of this relationship had been observed from temperate forest ecosystem, the species in this study might differ fundamentally from those studied in the literature from which the expected trade offs were derived. Because it had been found that the amount of green leaves displayed by the canopy impact light absorption and photosynthetic activities in forest ecosystems (Parker, 1995).

Moreover, there was also an unexpected negative relationship between SLA and Gs_{max}. Relationships between vegetative traits at specific sites do not always conform to the global patterns (Wright et al., 2004). It thus appears that at my savanna site SLA is influenced by other parameters than simply maximum photosynthetic rates.

I found no significant relationship between SLA and Gs_{max}, but species with low SLA have a wide variation in Gs_{max}. Increased maximum stomatal conductance was with decreased wood density as expected. But species with low wood density also had a wide variation of Gs_{max} rates. However, I predicted an increase in Gs_{max} with increased SLA. This result implies the resources allocated to the production of high density wood reduce the allocation of resources to other aspects of plant functioning. As the high wood density results in low hydraulic conductance hence, decreases the rate of stomatal conductance (Bucci et al., 2004, Hacke et al., 2001).

3.5.3 Relationships between vegetative traits and phenological metrics

The results demonstrated some trade-offs between vegetation traits and phenological metrics, but not all the trade-offs were significant. These correlations were important in demonstrating how different vegetation traits are represented between phenological metrics. For example the higher wood density of the DRSF

metric was one of the strongest patterns found. For examples species which are influenced by rain to flush require high rates of photosynthesis, which requires high rates of stomatal conductance, high leaf nitrogen and possibly high SLA. This is as expected as species with high wood density would be expected to flush with the availability of water. This make sense because the high wood densities is not an indication of the plants ability to store water and use it to rapidly put on a full canopy of leaves – as suggested by Borchert, (1994).

It also implies that DRSF might be an important phenological metric in savanna systems. It has been noted that allocation of resources to the production of wood of high density constrains other aspects of resource allocation (Bucci et al., 2004). This means that wood density might have impact in the variation of canopies in semi-arid tropical systems. It is important to note that plant species which green up quickly would exhibit high hydraulic conductance (Hacke et al., 2001). This will facilitate early bud break and hence increase rate of leaf expansion. However, Muller-Landau (2004), found that wood density was negatively correlated with overall growth rate – indicating that this strategy might have long-term consequences for the tree. Similarly, there is literature indicating that tree species with high wood density had high tree mortality (Muller-Landau, 2004).

3.5.4 Relationship between vegetative traits and PFTs

Brevi-decidous species (BDS) had a higher SLA and high leaf nitrogen, and low wood density and low Gs_{max}. These tree species tend to drop some of their leaves during growing season. However, contrary to the prediction BDS had higher SLA but not high as expected (Figure 3.2a). As expected species in dry sites with annual rainfall of 612. 94 mm are also expected to have high leaf nitrogen (Wright 2001).

Evergreen species had very low SLA and wood density. However it showed high $Gs_{max.}$ Leaves are costly for a tree to construct and maintain, and as evergreen have leaves for more than 9 months its SLA is expected to be low as a results.

Longer dormant season species (LDS) had low SLA and low leaf nitrogen (Figure 3.5a, c), but they had high wood density and high maximum stomatal conductance. LDS species flush their leaves before the first rains. Based on the literature I would have expected that with a low SLA and low leaf nitrogen the trees would also have a low maximum stomatal conductance and a high wood density (Roderick et al., 1999), also noted plants with high leaf nitrogen will also have high SLA and high photosynthetic rate. So there is some confusion in the data - the high maximum stomatal conductance of this strategy implies high photosynthetic rates but the low leaf nitrogen implies low photosynthetic rates (Mooney et al., 1981; Reich et al., 1997; Reich et al., 1995). I expected trees in this group to have high photosynthetic rates, which is only supported by the maximum stomatal conductance data. Clearly the life history implications of this novel savanna life history strategy still need to be understood.

Rain-stimulated species (RS) had the lowest SLA and low wood density, and high leaf nitrogen and high Gs_{max}. These species appear to flush only after the rains. These species can be categorised as "deciduous" but their low SLA is not consistent with findings, where high SLA was noted (Reich et al., 1995; Guillermo et al., 1985). As mentioned above, however, it could be that SLA at this site is more impacted by herbivory than by selection for high photosynthetic rates. However, high leaf nitrogen and high Gs_{max} were expected on this strategy. Nevertheless, the leaf nitrogen was not expected to be as high than that of LDS species (Reich et al., 1991), which was the case in this study. The high stomatal conductance in this strategy in consistent with other findings (Meziane and Shipley 2001; Meziane and Shipley, 1999). The low wood density of this strategy was expected as they only flush when the resources are available (water), it enable them to flush quickly (they had short green-up periods – Chapter 2).

3.5.5 Importance of family and genus distribution within PFTs.

Species which are closely related would be expected to have similar characteristics because they have a common ancestry (Antúnez et al., 2001; Villar et al., 1998). The distribution of species at family level shows that leaf phenology

in semi-arid savanna species is phylogenically conserved in some families, but not all.

However, it seems as the distribution is the same even at genus level but more data is need for species of the same genus to determine if the distribution is restricted. Species which keep their leaves for most of the time in the growing season were shown to be even distributed at genus level.

Chapter 3 analysed the importance of vegetative traits across semi-arid savanna trees. The main aim was to identify if there are associations amongst vegetative traits and between phenological metrics. My results largely reflected what has been found elsewhere with a few notable exceptions: in my study site SLA and leaf nitrogen were negatively, not positively correlated as would be expected from Wright et al., 2001; Reich et al., 1998). Despite the fact that there were some clear correlation between phenological traits and vegetative traits the three phenological groups identified in Chapter 2 were not clearly distinguished by their vegetative traits.

CHAPTER 4.0
CONCLUSION

4.1 IMPORTANCE OF PLANT FUNCTIONAL GROUPS

This study investigated the seasonal patterns of leaf display in a semi-arid savanna site in South Africa (Nylsvley Nature Reserve), with the aim of improving our understanding of phenological strategies used by savanna trees. I also aimed to determine the life history consequences of these strategies, and to demonstrate a data-driven approach to identifying PFTs as a step towards integrating information across a range of different savanna ecosystems on the globe. In order to identify PFTs 28 savanna trees were surveyed and monitored over 12 months. Eight phenological metrics were identified, and used together with four vegetative traits to assess trade-offs and life history consequences of different phenological strategies.

Basically my thesis distinguishes four main phenological life history strategies for savanna trees; 1: evergreen, which maintain leaf canopies through unfavourable conditions and have vegetation traits associated with long-leaf life-spans: reduced photosynthetic rates, but high water use efficiency. 2: Brevi-deciduous species which also maintain their leaves for most time throughout the year but losing some. Brevi-deciduous PFTs is mostly described in temperate region with species interchange leaves.

3: rain-stimulated species which have seasonal patterns of leaf display that are closely tied to the availability of soil moisture – greening up only after the first rains, and starting to drop leaves the moment soil moisture starts to decline. Interestingly these species have quite conservative vegetative traits – low specific leaf area (SLA), indicating that overall they follow a strategy focussing on water use efficiency and conserving resources, although other vegetative traits were not conclusive on this. This could be a consequence of phylogenetic contingencies –

all of the Combretaceae fall into this group, except *T. sericea* and this genus is characterised by low SLA and conservative water use. However, the general ecological pattern remains.

4: my final group consists of species with very short growing seasons that often green up before the first rains. While the other two groups could broadly be considered to characterise classic "evergreen" and "deciduous" functional types, this group is unique in that it displays clear patterns of leaf phenology but shows little relationship to soil moisture. Because this group's distinguishing characteristic of short growing season I was expecting traits related to high photosynthetic rates, which was demonstrated by its high Gs_{max} (Figure 3.5d), and perhaps a less conservative water use strategy. Leaf nitrogen is relatively high in these species.

In savannas some deciduous species are clearly following a conservative water use strategy, while others focus on fast gains and high risk. I have demonstrated this is a strongly related to how closely the species in question follows seasonal patterns of water availability.

In Chapter 1 I laid out four hypotheses which I aimed to test with this work:

1. Hypothesis 1: To assess if multiple leaf phenology strategies in savanna trees exist.
2. Hypothesis 2: Trees which display their leaves during the dry season must have access to a stored water source and will have low wood density.
3. Hypothesis 3: Trees species in the same family will fall into the same phenological functional types (PFTs) (i.e. phenology is phylogenetically conserved).
4. Hypothesis 4: Trees with the same phenological grouping will have the same vegetative traits (leaf, wood and physiological) and display similar trade-offs between traits.

My data support Hypothesis 1, but I got mixed support for Hypothesis 3 – with some families fitting expectations but some notable exceptions (Leguminoseae).

Hypotheses 2 and 4 could not be supported or refuted as I did not have enough statistical power to test this.

4.2 DIFFERENCES IN METHODS FOR ASSESSING PFTs AND THEIR IMPLICATIONS

Most previous studies of Plant Functional Types studies used methods which looked into either the amount of leaves or the timing of leaf onset and offset on the canopy to define PFTs (Prior et al., 2003; Williams et al., 1997; Borchert, 1994; Elliot et al., 2006; de Bie et al., 1998). In retrospect I also focussed largely on the timing of leaf onset and offset, which might explain why my analysis did not identify a clear evergreen strategy. Although the phenological functional types in my study were not a demonstrable improvement on the previous grouping identified in the literature, I do believe that I have demonstrated valuable ideas and methods that can be used to expand and generalise our understanding of savanna phenological functional types.

The first important finding is that it is ideal that in PFTs we move from subjective to automated (MClust) methods in order to reduce the biasness of the our identification. I have also demonstrated that it is important to clearly describe the phenological metrics, and to have a complete set of phenological metrics – both related to the timing of leaf on and off, and the amount of green leaf canopy over the year. I have also clearly indicated that savanna tree species require more than just two phenological categories, and that DGVMs that aim to realistically represent water use and photosynthetic rates in savannas need to distinguish between deciduous species that are driven by water availability, and those that are characterised by high risk, less water-dependent leaf display and vegetative traits.

4.3 HOW THE STRATEGIES MAY BE AFFECTED BY ENVIRONMENTAL CHANGE

Climate change will impact the ecosystem (Woodward, 1987). Already we have seen dramatic changes in plant growth determinants: CO_2 concentration, rainfall and temperature (IPCC, 2007), linked to human activities. In African savannas increase in CO_2 has been suggested to result in an increase in the abundance of savanna trees (Bond et al., 2003). These current changes in climate have been noted to impact a wide range of ecosystems and other biological processes (Parmesan, 2006). Biological events such as phenology have been noted to be responsive to temperature and much has been reported on the climate change to phenology (Menzel et al., 2006). CO_2 has almost doubled in the last century and is continuing to rise, we are expecting higher temperatures (up to 4 degrees higher in winter by 2100), and more variation in the seasonal patterns of rainfall. From the information I have gathered in this MSc thesis it should be possible to assess how different savanna tree PFTs will be affected by environmental change.

Short growing season species (longer dormant season species) are likely to be accessing water from stored reserves/deep water sources. Because of this in the short term, changes in rainfall might have less impact on these species seasonal patterns of leaf display than on the rain-stimulated species that are directly cued by soil moisture. However, in the long term, because these species follow a high-risk water use strategy (high Gs_{max}) (Figure 3.5d), they could be prone to mortality if they are maintaining actively-photosynthesising canopies during times when water is not available and their stored reserves become depleted.

The fact that high CO_2 is expected to increase water use efficiency (Borchert, 1994) might be a mediating factor here. Evergreen species (longer growing season species) are likely to be the least affected by changes in the seasonal distribution of rainfall as they have strategies to cope with periods of low water stress. However, because they maintain their canopies throughout the year, increased temperatures, and increasing winter temperatures in particular, might impose an increased stress on these species.

Rain stimulated species follow the seasonal patterns of rainfall. Changes in rainfall patterns will affect these species as there are stimulated by soil moisture to flush (Borchert, 1994). Early rains will influence the flush in these tree species, and late rains will also delay the flush. Most of species in semi-arid systems initiate leaf flushing after the first large rainfall (Jolly and Running, 2004). These species might be the most responsive to climatic changes, and therefore also, better adapted to these changes.

4.4 IMPLICATION OF DEFINING DISTINCT PHENOLOGICAL STRATEGIES FOR MODELLING

In plant ecology, a challenge to understand how climate and vegetation interact to define the past, current and future distribution of vegetation (Scheiter et al., 2013). These challenges have been addressed by modelling, and most global vegetation models use PFTs to model vegetation distribution using ecophysiological principles (Prentice et al., 2007). There have been some successes in addressing different questions related to vegetation modelling. For example, the Dynamic Global Vegetation Models (DGVMs) have predicted that most areas in the world would shift to be forest in the absence of fire (Bond et al., 2005). However, these models have shown some weakness in terms of their predictions, on based of how set of plant traits can define PFTs and secondly that these DGVMs does not represent competition in the system (Scheiter et al., 2013).

However, my study demonstrates that classing all savanna trees as deciduous which are driven by water availability is a large simplification of the different phenological strategies. One solution would be developing more detailed mechanistic descriptions of the functional types represented in savannas. An alternative approach, which is quickly gathering momentum, is to directly model vegetation traits, rather than plant functional types (Scheiter et al., 2013). This approach uses functional relationships between plant traits and environmental drivers to define which traits should be present in a system and how they should be organised. However, it also requires that functional relationships between

vegetative traits need to be better understood and modelled. My thesis contributes to this in savannas by supporting some of the theory, but highlighting some important site-specific differences. This can improve our understanding of plant functional types (PFTs) better to answer some plant ecology questions.

4.5 FUTURE RESEARCH

4.5.1 Problems with my research

Although three clear phenological types were defined using automated method, more clear description of phenological metrics is need in order to quantify the initiation of leaf out and leaf drop. The canopy monitoring was assessed on a monthly bases and I think a more regular of two to three times a month might give better results in distinguishing different leaf development stages. From this regular monitoring the exact date of leafing might be determined or be able to clearly define early-greening species. The four vegetative traits measured did not show good patterns and had a lot of scatter within three functional groups and if I had increased my replication from five to ten replicate and individuals, and not relied on the TRY database at all I might have had good data.

4.5.2 Mapping different PFT’s in space

The detailed information about the vegetation structure is important in assessing PFTs; from the leaf to the entire stand. One more potential follow up from this project would be to assess the relative dominance of different PFTs at regional scales and across continents. Potentially it is possible to use remotely sensed data for this, integrated by a network of ground-based observation sites.

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