# THE COPPICING OF A SAVANNA TREE SPECIES (*Terminalia sericea*) IN RELATION TO RESOURCE MANIPULATION AND DISTURBANCE

**Hloniphani Moyo**

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Doctor of Philosophy.

**JOHANNESBURG**

**2013**

**DECLARATION**

I declare that this thesis is my own work, unless specifically mentioned and acknowledged in the text. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any university. The thesis is structured in a format for publishing each research chapter. For the purposes of consistency, the reference style for the Journal *Annals of Botany* has been adopted for this thesis.

**14 October 2013**

Hloniphani Moyo

University of the Witwatersrand, Johannesburg, South Africa.

**ABSTRACT**

The growth and recovery of trees from disturbances such as fire and browsing is driven by the intensity of the disturbances and the availability of resources. In savannas, resprouting has become recognized as a key functional trait in plant ecology over the past decade. Although this may indeed be the case, there is still limited information about the physiology and growth strategies of resprouting trees. Available information about the influence of disturbance comes from ecosystems that are in many ways different from tropical and sub-tropical savannas. Therefore it is important to know and understand post-disturbance tree responses and limitations so as to establish sustainable use and management practices. This thesis reports the findings of a study, conducted in the Mpumalanga province of South Africa, aimed at achieving a better understanding of the influences of resource availability (water and nutrients) and disturbances (herbivory and repeated cutting) on the coppicing of a widely distributed savanna tree species that is both ecologically and economically important; *Terminalia sericea*.

To investigate the effects of resource availability, cut trees were exposed to different levels of water and nutrient (nitrogen and phosphorus) supplementation over a period of two years in a factorial experimental design. A number of coppice regrowth variables (e.g. shoot production, resprout shoot diameter and shoot length) were measured monthly, while the phenological responses (e.g. timing of leaf discolouration and fruit presence) were monitored every two weeks. The effects of disturbances were investigated in two separate experiments, in which cut trees were exposed to a five month browsing period and different cutting frequencies, respectively. Coppice regrowth variables were monitored for 12 months in trees exposed to browsing and for five months in trees exposed to different cutting frequencies. The effect of multiple cutting cycles on total non-structural carbohydrates and leaf chemistry (carbon, nitrogen and phosphorus) was measured.

There was evidence of self-thinning of coppice shoots within cut trees in all experiments in the second year of growth, with supplemented trees also recording lower shoot numbers. With shoot production higher in trees that received no resource addition, water and nutrients interacted synergistically, doubling shoot diameter and

shoot length for supplemented trees after 12-months of addition. The majority of the phenophases monitored peaked in the wet growing season. Supplemented trees changed colour from the typical green to senescent yellow later in the growing season than unsupplemented trees. Fruit presence occurred in the second year after cutting for supplemented trees. Shoot length and shoot diameter for unbrowsed trees were twice those for browsed trees, with leaf nitrogen and phosphorus content significantly higher for browsed trees compared to unbrowsed trees. Trees subjected to multiple cutting cycles recorded half the TNC levels, and half the resprout shoot diameter and shoot length of trees cut only once.

Results from this study demonstrate that self-thinning (*i.e.*, negative change in shoot number) is not primarily under resource control. By contrast, the findings suggest that shoot growth characteristics, the timing and duration of phenological stages in coppicing trees are resource-limited in savannas. Browsing induces an initial compensatory response through higher shoot production in browsed trees and should be kept minimal because, in the long run, browsed cut trees would take longer to recover lost biomass compared to unbrowsed cut trees. Repeated cutting significantly depleted non-structural carbohydrate reserves in stems, implying that repeatedly cut trees rely heavily on non-structural carbohydrate reserves for regrowth. The significantly lower shoot diameter and shoot length in repeatedly cut trees imply that the coppicing ability of a tree reduces as the cutting frequencies increase.

Such information can be vital in establishing the competitive growth ability of *T. sericea* in a multiple-species ecosystem affected by changes in resource availability as well as natural disturbances. With reference to multiple cut trees, a form of cutting or harvesting strategy should be in place that allows for sustainable regeneration of the study species. A threshold in terms of number of cutting cycles a tree can tolerate based on either maximum or minimum levels of reserve carbohydrates should also be established, as this has a direct effect on the coppice growth and survival.

**DEDICATION**

This thesis is dedicated to my late mother Miss Winnie Ncube.

## ACKNOWLEDGEMENTS

This study was conducted in collaboration with the University of Florida in a project with the title “Linking disturbance and nutrient limitation in the tropical savannas: tree-soil-microbial feedbacks in Lowveld savannas”. The project was funded by the Andrew Mellon Foundation and the Centre for Tree Health Biotechnology (CTHB) (University of Pretoria). The funds enabled a trip to the Universities of Florida and Missouri to carry out laboratory work on leaf and tree core samples. Valuable input from Dr Julia Reiskind and Professor Michelle Mack, University of Florida, is appreciated. Contributions from Professors Ed Witkowski and Kevin Balkwill, Drs Sally Archibald and Deanne Drake are also appreciated. The field assistants, Thabo Sibuya and Frank Nyathi are acknowledged for the hours spent in the sun writing on white paper! My family and Thulani are thanked for the support through difficult times when Wits Rural Facility was a lonely place to be. The assistance of Dr Ricardo Holdo, University of Missouri, for statistical analysis, encouragement and review of drafts is greatly appreciated. Lastly the supervisors in this work, Dr Wayne Twine and Professor Mary Scholes, are also acknowledged for time invested, the encouragement and patience shown throughout the doctoral process. It was a privilege working with them and something to treasure and refer to for a long time. To God be all the glory!

**TABLE OF CONTENTS**

DECLARATION ..... i
ABSTRACT ..... ii
DEDICATION ..... iv
ACKNOWLEDGEMENTS ..... v
TABLE OF CONTENTS ..... vi
GLOSSARY OF TERMS USED ..... ix
LIST OF FIGURES ..... x
LIST OF TABLES ..... xii
CHAPTER 1 ..... 1
GENERAL INTRODUCTION AND LITERATURE REVIEW ..... 1
1.1 INTRODUCTION ..... 1
1.1.2 Determinants of savanna ecosystems ..... 1
*1.1.2.1 Moisture availability* ..... 2
*1.1.2.2 Soil nutrient status* ..... 2
*1.1.2.3 Fire* ..... 3
*1.1.2.4 Herbivory* ..... 4
1.1.3 Tree responses to disturbances ..... 6
*1.1.3.1 Disturbances and allocation of resources* ..... 6
*1.1.3.2 Response through coppicing* ..... 7
1.1.4 Tree phenology in savannas ..... 8
1.1.5 Coppicing as a management tool in savannas ..... 9
1.1.6 Coppice management practices ..... 10
1.1.7 Human activities in savannas ..... 12
1.2 RESEARCH RATIONALE AND OBJECTIVES ..... 14
1.2.1 Aims and objectives ..... 16
1.2.2 Scientific contribution of the research ..... 16
1.2.3 The conceptual framework of the study ..... 18
1.3 STUDY SITE ..... 21
1.3.1 Biophysical characteristics ..... 21
1.3.2 Study species ..... 23
1.4 STUDY APPROACH AND THESIS STRUCTURE ..... 24
CHAPTER 2 ..... 27
EFFECTS OF WATER AND NUTRIENT ADDITION ON THE TIMING AND DURATION OF PHENOLOGICAL STAGES OF RESPROUTING *Terminalia sericea* ..... 27
ABSTRACT ..... 27
2.1 INTRODUCTION ..... 28
2.2 METHODS ..... 31
2.2.1 Study site ..... 31
2.2.2 Study species ..... 31
2.2.3 Experimental design ..... 31
2.2.4 Phenological stages monitored ..... 33
2.2.5 Statistical analyses ..... 34
2.3 RESULTS ..... 34
2.4 DISCUSSION ..... 39
2.5 CONCLUSIONS ..... 42
CHAPTER 3 ..... 43

EFFECTS OF WATER AND NUTRIENT ADDITION ON THE COPPICE RESPONSE OF CUT *Terminalia sericea* ..... 43
ABSTRACT ..... 43
3.1 INTRODUCTION ..... 44
3.2 METHODS ..... 47
3.2.1 Study site ..... 47
3.2.2 Study species ..... 47
3.2.3 Experimental design ..... 47
3.2.4 Morphological measurements ..... 47
3.2.5 Total non-structural carbohydrate (TNC) sampling and determination ..... 47
3.2.6 Confounding effects of browsing ..... 48
3.2.7 Statistical analyses ..... 49
3.3 RESULTS ..... 49
3.3.1 Interactive effects on the coppice response ..... 49
3.3.2 Effects of water and nutrient additions on coppice response ..... 52
3.3.3 Effect of water and nutrient additions on stem TNC levels ..... 55
3.3.4 Confounding effects: browsing ..... 55
3.4 DISCUSSION ..... 56
3.4.1 Effects of water and nutrients on coppice response of cut trees ..... 56
3.4.2 Effect of water and nutrients on stem TNC levels ..... 59
3.5 CONCLUSION ..... 60
CHAPTER 4 ..... 62
THE COPPICE RESPONSE OF RESPROUTING *Terminalia sericea* TREES IS NEGATIVELY INFLUENCED BY BROWSING ..... 62
ABSTRACT ..... 62
4.1 INTRODUCTION ..... 63
4.2 METHODS ..... 66
4.2.1 Study site ..... 66
4.2.2 Study species ..... 66
4.2.3 Experimental design ..... 66
4.2.4 Morphology measurements ..... 67
4.2.6 Browse proportion ..... 68
4.2.7 Statistical analyses ..... 68
4.3 RESULTS ..... 69
4.3.1 Morphological properties ..... 69
4.3.2 Foliar properties ..... 71
*4.3.2.1 Growth properties* ..... 71
*4.3.2.2 Changes in foliar chemical properties* ..... 72
4.4 DISCUSSION ..... 72
4.4.1 Effects on morphological responses ..... 73
4.4.2 Effects on foliar chemical properties ..... 75
4.5 CONCLUSION ..... 77
CHAPTER 5 ..... 78
THE EFFECTS OF REPEATED CUTTING ON COPPICE RESPONSE OF *Terminalia sericea* ..... 78
ABSTRACT ..... 78
5.1 INTRODUCTION ..... 79
5.2 METHODS ..... 82
5.2.1 Study site ..... 82
5.2.2 Study species ..... 82

5.2.3 Experimental design ..... 82
5.2.4 Morphology measurements ..... 84
5.2.5 Chemical analyses of the above ground components ..... 84
*5.2.5.1 Above-ground storage analysis* ..... 84
*5.2.5.2 Foliar analysis* ..... 85
5.2.6 Statistical analyses ..... 85
5.3 RESULTS ..... 86
5.3.1 Effects on coppice response ..... 86
5.3.2 Effects on total non-structural carbohydrates (TNC) ..... 88
5.3.3 Effects on foliar C, N and P levels (%) ..... 88
5.4 DISCUSSION ..... 89
5.4.1 Effects on coppice response ..... 90
5.4.2 Effects on stem TNC levels ..... 91
5.4.3 Effects on foliar properties ..... 92
5.5 CONCLUSION ..... 94
CHAPTER 6 ..... 96
THE COPPICING OF A SAVANNA TREE SPECIES (*Terminalia sericea*) IN RELATION TO RESOURCE MANIPULATION AND DISTURBANCE ..... 96
6.1 The conceptual framework ..... 96
6.2 Discussion of ecological findings and additional insights ..... 99
6.2.1 The importance of coppicing ..... 99
6.2.2 Coppicing in relation to resource limitation ..... 100
6.2.3 The effects of disturbances on coppicing ..... 105
6.3 The height of resprouting shoots: browsing, cutting and coppicing nexus ..... 109
6.4 Knowledge contribution ..... 113
6.4.1 Self thinning ..... 113
6.4.2 The effect of water and nutrient supplementation ..... 113
6.4.3 Browsing effects ..... 114
6.4.4 Repeated cutting effects ..... 115
6.4.5 Browsing *vs* repeated cutting effects ..... 115
6.5 Management considerations and recommendations ..... 115
6.6 Suggestions for future research arising from the study ..... 117
7. REFERENCES ..... 119

## GLOSSARY OF TERMS USED

**Browsers** – defined as any animal that feeds on small twigs, leaves and young shoots of trees or shrubs (Scholes and Archer, 1997, Bergstrom, 1992).

**Coppicing –** implies the process when a tree develops secondary replacement trunks from adventitious buds (Hardesty, 1987, Del Tredici, 2001). The term is used inter-changeably with resprouting and in some instances regeneration or sprouting.

**Disturbance –** any event that changes the physical environment and disrupts ecological processes (Li et al., 2004).

**Herbivory –** refers to the activity by any animal that eats living plant tissues (Crawley, 1983).

**Resource allocation –**refers to a plant's ability to utilize nutrients, or stored carbon, when compensating for tissue loss due to browsing, fire and cutting (Rooke et al., 2004).

**Savanna** – these are ecosystems characterized by a continuous herbaceous layer and discontinuous woody layer (Sankaran et al., 2004, Scholes and Archer, 1997).

**Sustainable harvesting –**harvesting such that the rate of biomass removed is less than or equal to the rate of biomass regeneration.

**Total non-structural carbohydrates** – These are sources of energy, especially in the form of starch, that enable plants to resprout after a disturbance (Lloret and Lopez-Soria, 1993, Bell and Ojeda, 1999). Referred to as either the carbon reserves, stored reserves or stored carbohydrates.

**Woodland –** defined as vegetation formations that are mostly dominated by trees, not to the extent of overlapping canopies and also not excluding the growth of other forms of vegetation such as grasses or shrubs (Scholes, 2004).

## LIST OF FIGURES

### Chapter 1

Figure 1.1. Conceptual framework for factors hypothesized to influence coppicing in savanna trees. ..... 20
Figure 1.2. Location of the study site WRF (Wits Rural Facility) in the Limpopo Province, South Africa (Adapted from Neke, (2004)). ..... 22
Figure 1.3. A) long-term mean monthly rainfall distribution (1992-2010) for the Wits Rural Facility and B) cumulative monthly rainfall data for the duration of the study period (September 2010-September 2012)..... 22
Figure 1.4. Study structure for the investigation of the coppicing of a savanna tree species (*T. sericea*) in relation to resource manipulation and disturbance. ..... 26

### Chapter 2

Figure 2.1 Factorial experiment designed to investigate the influence of water and nutrient additions on the coppice response of harvested trees.....33
Figure 2.2. Changes in phenological stages of resprouting trees as a result of water and nutrient additions to resprouting trees; A) bud presence, B) leaf presence, C) discoloured leaves, D) fruit presence and E) average number of leaves..... 38

### Chapter 3

Figure 3.1. Effects of water and nutrient addition on A) shoot production, B) shoot diameter, C) shoot length and D) resprout ratio between September 2011 and September 2012.....51
Figure 3.2. The effect of water and nutrient addition on A) shoot production (calculated as number of shoots per unit area of original stump circumference), B) shoot diameter, C) shoot length and D) resprout ratio between September 2011 and September 2012.....54
Figure 3.3. The changes in browsing proportion on resprouting trees supplemented with water and nutrients from December 2010-September 2012.....56

### Chapter 4

Figure 4.1. The changes in A) shoot production (calculated as number of shoots per unit area of circumference), B) shoot diameter, C) shoot length and D) resprout ratio of cut trees subjected to a five month period of browsing..... 70
Figure 4.2. A) increment and B) stomatal conductance of leaves for browsed and unbrowsed trees..... 71
Figure 4.3. Mean leaf levels (%) of A) carbon, B) nitrogen and C) phosphorus due to exposing resprouting harvested trees to browsing for a period of five months.. ..... 72

### Chapter 5

Figure 5.1 The diagrammatic representation of the treatments in the study in three sites showing the three treatments.....83

Figure 5.2. The monthly effects of exposing *T. sericea* to different cutting regimes on A) shoot production, B) mean number of leaves, C) resprout shoot diameter and D) resprout shoot length from October 2012 to February 2013.. ..... 87
Figure 5.3. Mean (dry weight) total non-structural carbohydrates (TNC) in three harvesting regimes..... . 88

**Chapter 6**

Figure 6.1. The expanded conceptual framework of the elements brought together in the discussion.. ..... 97
Figure 6.2. The height recovery of resprouting trees, A) resprouting in repeatedly browsed trees and B) resprouting in repeatedly cut trees.....112

## LIST OF TABLES

### Chapter 3

Table 3.1. Changes in TNC (mg $g^{-1}$ DW) levels between September 2011 and April 2012 as a function of water and nutrient additions. ..... 55

### Chapter 5

Table 5.1. Mean nitrogen, carbon and phosphorus concentrations (%) of Uncut and Cut 6-times trees, (s.d. = standard deviation)... ..... 89

# CHAPTER 1

# GENERAL INTRODUCTION AND LITERATURE REVIEW

## 1.1 INTRODUCTION

Savannas are ecosystems characterized by a continuous herbaceous layer and patchy woody layer (Sankaran et al., 2004, Scholes and Archer, 1997). These ecosystems support an abundance of wildlife and livestock in Africa, and provide a range of other livelihood sources for humans, including firewood, wild foods and construction materials (Shackelton et al., 2004). Savanna woodlands cover almost one third of the total surface area of South Africa (Scholes and Archer, 1997, Scholes and Walker, 1993), supporting almost 9.2 million people living in rural settlements (Shackleton, 2001). Savanna systems are diverse and occur over a wide range of bioclimatic conditions (Sankaran et al., 2005, Scholes, 1987, Higgins et al., 2000). Land-use practices in savannas vary widely, ranging from conservation to commercial livestock farming and communal multiple-use systems (Sunderlin et al., 2005, Shackleton, 1997).

### 1.1.2 Determinants of savanna ecosystems

Savannas are among the most striking vegetation types because of the co-existence of tree and grasses (Scholes and Archer, 1997). Savanna structure and productivity are determined by the interactions of four major determinants; moisture availability, soil nutrient status, herbivory and fire (Scholes and Walker, 1993, Shackleton, 1997, Scholes and Archer, 1997, Zida et al., 2007, Kraaij and Ward, 2006). Interactions amongst the four determinants can either be synergistic or antagonistic, resulting in high levels of productivity (reflecting positive feedback). Savanna determinant interactions (*e.g.* fire and herbivory) can also result in negative feedback loops resulting in a wide range of impacts including loss of biodiversity, soil and water loss and reduced ecosystem services (reflecting non deterministic variation) (Scholes and Archer, 1997).

*1.1.2.1 Moisture availability*

Moisture availability is a major factor influencing the distribution and productivity of the earth's vegetation and is considered a critical driver of savanna structure (Sankaran et al., 2005). Moisture availability affects photosynthesis through changes in plant water potential and increasing leaf growth, as well as having direct influence on the growth of plant parts such as the distribution of roots (McMichael and Quisenberry, 1993, Liedloff and Cook, 2007). In savannas, the dependence of maximum tree cover on rainfall has been shown to peak between 200-700 mm in mean annual precipitation (Sankaran et al., 2008). However, thresholds can be reached when any further increases in mean annual precipitation do not result in further increases in tree growth, as suggested by Sankaran et al. (2005); Sankaran et al. (2008); Fensham et al. (2005) and Bond et al. (2005).

Moisture availability for plant production in savannas is limited by competition, inter-annual variation of rainfall and the partitioning of rainfall between infiltration, interception losses and runoff (Scholes and Archer, 1997, Scholes, 2009). In ecosystems such as savannas, there is a strong seasonal alternation between warm wet and cool dry seasons, which characterises savanna structure from that of forest, grassland and desert ecosystems (Scholes and Archer, 1997). Such seasonal moisture availability may contribute to an increase in fuel load during the cool dry season, increasing the possibility of fires (Govender et al., 2006).

*1.1.2.2 Soil nutrient status*

The availability of soil nutrients, and particularly soil nitrogen, is an important determinant of ecosystem and community dynamics for grasslands and savannas, contributing towards plant growth as well as production (Craine et al., 2009). Soil nutrient status is often correlated with vegetation growth (Singh, 2004, Bond et al., 2005) through soil moisture, because changes in soil water status directly impact root-nutrient relationships since nutrients are required to be in solution for assimilation (McMichael and Quisenberry, 1993). Therefore, changes in soil moisture levels have direct effects on root-nutrient interactions (Scholes and Archer, 1997, Sankaran et al., 2008). Most of the factors that increase tree growth and establishment are

environmental factors that interact with the soil nutrient status, increasing leaf growth and development of the root system in savannas (McMichael and Quisenberry, 1993, Scholes and Archer, 1997). Although root development is largely under genetic control, high soil nutrient status enhances initiation, growth and root length of root branches during germination and establishment of plants (McMichael and Quisenberry, 1993). In savannas, the distribution of fine-leafed and broad-leafed savannas is determined by soil nutrients and texture, with the former occurring on more, clay-enriched soils than the latter (Scholes et al., 2002). Fine-leafed savannas indicate ecosystems with palatable grasses, with few fires and are sometimes referred to as eutrophic or nutrient-rich savannas (Scholes and Walker, 1993, Scholes et al., 2002). On the other hand, broad-leafed savannas reflect more frequent fires, with less palatable grasses and are at times referred to as dystrophic or nutrient poor savannas.

In order to understand the dynamics of nutrient-limited savannas, it is important to know which nutrients primarily limit growth and primary production, as this would also be useful in informing conservationists on the best management practices for savanna ecosystems (Craine et al., 2008). It also important to understand nutrient concentrations on different soil types and textures because of an established relationship between soil texture, nutrient availability as well as moisture availability (Sankaran et al., 2008).

*1.1.2.3 Fire*

Fire is generally regarded as the dominant factor limiting savanna trees from reaching their resource-driven growth potential (Sankaran et al., 2005, Higgins et al., 2000, Bond et al., 2005). Fire's major impact on savanna structure is exerted through its effects on plant recruitment, mortality on seedlings as well as its impacts on subsequent plant growth rates (Murphy et al., 2010). Mortality effects are especially on seedlings burnt before establishing, whilst on the other hand some seeds need fire to break dormancy before germinating (Higgins et al., 2000, Shackleton, 1997, Holdo, 2005, Daly et al., 2000). The effects of fire in savannas, although not yet fully understood (Midgley et al., 2010), depend on the frequency, season of occurrence, type and the intensity of fire (Govender et al., 2006). Globally, fire has a significant role in the carbon cycle and it also acts as an ecosystem growth regulator with

implications for climate change and plant regeneration (Van Langevelde et al., 2003, Higgins et al., 2000). Fire interacts with other forms of disturbance such as herbivory to increase tree mortality. An example of this process is offered by the case of elephant browsing, which reduces tree height, thus bringing trees into the flame zone (Holdo, 2005, Roques et al., 2001, Zida et al., 2007). Also, bark removal by elephants has been suggested to increase fire damage, thus impacting significantly on the post-fire tree responses (Midgley et al., 2010, Moncrieff et al., 2008). When interacting with herbivory, fire affects grazing through altering large scale foraging patterns, while grazers influence incidents of fire by reducing fuel load, thereby decreasing the spread of fires in an ecosystem (Archibald et al., 2005). Other authors, *e.g.* Holdo et al. (2009) have instead suggested that the presence of herbivores, such wildebeest, reduce the impact of fire, facilitating the growth of trees. Without fire, large areas in savannas could potentially develop into closed woodlands, but this is entirely dependent on the total amount of rainfall and season of distribution (Govender et al., 2006).

*1.1.2.4 Herbivory*

Plant-herbivore interactions have an important role in determining not only the structure of savanna ecosystems, but also the re-establishment and population of recruiting seedlings in ecosystems such as savannas and Mediterranean forests (Midgley et al., 2010). Herbivory is often an important force limiting the recovery of savannas from disturbance while at the same time maintaining ecosystem structure (Teich et al., 2005, Shackleton, 1997). Herbivores are selective and will consume ecologically important plant parts such as shoot-tips and leaves (Du Toit, 1990, Danell et al., 1994, Fernando et al., 2008). In doing so, herbivores possibly alter resprouting and branching patterns of trees. Herbivores generally seek to maximise high digestible energy and nutrient intake and will preferably feed on nutrient rich plants and plant parts (Skarpe et al., 2000, Owen-Smith and Cooper, 1987). When browsed, biomass and plant fitness are reduced, and plants will respond through replacing lost tissue, *i.e.* through showing partial or total compensation (Fornara and Du Toit, 2007). Selective feeding by herbivores modifies the competitive relationships for resources between the component plant species. It can also act to increase diversity, by reducing the dominance of vigorous plants that are intolerant of

grazing/browsing, and enhancing the spread of less competitive, more tolerant plants (Crawley, 1983).

The frequency and intensity of browsing and grazing changes with seasonal moisture availability (Scholes, 2009, Mbatha and Ward, 2010). This is because rainfall is linearly related to above-ground net primary productivity and forage availability, which partially determines grazing capacity. Grazing and fire both potentially reduce productivity, and at times interact with each other (Govender et al., 2006). Grazing reduces the accumulation of fuels and thus reduces the incidences or impact of fire, while fire can reduce, or increase (in the case where dead grass is unpalatable *e.g.* in the sourveld), the availability of forage to grazers (Wiegand et al., 2006, Sankaran et al., 2008). Grazing also creates gaps in the grass layer, thus making below- and above-ground resources (e.g. soil moisture, nutrients and light) available for establishing tree seedlings (Sankaran et al., 2008, Scholes, 2009). Bush encroachment of trees and shrubs into what were formerly sparsely treed grasslands may possibly occur as a result of intensive grazing, and this contributes to the decrease in grass production (Scholes and Archer, 1997, Ward, 2005, Roques et al., 2001, O'Connor and Crow, 1999). An increase in woody plant density also increases the grazing pressure because grazer populations are not always reduced based on tree density (Scholes and Archer, 1997).

Herbivores can be used as a tool to help maintain landscape diversity for conservation purposes. In some instances, browsers can be beneficial in restricting bush encroachment (Pepin et al., 2006). The impact of large herbivores, such as elephants, may change the structural composition of woody plants (Baxter and Getz, 2005). For example, elephant browsing and damage at times result in an increase in grass biomass, which may intensify the fire hazard resulting in a possible decrease in species richness (Baxter and Getz, 2005). Severe browsing also contributes to lower woody species diversity and reduction of competition through the removal of tall trees (Teich et al., 2005, Shackleton, 1997). However, over time, a low population of browsers in an area leads to bush encroachment because mature trees have a competitive and suppressive effect on grass growth which leads to low grass production (Scholes, 2009). Continuous browsing can reduce tree growth by reducing photosynthetic area and also by reducing the plant’s capacity to restore carbohydrate

reserves after a disturbance (Crawley, 1983). Herbivores influence nutrient cycling through the urine, trampling and dung deposits (Shackleton, 1997, Kohyani et al., 2008).

### 1.1.3 Tree responses to disturbances

#### *1.1.3.1 Disturbances and allocation of resources*

Plants are subjected to various forms of disturbances and stress factors that affect their development, production and survival. Disturbances such as fire reduce the dominance of established plants. For a plant to respond to a disturbance, it needs surviving meristems and stored reserves to support regrowth (Bond and Midgley, 2001, Tainton, 1999). The response pattern in plants after a disturbance is affected by the intensity of the disturbance involved and the time of year when the disturbance occurs (Li et al., 2004, Tainton, 1999). Responses are also dependent on the growth stage of the plant and growth conditions affecting the plant after a disturbance (Coley and Barone, 1996, Danell et al., 1994, Rooke et al., 2004). For example, under environmental stress and after a herbivory event, plants can respond by switching the function of reproductive structures to vegetative ones (Lehtila and Syrjanen, 1995).

Plants allocate their net energy production from photosynthesis towards vegetative growth or regrowth (compensation), defence, carbon storage and reproduction (Kurokawa et al., 2004, Chiariello and Roughgarden, 1984). Energy directed towards storage depletes direct investment in either vegetative growth or reproduction, thereby delaying reproductive processes (Chiariello and Roughgarden, 1984, Bond and Midgley, 2001). Also, such allocation results in a reduction in reproduction by an amount equivalent to the metabolic cost of storing and mobilizing the carbon storage. When trees experience herbivory or fire disturbances, they change their allocation of resources towards defence and a temporary nutrient deficiency is experienced, thus limiting growth. Therefore, carbon may be directed towards storage leading to reduced regrowth ability of a plant (Katjiua and Ward, 2006a).

*1.1.3.2 Response through coppicing*

Coppicing is a common response strategy of trees to damage, enabling survival after severe disturbances such as cutting (Kaschula et al., 2005b, Hardesty, 1984). It is a different strategy used by trees when compared to new growth initiated from an existing shoot after *e.g.* a browsing event. Unlike grasses, woody plants are not as well adapted to intensive or severe disturbances because their meristematic tissues (growing zones) are aboveground where disturbances mostly occur (Tainton, 1999). The ability of a tree to coppice, which is the production of vegetative shoots at the base of the stem or sprouts arising from a stump, is one such response strategy used by woody plants to recover some of the biomass initially lost after a disturbance (Kaschula et al., 2005b, Hardesty, 1984).

Regrowth of trees through coppicing is more obvious in dry savanna ecosystems than in the wet tropics because there is a lower probability of successful regeneration through seeds and also due to higher incidences of herbivory and drought (Del Tredici, 2001). In addition, tree bases are less likely to decay in dry savanna ecosystems than in wet ones, implying that trees in these savannas are more likely to regenerate vegetatively through coppicing (McLaren and McDonald, 2003, Brudvig and Asbjornsen, 2008). Various factors, such as the height of the harvested tree stump, harvesting method, and the age of the tree, influence coppice regrowth in woody plants, as shown by Seymour (2008); Shackleton (2001); Sennerby-Forsse and Zsuffa (1995); Krauss and Allen (2003); Kaschula et al. (2005b) and Tang et al. (1999). The coppicing of a tree species is determined in part by genetic factors (Hardesty, 1987, Tang et al., 1999). Some trees do not regenerate or sprout at all (Sennerby-Forsse and Zsuffa, 1995), while others do so variably depending on soil and climatic conditions (Hardesty, 1987, Ibrahima et al., 2007). The age of the plant also affects coppicing since coppicing varies during the life span of a plant. Production of sprouts may decrease in a plant with an increase in age due to bark thickening (Hardesty, 1987).

Coppice shoot development and structure depends on position, abundance and activity of the remaining meristems on the stump interacting with environmental factors such as moisture availability and soil nutrient status (Sennerby-Forsse and Zsuffa, 1995,

Miller, 1999). After a cutting event, the early growth rate of coppice shoots is faster than seedlings or cuttings, because coppice shoots benefit from the already established existing root system (Forrester et al., 2003, Hardesty, 1984). A high number of coppiced shoots per unit area results in rapid leaf area development, leading to fast crown closure and efficient utilization of available space. Coppice shoots also have an early onset of growth and have a continuous development of new nodes until late into the dry season (Laureysens et al., 2005).

### 1.1.4 Tree phenology in savannas

Plant phenology is the study of the timing of the development of vegetative and reproductive plant parts and the relationship occurring between specific plant events (Seghieri et al., 2009, Fenner, 1998). Knowledge of the phenological behaviour of tree species is important for understanding community structure, function and regeneration, and predicting effects of climate change on vegetation (Seghieri et al., 2009, Childes, 1989, Broadhead et al., 2003, Williams et al., 1999). Phenological studies are also important because the phenology of the plant acts as an indicator of plant responses to stressful or favourable environments (Sekhwela and Yates, 2007, Williams et al., 1999). Coppicing affects plant phenology. For example, in cut trees, Hardesty (1984) has proven that coppicing affects phenology in plants, as evidenced when leaf production occurred during the dry season in cut trees in Brazil. The trees maintained the green foliage for the duration of the dry season. This gives a cut tree stump a competitive advantage as it has access to more belowground resources than seedlings.

The study of community phenology can contribute towards the prediction of major influences of biotic and abiotic factors that determine the different plant growth phases (Shackleton, 1997). For instance, increased soil moisture levels trigger leaf emergence (Shackleton, 1997, Broadhead et al., 2003). While phenology is affected by temperature, water and nutrients, herbivory acts a selective force especially against young leaves vulnerable to attack, leading to trees flushing in the dry season when insects are least abundant (Fenner, 1998). Diversity in an ecosystem is maintained through having different species that have varying phenological patterns, thereby reducing chances of competition for the same pollinators, resources and seed

dispersers (Cleland et al., 2007). For example the timing of growth and onset of senescence is important in determining growing season length of different tree species, therefore also affecting carbon uptake in an ecosystem (Cleland et al., 2007).

In savannas, the timing and duration of leaf presence affects processes such as carbon assimilation, water and energy exchange as well as forage availability (Archibald and Scholes, 2007). Also, predicting phenological patterns is complicated because of the unpredictability of rainfall distribution in season and also because it is difficult to separate the phenological behaviour of trees and grasses (Archibald and Scholes, 2007).

### 1.1.5 Coppicing as a management tool in savannas

Coppicing is generally the primary regeneration mechanism after a woody plant has been cut or severely damaged, where stem and roots remain in place (Forrester et al., 2003). In Britain, coppicing has been used as a wood production tool for thousands of years (Fuller and Warren, 1990). It has been proposed as a method for minimizing damage to indigenous vegetation through sustainable fuelwood production (Kennedy, 1998). This is because coppice shoots grow faster than seedlings and they exhibit apical dominance, producing woody material for homestead utilization (Kennedy, 1998, Hardesty, 1987). Additionally, allowing trees to regrow through coppicing ensures that there is limited soil disturbance, considering that the tree's root establishment remains intact. This results in reduced soil erosion and loss of nutrients from the soil as suggested by Kennedy (1998).

As a management tool for improving biomass yield, trees of bigger size can be harvested as these potentially produce many coppice shoots, while increasing the height at which trees are harvested also increases the number of coppice shoots produced (Shackleton, 2001). However, harvesting trees of bigger size should be done with caution considering that larger trees create a microhabitat for micro-organisms. Cutting larger trees also reduces sexual reproduction because larger trees have higher seed production compared to smaller trees. It also created bigger patches, thus exposing the soil to *e.g.* soil erosion (Franklin and Forman, 1987). Cutting trees increases the availability of water and nutrients by removing the lower quality and

older stems to focus growth on future tree parts, and it also increases light penetration to underlying vegetation (Boivin-Chabot et al., 2004, Hardesty, 1984). Managing a coppice cycle maintains a very diverse ecosystem structure, and is attractive to many different plants and animals such as birds (Fuller and Warren, 1990).

The resprouting ability of a plant can have major impacts on tree recovery and re-establishment. This is because the following can be reduced:

- turnover of populations,
- the effects of severe cutting or severe fires,
- ecosystem dependence on seed production and germination for population maintenance and growth, because it is not a reliable means of re-establishment, especially where resources such as water are limited (Bond and Midgley, 2001).

A coppice cycle in a woodland where firewood is continuously harvested maintains links with traditional practices because for rural people, firewood is still the major source of cooking energy in the communal areas, as it was in years gone by (Mason and MacDonald, 2002). As a result of the ongoing high demand for firewood, collection consists of cutting even the green coppice of a previously harvested tree stump (Avohou et al., 2011). This reduces the overall productivity of an ecosystem that supplies the bulk of coppices (Avohou et al., 2011). Rotational harvesting strategies can thus be implemented that maintain the community structure, ensuring that the removal of excess production will not alter the production and sustainability of the ecosystem (Shackleton, 1993).

### 1.1.6 Coppice management practices

Sustainable utilization is defined as when the total woody biomass removed is less than or equal to the total annual growth (Lawes and Obiri, 2003, Shackleton, 1997, Chirwa et al., 2008). A major challenge in savanna ecosystems is to maintain the biodiversity and composition of the ecosystem, while at the same time meeting human demands of savanna products such as firewood (Shackleton et al., 2004). While selective harvesting of such resources as firewood has less severe consequences on

biodiversity and ecosystem function than complete removal, such harvesting has to be monitored and managed closely such that ecosystem structure and function are not degraded. For example, wood is a renewable source of energy if utilized sustainably (Shackleton, 1997).

Sustainable practices are those that take into consideration regeneration and the long-term functioning of the harvested ecosystem in the cases where there is no harvestable dead-wood. In a sustainable tree utilization practice, such as a rotational cutting cycle, selected trees are left to grow whilst others are clear-cut, such that a section of the tree cover is maintained and the soil is protected from erosion and direct rain-drop impact. Cutting cycles can be introduced in harvesting areas whereby an area is divided into blocks big enough to allow for continuous harvesting. Trees are clear-felled in rotating cycles giving enough time for regrowth for the next harvest. Selective cutting of trees can be done such that branches or stems are felled from trees continually but selectively, with replanting strategies implemented as cutting takes place. In ensuring sustainable utilization, the area utilized can be divided into segments such that cutting cycles can be introduced for the purpose of planning and to limit over-exploitation. Dead trees and unwanted trees can be removed using this type of harvesting, thereby improving growth rates of remaining trees (Shackleton and Clarke, 2007, Chirwa et al., 2008).

Selective and sustainable cutting can also include different harvesting intensities leaving branches with leaf material. This way, trees are able to recover lost biomass through photosynthesis. Trees can also be harvested at different times of the year, and because the regenerative capacity of trees varies with time of the year it is cut (Kozlowski, 2002), trees recover at different times enabling a harvestable biomass to be available in rotational manner. In Malawi, Abbot and Lowore (1999) reported that a cutting cycle of between 3-5 years is recommended for the production of firewood and poles, whereas in Sudan, which is more arid, Nygård et al. (2004) recommended a rotation period that is longer (approximately 4-6 years) for a larger proportion of firewood production.

The utilization of savanna woody plants involves the partial or complete removal of the canopy and stems on a regular basis and as a result the amount of resources

supplied to the plant and the frequency of utilization may significantly affect the regrowth and functioning of resprouting shoots (Eggleton et al., 2007). When harvesting, the availability of resources, the rate of harvesting and the cyclic renewal of available resources such as moisture have to be considered (Gaugris et al., 2008). Management should focus on strategies that do not significantly reduce biomass in a woodland ecosystem or severely affect the regeneration or recruitment potential in that ecosystem (Lawes and Obiri, 2003). Sustainable harvesting practices should also introduce institutional arrangements that allow for natural resource management with community participation being emphasized.

An example of such an institutional arrangement that also involves the community is community based natural resource management (CBNRM) (Thakadu, 2005, Kaschula et al., 2005a, Eriksen and Watson, 2009). Such initiatives help balance the demand for savanna products, social sustainability as well as resource sustainability, with the goal being the community utilizing and managing its own resources sustainably through linking scientific information and policies involved in utilizing the resources (Kaschula et al., 2005a). Sustainable harvest practices and management strategies can be implemented and monitored through embracing more participatory interactions with local communities and stakeholders such as local municipalities (Seydack and Vermeulen, 2004).

### 1.1.7 Human activities in savannas

Over thousands of years, human activities have influenced the production, structure and diversity of savanna ecosystems through cutting trees for firewood, land clearing for agricultural practices and livestock rearing (Scholes and Archer, 1997, Luoga et al., 2004). There is concern about unsustainable harvesting of trees in savanna communal lands, primarily for firewood (Shackleton and Clarke, 2007, Pote et al., 2006). An increase in human density has increased the pressure on ecosystem resources, in the process negatively influencing growth, production and sustainability in savannas (Houehounha et al., 2010, Kaschula et al., 2005a, Shackelton et al., 2004). This has happened through intensive harvesting practices which put more pressure on natural resources, posing a real challenge for nature conservation practices (Seydack and Vermeulen, 2004).

Clearing of trees for various purposes has led to patchy and degraded vegetation being produced, increasing costs of other economic activities such as farming through causing soil erosion, a decline in soil fertility, reservoir sedimentation and flooding (Scholes and Archer, 1997). Natural ecosystems have been transformed by different land-uses, such as land clearing for crop farming and urbanization, which have led to significant woody biomass losses (Scholes and Archer, 1997). Remote areas still rely on firewood as a source of power, with alternative energy sources such as paraffin and gas difficult to afford for most households (Twine et al., 2003, Shackelton et al., 2004).

In developing countries, authorities are faced with a challenge; to limit tree cutting for firewood so as to reduce overcutting, thus forcing people to shift to other sources of energy which may even be more costly; or to allow continued utilization in the current manner which may lead to total depletion of woody plant material due to overcutting (Allen, 1985, Shackleton et al., 2004, Pote et al., 2006). Indirect utilization of ecosystem resources for human benefits, such as the browsing and grazing of livestock, can be beneficial in contributing towards biodiversity conservation (e.g. possible seed dispersal can increase tree or grass species diversity). However, this utilization must ensure that economic gains are not only profitable but also sustainable in the long term (Crook and Clapp, 1998).

In communal areas, local management systems, governance and institutions in charge are frequently weak, at times lacking in skills, capacity and adequate finances (Shackleton et al., 2004). Therefore, these management systems are under pressure to manage energy security strategies (Shackleton et al., 2004). Compared to private areas, communal savanna areas have multiple users (e.g. different homesteads herd livestock in one communal grazing area) often with high human densities, at times leading to unsustainable use of land. Factors such as high poverty levels in such densely populated areas have contributed to such unsustainable use (Wessels et al., 2011).

## 1.2 RESEARCH RATIONALE AND OBJECTIVES

In systems prone to disturbances, such as savannas, the ability of trees to coppice is a key attribute to their resilience and productivity (Shackleton, 2001, Kaschula et al., 2005b) because coppice growth is tolerant of drought and nutrient poor soils (Kennedy, 1998, Kaschula et al., 2005b). However the ability of a woody plant to coppice and remain vigorous largely depends on the severity of the disturbance with reference to above ground biomass, availability of water and nutrients, and also on the availability and mobilization of resources above and below-ground (Nzunda et al., 2008). It is important to know how the various factors such as availability of water and nutrients and stored non-structural carbohydrate reserves interact in order to influence coppice growth. Such information is essential for assessing the ecological impacts of disturbances impacting trees, and for designing management strategies aimed towards sustainable production of coppice, e.g. for fuelwood.

The factors that drive ecosystem function in savannas include availability of resources (water and nutrients), interacting with disturbances that include fire, herbivory and human activities such as selective cutting (Luoga et al., 2004, Archibald et al., 2005). The availability of soil moisture and nutrients are important structural determinants in savannas because they facilitate the influence of other determinants such as herbivory and fire through increasing plant growth and distribution when in abundance (Scholes and Archer, 1997, Scholes, 1987, Sankaran et al., 2005). The seasonal availability of soil moisture in particular, is thought to control the duration of the growth period, while nutrients govern the growth rate during that period (Scholes and Walker, 1993). Soil moisture also has a major influence in determining the onset of germination and seedling establishment (Wilson and Witkowski, 1998).

In some areas, herbivores such as elephants, open up areas through pushing trees and increasing grass biomass, while in other areas savannas are transformed to shrubland with less grass biomass (Scholes, 2004). Elephants also have important ecological roles on savanna dynamics such as influencing nutrient cycling and seed dispersal (Baxter and Getz, 2005). Elephant tree damage can substantially change savanna structure and influences species composition through opening up previously shaded areas (Banda et al., 2006). Through removing the canopy, elephants also promote the

spread of fire by facilitating grass growth (Holdo, 2007). Overall, the habitat modification that results from high elephant densities likely alters the compositional, structural and functional diversity of ecosystems (Baxter and Getz, 2005).

Humans have interacted with savanna ecosystems for millennia and contribute substantially to the structure, distribution and composition (Scholes and Walker, 1993, Marchant, 2010). This human-ecosystem interaction has a possibility of endangering savanna sustainability in the long run and affecting tree species distribution (Marchant, 2010). Through an increase in the intensity of utilization in recent years, the availability of natural resources such as wood from trees has decreased considerably (Shackleton et al., 2004). Since savannas are anticipated to be among ecosystems that will be exposed to future changes in land use and climate (Scholes and Walker, 1993) and also because these are disturbance prone areas (Shackleton et al., 2007, Neke et al., 2006), a thorough understanding of factors that structure savanna communities is urgently required to guide management efforts for sustainable utilization.

There is a need to understand the implications of the interaction of site and climatic factors, such as soil fertility and moisture availability on the resprouting of cut trees, so that the long term productivity and sustainability of woodlands can be managed (Neke, 2004, Neke et al., 2006, Pote et al., 2006). Although resprouting has become recognized as a key functional trait in plant ecology over the past decade (Lawes and Clarke, 2011), there is still limited information about the physiology and growth strategies of resprouting trees (Neke, 2004, Pote et al., 2006). Also, there are few data indicating how soil nutrient limitation and soil moisture interact to influence the physiological processes involved in the response of trees to cutting (da Silva et al., 2008, Henderson and Jose, 2010). Available information about the influence of disturbance and cutting frequency comes from ecosystems that are different when compared with savannas. In this context, understanding post-cutting resprouting limitations is important for establishing plans for sustainable use and management of coppice resources (Lawes and Clarke, 2011).

### 1.2.1 Aims and objectives

The aim of this study is to investigate the effect of water and nutrient availability, and disturbances, on the coppice growth of a savanna tree species.
The specific objectives and hypotheses of the study are to:

1. Investigate the effect of water and nutrient addition on the timing and duration of phenological stages of cut trees.

**Hypothesis**- Adding water and nutrients to cut trees causes a shift in the timing and duration of phenological stages of resprouting trees in ways that favour growth.

2. Investigate the effect of water and nutrient addition on the coppice response and the stored carbohydrate reserves in stems of cut trees.

**Hypothesis**- Adding water and nutrients to cut trees increases the coppice response and stem total non-structural carbohydrates of resprouting trees.

3. Investigate the effect of browsing on the coppice growth of cut trees.

**Hypothesis-** Exposing resprouting trees to browsing decreases coppice response.

4. Determine how repeated cutting of trees affects regeneration and the stored carbohydrate reserves in stems.

**Hypothesis**- Repeated cutting reduces coppice response.

### 1.2.2 Scientific contribution of the research

- This research investigates the possible interactive effects of adding water and nutrients on the coppice regrowth of cut tree stumps. There is limited information about the effects of water and nutrient interactions on coppice regrowth in savanna trees. Most research in the past has focused on ecosystems different to savannas in terms of the seasonality of water distribution. Studies that can be referred to in savannas have focussed more on seedling establishment as well as forest plantation trees (Coyle and Coleman, 2005, Scogings and Mopipi, 2008, Wilson and Witkowski, 1998). This study set out to contribute towards this lack of information through experimental manipulations by cutting trees.

- It is important to understand how water and nutrient availability influences tree regrowth, not only to understand the change in coppicing ability of a tree species due to resource availability, but also to evaluate how changes in resource availability in an ecosystem may impact on a tree's ability to restore depleted stem reserves. Therefore, this study set out to determine the effects of adding water and nutrients on the stem total non-structural carbohydrate storage after cutting trees.
- With a number of studies proposing that either temperature or water availability play a pivotal role in controlling phenological changes (Archibald and Scholes, 2007, Childes, 1989, Chidumayo, 2001, Seghieri et al., 1995), this study offered an opportunity to test the role played by two savanna determinants (water and nutrients) in controlling plant events such as the timing of leaf discolouration in an African savanna. Also, Jenerette et al. (2010) mention that the sensitivity of tree phenology to soil water fluctuations is not well understood; this study had the objective of filling this gap. Most phenological studies have focused on mature trees, and this study offers a unique opportunity to monitor the response and persistence of cut resprouting trees.
- There is limited information about the response of resprouting trees to browsing. Most of the research has focused on how seedlings or mature trees respond to either defoliation or simulated browsing. Through exposing resprouting trees to a certain period of browsing, this study offers an opportunity to investigate the effects on trees at a different physiological state, in terms of e.g., growth, compared to mature trees or seedlings.
- A tree can only tolerate disturbances/cutting cycles to a certain level (Landhausser and Lieffers, 2002). Therefore, a resprouting tree has to compromise between replenishing depleted reserves and supporting existing plant parts at the same time (Schutz et al., 2009). This research, through the multiple cutting experiment, sheds light on the influence of repeated cutting on stored resources, which has implications for tree vigour and survival under intensive harvesting practices. Also, this information would be critical in savannas considering that these are disturbance prone ecosystems.

### 1.2.3 The conceptual framework of the study

The structure, production and dynamics of savanna ecosystems are largely affected by resource availability and the prevalence of disturbances (Sankaran et al., 2008, Sankaran et al., 2005). In savannas, disturbances (e.g. fire, herbivory and human cutting) occur frequently and unpredictably (Iwasa and Kubo, 1997, Lawes and Clarke, 2011). In such ecosystems, trees are subjected to various forms of disturbances and stress factors that affect their development, production and survival (Scholes and Archer, 1997). As a response strategy when damaged, some trees have the capacity to coppice; to produce resprouting shoots at the base of the stem or arising from the stump (Kaschula et al., 2005b, Hardesty, 1984).

Although resprouting has become recognized as a key functional trait in plant ecology over the past decade (Lawes and Clarke, 2011), there is still limited information about the physiology and growth strategies of resprouting trees (Neke, 2004, Pote et al., 2006). Also, there is little data indicating how soil nutrient limitation and soil moisture interact to influence the physiological processes involved in the response of trees to cutting (da Silva et al., 2008). Available information about the influence of disturbance and cutting frequency is from ecosystems that are structurally and functionally different from savannas. In this context, understanding post-cutting resprouting limitations is important for establishing plans for sustainable use and management of savanna coppice resources (Lawes and Clarke, 2011). The aim of this study was to investigate the effect of water and nutrient availability, and disturbances, on the coppice growth of a savanna tree species.

The conceptual framework developed for this study considers coppice growth at the scale of the tree; individual coppice shoots, and leaves on shoots as contributing towards the overall coppice regrowth (Fig. 1.1). Interacting with each other, internal processes and resources, or the within-tree factors (cell growth and metabolism, reproduction, stored reserves and photosynthesis), are considered to influence coppice regrowth. Cell growth and metabolism includes processes such as cell expansion, cell division and processes such as respiration (Chapin III, 1991, Chapin III et al., 1993, Abe et al., 2003, Chaves et al., 2003).

The internal factors are, in turn, also considered to be influenced by coppice regrowth in a feedback loop. For instance, the product of photosynthesis is used in the production of coppice shoots or, in the long term, can be diverted towards the production of reproductive parts such as flowers and fruits. As shoot production increases, there is an increase in leaf area, which in turn increases photosynthesis. Alternatively, an elevation in the rates of photosynthesis would be as a result of an increase in coppice regrowth (e.g., increase in shoot numbers that would potentially increase leaf numbers and also leaf area), including factors such as elevated foliar nitrogen. Consequently, in both scenarios, elevated levels of photosynthesis would result in an allocation of carbon towards increased coppice growth and also towards an increase in the amount of stored TNC reserves.

The framework also considers the external drivers that influence coppice regrowth, namely the resource drivers (availability and seasonality of resources) and the disturbance drivers (browsing and repeated cutting) (Fig. 1.1). The data obtained from the addition of water and nutrients, as well as exposing trees to browsing and multiple cutting disturbances were used to refine the conceptual framework. The dashed boxes in the conceptual framework are the quantifiable variables that help explain the extent of the influence of each factor and each driver on coppice regrowth.

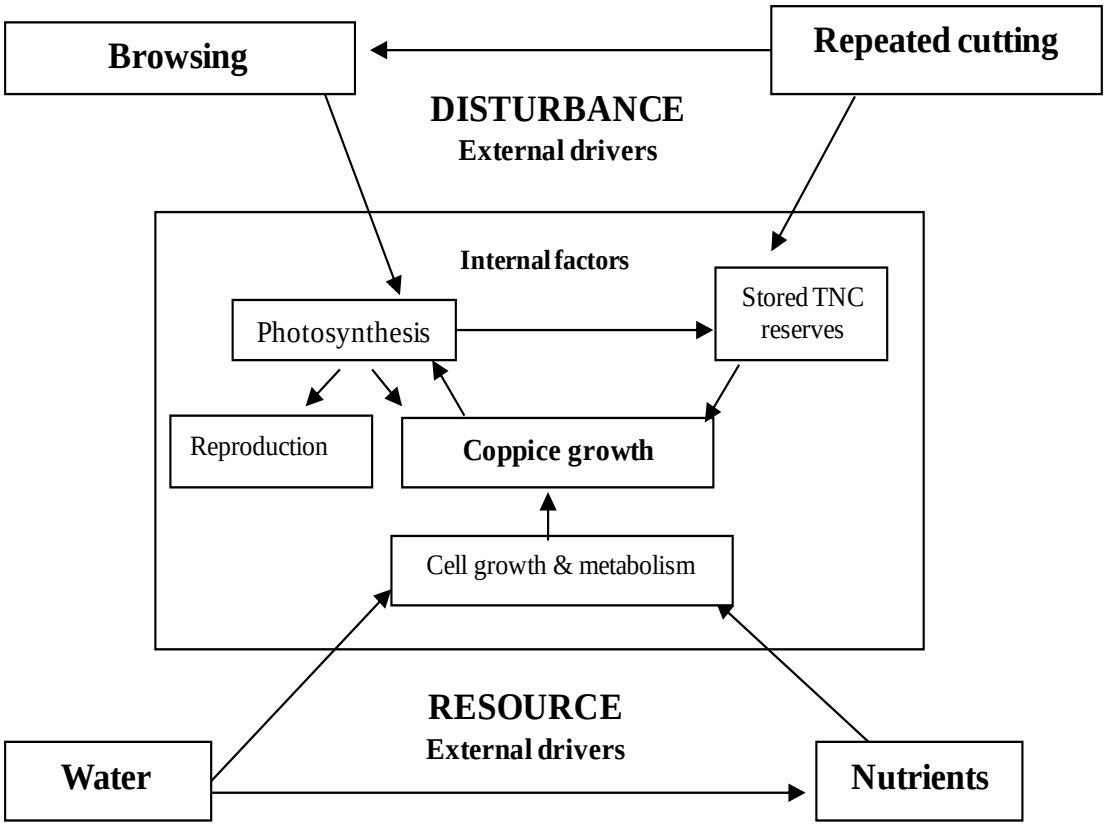



**Figure 1.1.** Conceptual framework for factors hypothesized to influence coppicing in savanna trees.

## 1.3 STUDY SITE

### 1.3.1 Biophysical characteristics

The study was carried out at the Wits Rural Facility (WRF), a 350 ha research station of the University of the Witwatersrand, in the central savanna Lowveld area (Fig. 1.2) of Limpopo Province, South Africa ($24^{o}$ 30′ S; $31^{o}$06′ E). The region is semi-arid, with a mean rainfall of approximately 650 mm per annum, concentrated in the summer season (October to April), mainly in the form of convectional thunderstorms (Fig. 1.3A) (Kaschula et al., 2005a, Shackleton, 1997, Neke et al., 2006). During the study, rainfall received between September 2010 and September 2011 was 825 mm, while 915 mm was received between September 2011 and September 2012 (Fig. 1.3B). The mean annual temperature is $22^{o}$C (Neke et al., 2006, Shackleton, 1993). Droughts are common and may occur as often as once in every 4 years (Neke, 2004). The most common soil types in this region are the shallow sandy nutrient poor lithosols, underlain by granitic gneiss (Shackleton, 2001, Neke et al., 2006, Kaschula et al., 2005a, Kaschula et al., 2005b).

The vegetation is dominated by tree species in the Combretaceae (e.g. *T. sericea*) as well as Mimosaceae (e.g. *Acacia gerrardii* Benth) families, characteristic of the Mixed Lowveld Bushveld vegetation type (Shackleton, 2001, Neke et al., 2006, Shackleton, 1993). The dominant grasses include *Panicum maximum* Jacq, and *Hyperthelia dissoluta* (Nees) Clayton (Shackleton, 1993).

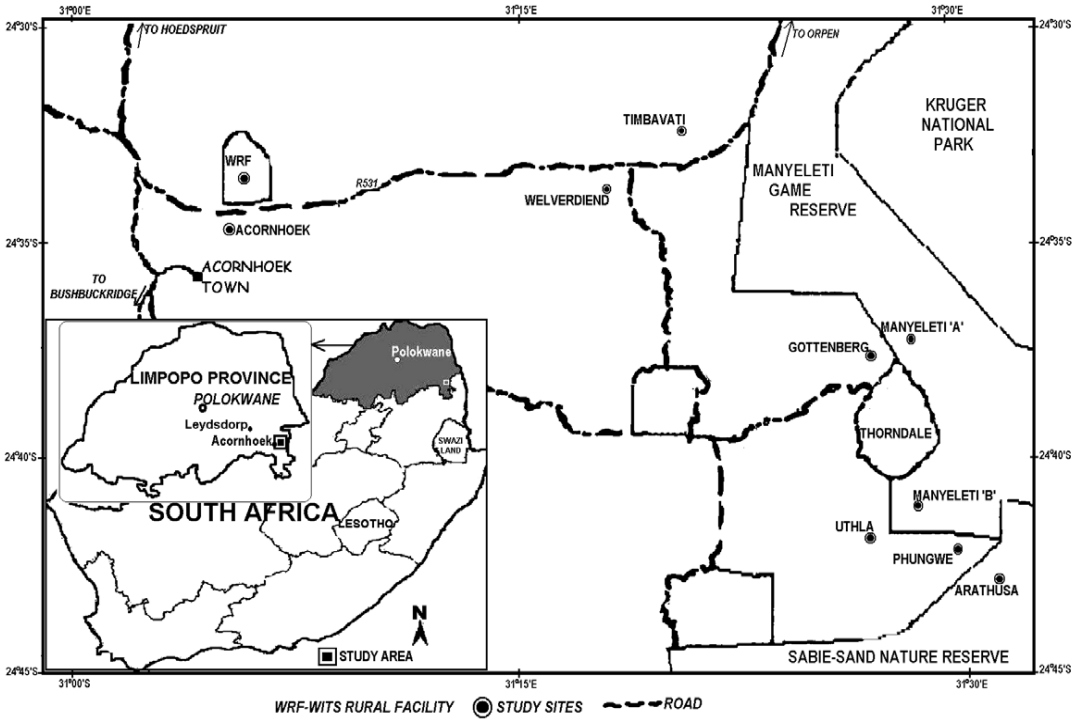



**Figure 1.2.** Location of the study site WRF (Wits Rural Facility) in the Limpopo Province, South Africa (Adapted from Neke, (2004)).

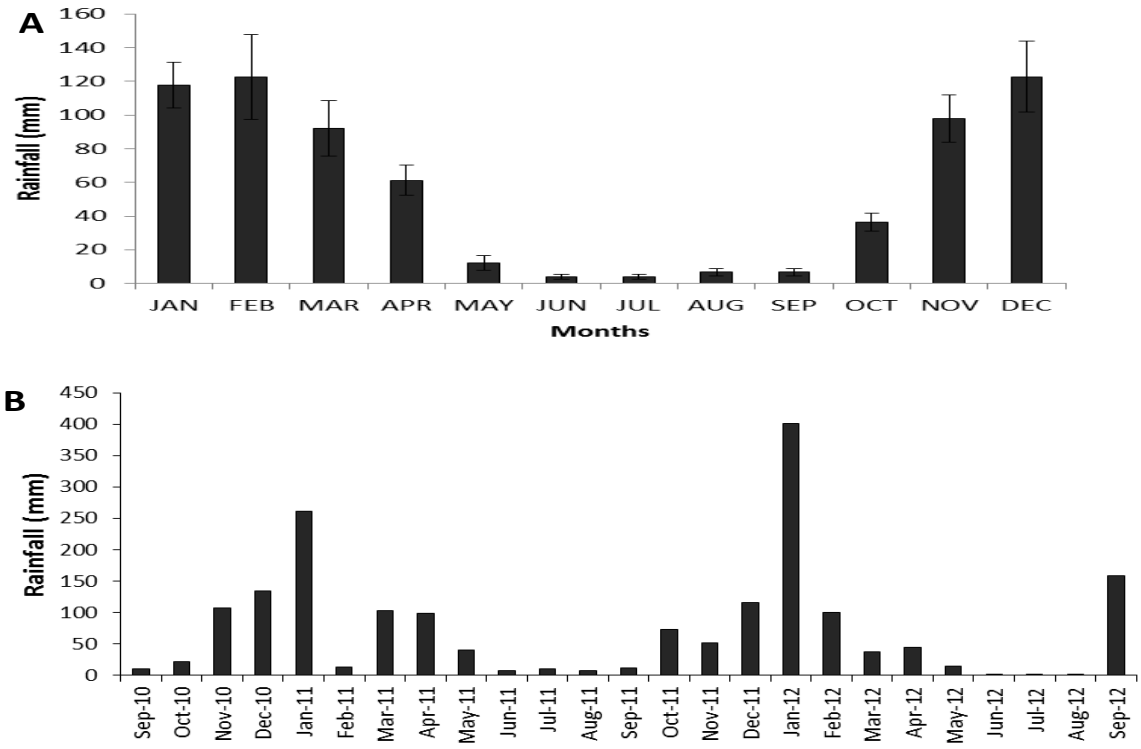



**Figure 1.3.** A) long-term mean monthly rainfall distribution (1992-2010) for the Wits Rural Facility and B) cumulative monthly rainfall data for the duration of the study period (September 2010-September 2012). January 2012 received exceptionally high amounts of rainfall compared to other January figures for the past 18 years. Data courtesy Dr. Wayne Twine.

### 1.3.2 Study species

The species chosen for this study was *Terminalia sericea* Burch. ex. DC, also known locally as silver cluster leaf. It is a common tree species in dystrophic savannas occurring from Tanzania and the Democratic Republic of Congo, southwards to Angola, Namibia, Zimbabwe, Botswana and South Africa (Coates-Palgrave, 2002), and is widespread in WRF and the surrounding areas. *T. sericea* is a medium sized semi-deciduous tree species, growing (when uncoppiced) as a single-stemmed tree reaching up to 8 m in height or a multi-stemmed shrub 4-6 m tall (Coates-Palgrave, 2002). The grey bark is deeply fissured, and the young leaves have silver hairs, giving the tree a characteristic silver appearance.

The species is common in the lowveld, bushveld and bush savanna vegetation types of South Africa. It tolerates drought and adapts well to saline soils (Griffiths, 1959). *T. sericea* is particularly prolific on the mid-slope seep-lines of these ecozones, where it grows in dense groups of various sizes forming thickets producing a very large biomass (Amri, 2011). It forms dense thickets when cut or burnt, preventing the growth of grass and although the nutritional value is low, leaves and young shoots are eaten by elephant, giraffe, kudu and impala (Coates-Palgrave, 2002, Katjiua and Ward, 2006b). The species in this study is mainly used for firewood and making charcoal, and is also used for medicinal purposes such as curing diarrhoea, in rural communities (Carr, 1994). Timber from *T. sericea* is hard and heavy and is used for construction purposes (kraals, fence posts etc.), with the roots used for strength during hut construction (Scholes, 2004). *T. sericea* was chosen as the study species for the following reasons;

- It is typically abundant in dense stands in the study area,
- It is known to coppice vigorously,
- It is the widely used as a source of firewood in southern Africa,
- More knowledge of its regenerative capacity can contribute to management recommendations for sustainable utilization. This is because it is such an important part of the everyday life of communal villagers, contributing

financially when wood is sold or through burning as a source of energy (Shackleton, 1993, Neke, 2004, Shackleton et al., 2004).

## 1.4 STUDY APPROACH AND THESIS STRUCTURE

This section gives an overview of the study approach. Detailed descriptions of the study designs and methods are presented in each of the data chapters (chapters 2-5). This study accomplished its objectives by using an experimental approach to examine the coppicing of cut trees under different experimental conditions in which resources and disturbances were manipulated. The research chapters of this thesis are written in the format of scientific papers to be submitted in internationally accredited scientific journals. Presenting and writing a thesis in a paper format results in some inevitable repetition, especially in the introduction and methods sections. Following this introductory chapter, Chapters 2 to 5 each focus on specific research objective (Fig.1.4). The Discussion chapter then integrates and combines findings from each research chapter, describing the overall ecological implications of the study.

**Chapter 2 and 3*: Resprouting trees supplemented with water and nutrients***- With the emphasis of the study focusing on the coppice response of cut trees, in these two chapters, the effects of resource manipulation on cut trees were determined (Fig. 1.4). Coppice response (e.g. resprout shoot length and resprout shoot diameter), changes in stem storage total non-structural carbohydrates (TNC) and the timing of phenological stages of cut trees were investigated by manipulating water and nutrient levels in a 3x3 factorial experiment. Ten trees were selected per plot, with the number totalling 270 for the experiment. Trees were cut at a height of approximately 25 cm from the ground. Water was supplemented through obtaining average monthly long-term (18 years) rainfall data for the study site from data files and manipulating three treatments, while a commercially available fertilizer, ammonium phosphate (mixed N:P:K:Zn), was added as a nutrient supplement. Stem TNC was sampled at the beginning and at the end of the 2011 growing season (i.e. in September 2011 and April 2012). Tree coppice response was monitored monthly, while phenological changes (e.g. timing of leaf bud production and timing of leaf discolouration) were observed and recorded fortnightly.

**Chapter 4:** ***Browsing effects on resprouting trees***- In this chapter, the emphasis shifted from resource manipulation to test the effects of natural disturbances on tree responses, both morphological and physiological. The presence of antelope (e.g. kudu and impala) in the facility allowed for this study to explore the effects of browsing in a split-plot experiment. Trees were cut and half the plots were fenced off immediately after cutting. The other plots were left unfenced and therefore browsed for about 5-months, and subsequently fenced off. The coppice response was then monitored for about a year while stomatal conductance and leaf expansion were sampled at the beginning of the first growing season after exposure to browsing. Although the density of browsers (antelope) in the facility was not determined, the numbers were probably lower in the facility compared to browser population (especially goats) in a communal village.

**Chapter 5:** ***Trees exposed to multiple cuttings***- This study focused on comparing the coppice response of trees exposed to multiple cuttings (eight cutting events) with those that received fewer cutting cycles (one and two cutting events respectively) in a completely randomized experiment. Trees exposed to eight cutting cycles were cut every three months (based on the 2-year time frame for data collection), trees cut twice were cut at the beginning of the study (September 2010) and also in September 2012. Trees cut once were only cut in September 2012. Some studies have suggested that trees remobilize stored nitrogen for use in regrowth instead of stored carbohydrates (Druege et al., 2000, El Omari et al., 2003, Wendler et al., 1995, Millard and Proe, 1992). This study did not investigate nitrogen and stored stem carbohydrate reserve remobilization, but instead quantified and compared the amount of carbohydrate reserves (mainly in the form of starch) remobilized across the different cutting regimes. Tree coppice response was monitored monthly while stem TNC was sampled after six cutting cycles for the multiple cut trees, after one cutting event for trees cut twice and before any cutting was done for trees cut once over the study period.

**Chapter 6** ***Synthesis*****:** General discussion of research findings with particular reference to the implications of resource availability and disturbance for the sustainability of repeated harvesting of trees for fuelwood.

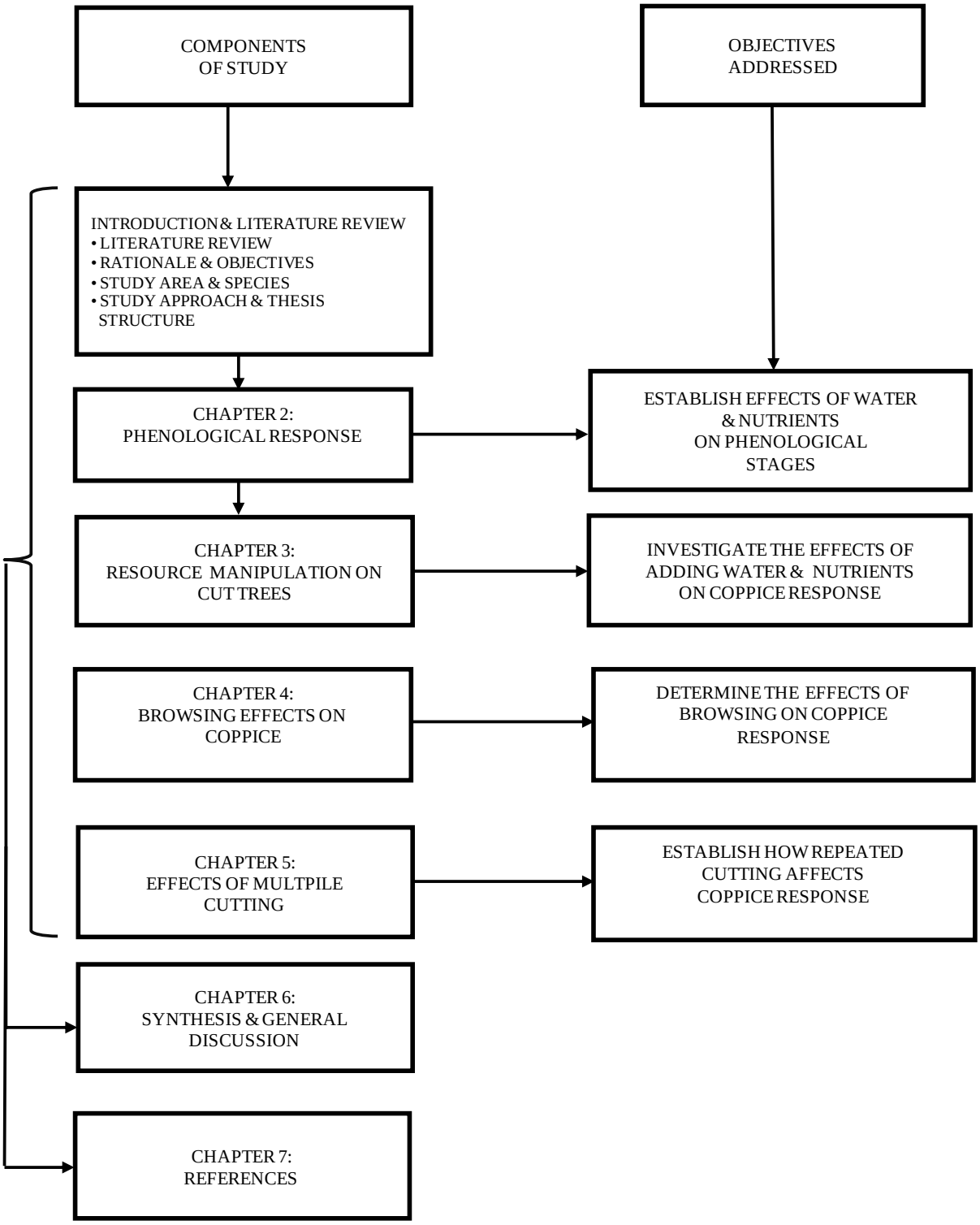



**Figure 1.4**. Study structure for the investigation of the coppicing of a savanna tree species (*T. sericea*) in relation to resource manipulation and disturbance.

## CHAPTER 2

## EFFECTS OF WATER AND NUTRIENT ADDITION ON THE TIMING AND DURATION OF PHENOLOGICAL STAGES OF RESPROUTING *Terminalia sericea*


## ABSTRACT

The seasonal duration of leaf flushing, flowering and fruiting determine the growth and survival of coppicing trees. There is limited information about the factors that affect phenology of coppicing trees. This study examined the effects of water and nutrient additions on the phenology of resprouting *Terminalia sericea* trees in a semi-arid savanna in South Africa. Cut trees were exposed to different levels of water and nutrient (nitrogen and phosphorus) supplementation over a period of two years in a factorial experiment. Phenological stages monitored fortnightly included bud presence, leaf presence and fruit production. Leaf presence followed a similar distribution to bud presence, peaking during the wet season (December-March). Change in leaf colour from the typical silvery green to yellow was delayed to later in the wet season, while higher leaf numbers were recorded during the wet seasons for trees supplemented with water and nutrients. Although generally low throughout the study in all treatments, fruit presence was mainly in supplemented trees. Results indicate that the increase in water and nutrient availability has direct consequences for extending the growing season of resprouting trees. This extension has positive effects on increasing the photosynthetically active period, thus potentially increasing the carbon gain and growth of trees. Plant growth and the duration of carbon assimilation are important because disturbances, such as tree cutting, have implications for productivity when growth can only occur during certain times of the year.



*Key words*: Phenology, water, nutrients, phenophases, harvesting.

## 2.1 INTRODUCTION

Phenology is the study of the annual growth cycle of plants with respect to the timing of their flowering, fruit production, development of new leaves and leaf senescence (Norman, 1989, Seghieri et al., 2009, Chidumayo, 2001). The timing of these different phenological stages, *e.g.* timing of leaf emergence has implications for the duration of the photosynthetically active period. This is important for carbon assimilation. Phenology is a dominant and often overlooked aspect of plant ecology, from the scale of individual tree species to whole ecosystems (Cleland et al., 2007). Phenology has been particularly overlooked in relation to resprouting and coppicing, with most published data referring primarily to undamaged mature trees (Chidumayo, 2001, Archibald and Scholes, 2007). The main task in monitoring plant phenology is to observe and record the periodically recurring growth stages and to observe the regularities and dependency of these stages on environmental conditions. The timing of tree phenological events is crucial for the survival, and regrowth, of trees in most environments as it is a trait highly responsive to changes in environmental conditions (Pinto et al., 2011).

At the ecosystem level, interactions between the environment and plant growth stages include influences of rainfall and temperature on the timing of different plant phenophases such as production of leaves and fruits (Rich et al., 2008). These are important interactions because the timing and extent of change of leaf characteristics are key tree responses which may be affected by climate change and prevailing fluctuations in rainfall and temperature (Archibald and Scholes, 2007). Vegetation production, species distribution and plant adaptability to changes are all plant traits that potentially change as a result of changes in the climate (Rich et al., 2008, Shackleton, 1999, Shackleton, 1997, Dreyer et al., 2006).

It has been proposed that phenological changes are controlled by temperature and photoperiod duration in temperate and high altitude climates (Vitasse et al., 2011, Damascos et al., 2008, Menzel, 2002, Williams et al., 1997, Chmielewski and Rötzer, 2001, Archibald and Scholes, 2007). There have also been suggestions that temperature determines the timing of phenological changes in southern Africa (Chidumayo, 2001, Childes, 1989, Seghieri et al., 2012). However, in savannas,

water, and not temperature, has often been reported as more limiting (Scholes and Walker, 1993, Archibald and Scholes, 2007, Sankaran et al., 2008, Broadhead et al., 2003). Seasonal rainfall fluctuations and limitations are therefore likely to determine the distribution of phenological events, because water is considered the most important environmental factor that determines growth, development and distribution of plants in savannas (Borchert, 1994, Archibald and Scholes, 2007, Seghieri et al., 1995, Sankaran et al., 2008). For instance, in Brazil, soil nutrient availability was demonstrated to be less important than water availability for phenological stages such as leaf flushing and leaf fall in *Senna multijuga* (Rich), with nutrient availability more important than water for flowering and fruiting (Cardoso et al., 2012). In an African savanna, leaf emergence of woody and bushy vegetation was concentrated late in the dry season and early summer, while leaf senescing peaked in June (Shackleton, 1997). Peak leaf-green up was recorded during high rainfall periods in January and May in a miombo woodland (Chidumayo, 2001). In the Cape region of South Africa, flowering of *Oxalis* was shown to peak in late autumn to early winter (May to July), after the onset of winter rains (Dreyer et al., 2006). Flowering then declined with an increase in rainfall (Dreyer et al., 2006).

While taking into account the direct role of water availability in plant phenology, water may also have an indirect effect by influencing nutrient availability through acting as a medium for transporting nutrients to different plant parts (Shackleton, 1999, Scholes and Walker, 1993). Wielgolaski (2001) reported a negative correlation between soil nutrient content and growth stages that included leaf bud break and flowering for *Betula pubescens* Ehrh., and *Salix caprea* L., along a coastal-continental gradient just above sea level in Norway. In an African savanna in the Kruger National Park in South Africa, green-up of a savanna broad-leafed tree species *Combretum apiculatum* (Sond) occurred later in the growing season (mid-November) while for fine-leafed *Acacia nigrescens* (Oliv) Benth, it started a month earlier in October before significant rains fell in November (Archibald and Scholes, 2007). For the Mediterranean shrubs *Cistus salviifolius* L. and *Cistus ladanifer* L., leaf production was reported to begin between October and November, reaching peak values by March (Simoes et al., 2008).

In semi-arid environments, understanding the effects of predicted increases in rainfall on the length of the growing season may contribute towards evaluating the influence of climate change on species distribution and ecosystem structure (Rich et al., 2008). This is because predicting climate change and rainfall fluctuation effects on timing of phenological trends is still limited, possibly due to genetic variation in plants and differences in sensitivity to seasonal changes in temperature and precipitation (Seghieri et al., 2009, Childes, 1989, Damascos et al., 2008, Chmielewski and Rötzer, 2001, Wielgolaski, 2001, Jolly et al., 2005). Consequently, responses of trees to changes in rainfall distribution interacting with soil characteristics need accurate predictions. This is because they have a bearing on future biomass production and composition of vegetation in both individual trees and the ecosystem as a whole. Tree responses are also important because different species' phenological responses to environmental changes are of particular significance when individual tree-level responses can be translated to whole ecosystem-level responses (Williams et al., 1999). There is also a necessity for studies that address overall individual and ecosystem plant phenological responses, relating changes in community structure to environmental influences such as rainfall (Rich et al., 2008), including effects of soil nutrient status (Wielgolaski, 2001, Cardoso et al., 2012).

This study set out to investigate the effects of water and nutrient addition on the timing of phenological stages of coppicing *Terminalia sericea* trees. Experimentally cut trees supplemented with water and nutrient addition were compared with unsupplemented trees. The question asked was: how does an increase in resource availability influence the timing and duration of the phenological stages in coppicing trees? By altering the length of the growing season, climate change, in the form of rainfall changes and temperature fluctuations, can have direct influences on other ecosystem and plant processes such as leaf growth (Archibald and Scholes, 2007). Following this reasoning, it was hypothesized that water and nutrient additions will cause late dry season leaf flush and extend leaf survival into the subsequent dry season, thus potentially extending the growing season. Therefore, a longer growing season would result in an increase in overall biomass productivity. This would be caused by supplemented trees photosynthesizing for longer and accumulating carbon for extended periods compared to trees with no water and nutrient addition.

## 2.2 METHODS

### 2.2.1 Study site

The study site is described in detail in Chapter 1.

### 2.2.2 Study species

The study species is described in detail in Chapter 1.

### 2.2.3 Experimental design

A 3x3 factorial experiment (nine plots) replicated in three sites, was established in September 2010 to determine the effects of water and nutrient addition on the coppice response of *T. sericea*. Each plot measured approximately 100 $m^2$, with each treatment sub-plot about five metres from the nearest sub-plot. Ten trees were selected per plot, with the number totalling 270 for the experiment. Single-stemmed trees were selected based on initial tree stump diameter; which was standardized (from 5-9 cm) to control its effects on coppice response. In cases where single-stemmed trees could not be used, multi-stemmed trees of a combined diameter ranging between 5 and 9 cm were used. Stems of such diameter range were considered medium-sized and were chosen because larger stems have been suggested to take a shorter time to respond to a cutting event, positively influencing initial coppice growth through having a larger size of the residual root system (Shackleton, 1997).

Tree cutting in this study, which was done only once for this study, was conducted manually using a chain-saw towards the end of the dry season in September 2010. Trees were cut at a height of approximately 25 cm from the ground, since research has shown that the production of resprouting shoots increases with cutting height (Shackleton, 1997, Khan and Tripathi, 1986, Ibrahima et al., 2007, Kaschula et al., 2005b). The height used in this study was kept constant to minimize its effects on resprouting trees.

A 30 cm radius was marked around each tree and grass cleared to reduce competition for water and nutrients. Grass was also cleared for trees that were not supplemented with water or nutrients. Average monthly long-term (18 years) rainfall data for the WRF records was used to derive water treatments. Water addition treatments were as follows;

i. Control ($W_0$) - no water additions through-out the study,
ii. Low ($W_+$) – trees were supplemented with an amount of water 0.5 times the long-term mean rainfall for that month and,
iii. High ($_{W++}$) – trees were supplemented with the long-term mean rainfall for that month.

This monthly amount of rainfall (Fig. 1.3A, Chapter 1) was then divided by four to obtain weekly amounts for supplementing trees for a period of about 18 months beginning in September 2010. Water was applied next to the base of each stump, within the 30 cm radius.

For the experimental plots that had nutrient additions, nitrogen (N) and phosphorus (P) were supplied in a commercial fertilizer as ammonium phosphate. A commercial dry fertilizer blended as 4:3:4:1 (N, P, K, Zn) and mixed according to 120 g/kgN and 90 g/kgP was purchased. Fertilizer additions were as follows;

i. Control ($N_0$) – no fertilizer additions through-out the study,
ii. Low (N+) – 0.13 g of N and 0.1 g of P per tree, and
iii. High (N++) – 0.27 g of N and 0.2 g of P per tree.

Fertilizer additions were applied once at the beginning of each of the two growing seasons over which the study was conducted; in October 2010 and October 2011. The annual high N treatment equated to roughly 3 % of total soil N of 3310 kgN/ha, recorded by Scholes et al. (2003), similar soils in the Kruger National Park. The dry fertilizer was applied within the 30 cm radius, by coring a hole next to the base of the stump with a diameter of about 3 cm and a depth of 10 cm and depositing the fertilizer into the hole. Fertilizer was added after the first rains fell in October 2010 and also in October 2011. Within the 30 cm radius, water and nutrient additions were randomized as illustrated in the diagram (Fig. 2.1). The distance from the nearest sub-

plot was estimated to be about five metres, which was assumed to be great enough to preclude overlap between treatments, since applications were at the base of each tree. Although other tree species co-exist with the study species, *T. sericea* dominated the experimental plots. As such, the probability of other tree species having an overlap effect was minimal.

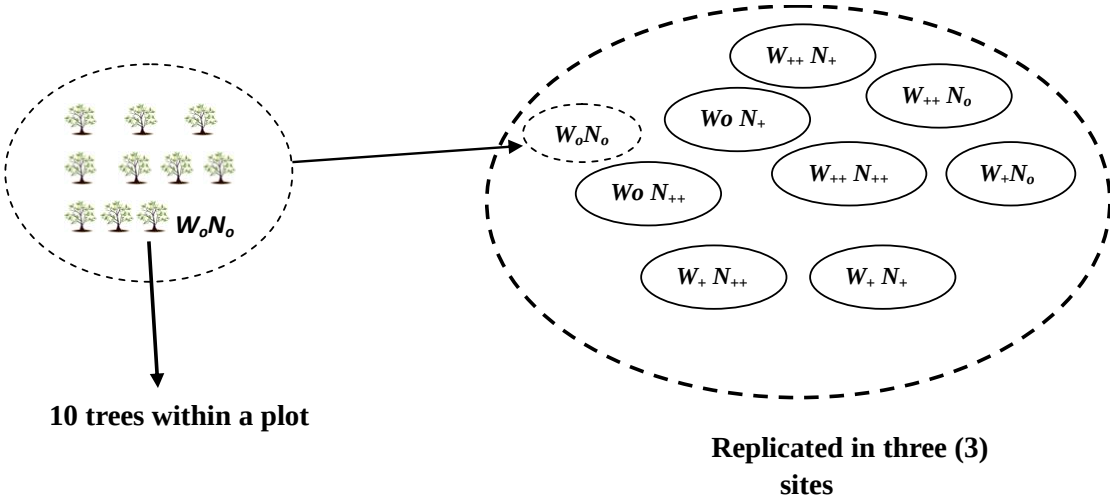



**Figure 2.1.** Factorial experiment designed to investigate the influence of water and nutrient additions on the coppice response of harvested trees.

### 2.2.4 Phenological stages monitored

Every two weeks (from December 2010 to September 2012), different phenological stages were estimated visually for each resprouting tree.

Phenological stages monitored fortnightly were:

(i) Leaf bud initiation - described as the proportion of foliage that consisted of leaf bud initials (juvenile and unexpanded leaves) on a tree. Leaf bud initials were estimated as 100 % (when leaf bud initial presence on a tree was at maximum), 75 % (when leaf bud initial presence on a tree had reduced by about 25 % from the previous estimated presence), and so on.
(ii) Presence of yellow leaves (% yellow leaves) - estimation of foliage that showed any slight discolouration or change from the normal silvery-green colour to yellow, brown etc. of present leaves on the tree. Classification was estimated as 100 % (when all the present leaves on the tree had changed from the normal leaf colour

appearance), 75 % (when 25 % of leaves present on the tree were the normal silvery-green colour), and so on.
(iii) Leaf presence - classification was estimated as 100 % (when leaf presence on tree branches was at maximum), 75 % (when leaf presence covering resprouting shoots had dropped by about 25 %), and so on.
(iv) Fruit presence - described as the prevalence of trees with fruits within a treatment. A tree was defined with a 'yes' when fruiting and a 'no' when it did not have fruits.
(v) Number of leaves produced per monitored shoot - the longest resprouting shoot was selected and marked. Leaves were counted monthly on this monitored shoot.

### 2.2.5 Statistical analyses

These data were averaged each month to obtain mean monthly proportions (%). To test for the effect of adding water and nutrients, the monthly proportions were transformed using arcsine square root for analysis with linear mixed models using SAS proc GLM. Tree responses were compared across treatments using Tukey's *post hoc* test to compare means at $\alpha<0.05$. To control for the influence of site by site variation on the monitored tree responses, site was included in the analysis as a random effect for the mixed model analysis. When significant interaction effects were detected, a simple effects analysis was used to test for water and nutrient effects at each treatment level.

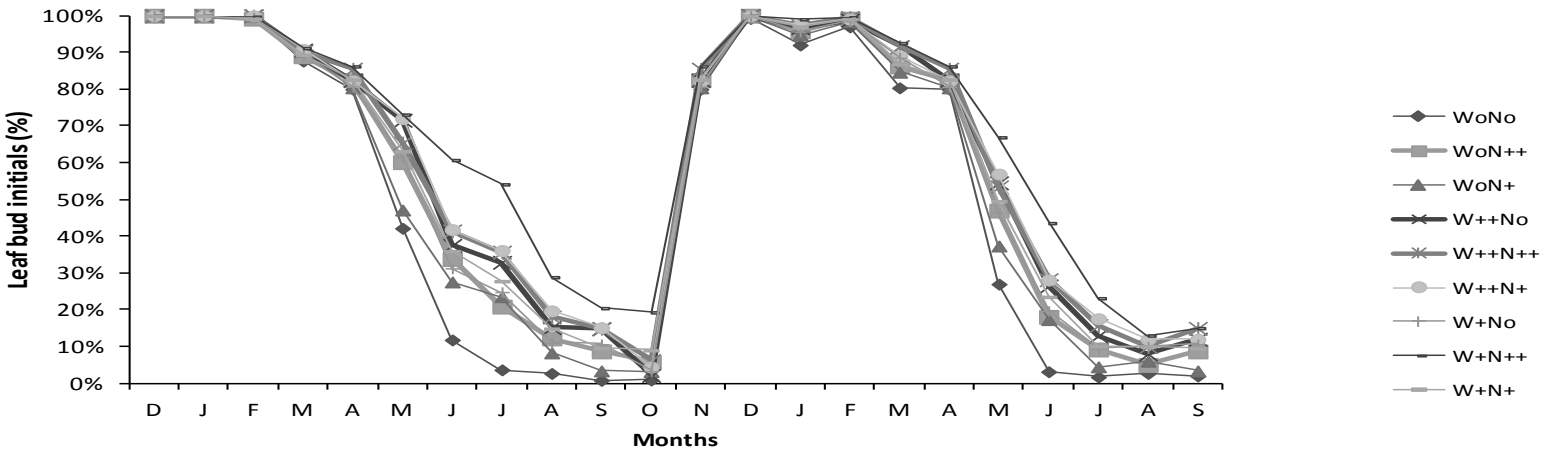
## 2.3 RESULTS

For all the phenology stages monitored, the effect of water and nutrient addition varied depending on the particular month and season, with peak levels of fruit presence, leaf presence, leaf bud initiation and average number of leaves recorded during the growing season months (between November and April). The lowest levels of these were found in the dry season months (between May and October) of each year. Leaf bud initials peaked between December 2010-March 2011 ($F_{19.88}=9.74$; $p<0.05$) for the $W_{+}N_{++}$ treatment, during the first year of water and nutrient addition, with the same trend observed between December 2011 and March 2012. Also, leaf presence peaked between the months December 2010 and April 2011 ($F_{19.88}=17.77$; $p<0.05$) while in the second year from November 2011 until April 2012 ($F_{19.88}=7.24$;

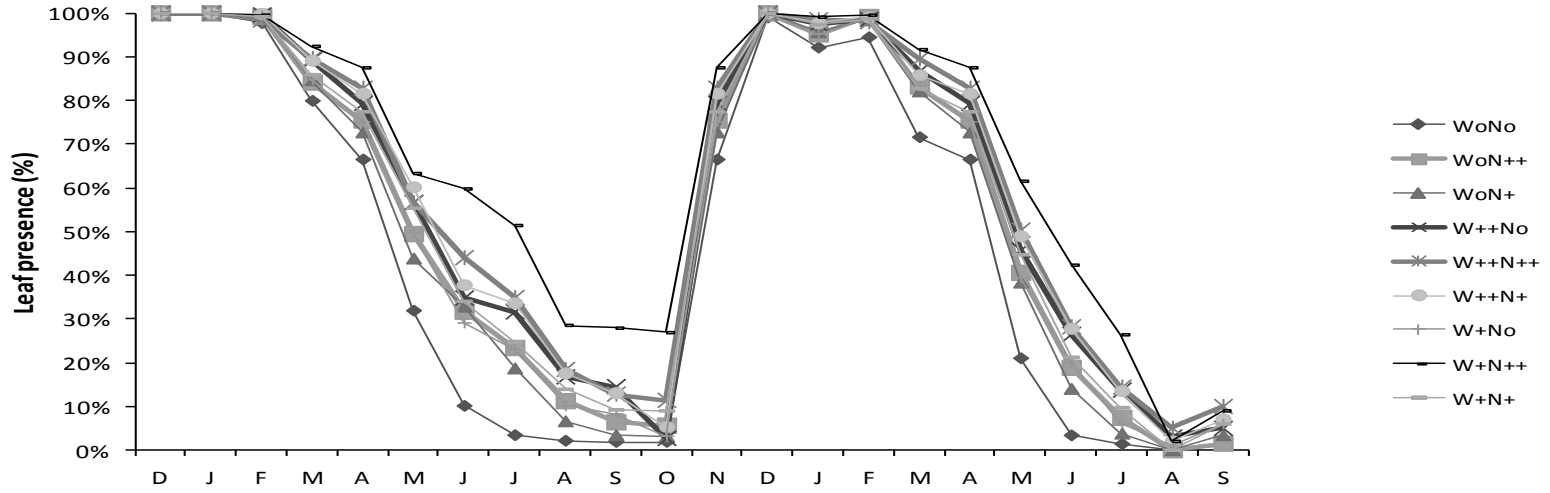
$p<0.05$) for the $W_{+}N_{++}$ treatment. Leaf presence reduced in the months during the dry season, *i.e.*, between April and October, with the $W_{+}N_{++}$ treatment trees recording about 30 % leaf presence in September of both 2011 and 2012 late dry seasons (Fig. 2.2B).

Peak leaf yellowing (leaf discolouration) was observed between the months of August and October (Fig. 2.2C), with $W_0N_0$ trees recording peak yellow leaves in September 2011 ($F_{19.88}=12.21$; $p<0.05$) and September 2012 ($F_{19.88}=6.07$; $p<0.05$). Peak fruit production was reached in the months between November 2011 and March 2012 ($F_{19.88}=4.29$; $p<0.05$); with notable treatment combinations $W_{+}N_{++}$ and $W_{++}N_{++}$ recording highest fruit production values (Fig. 2.2D). Highest leaf numbers were recorded in the $W_{+}N_{++}$ treatment trees ($F_{19.88}=18.48$; $p<0.05$) during the second growing season in April 2012 (Fig. 2.2E).

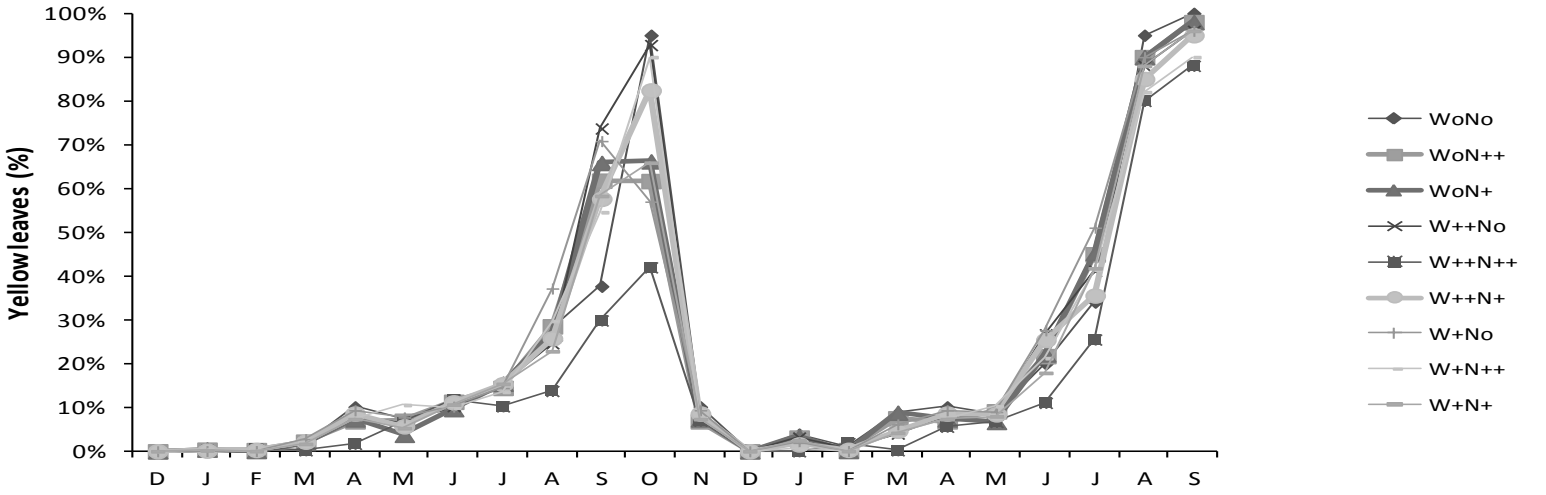
**A**


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Leaf bud initials (%)
D J F M A M J J A S O N D J F M A M J J A S
Months
WoNo
WoN++
WoN+
W++No
W++N++
W++N+
W+No
W+N++
W+N+

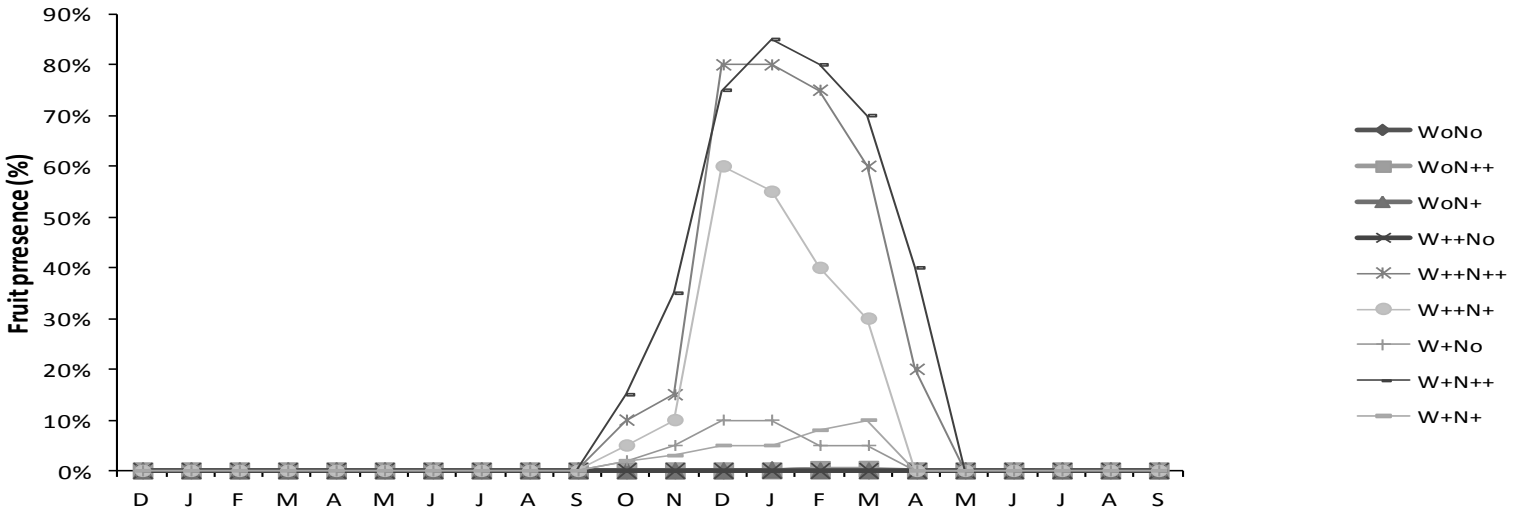
**B**


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Leaf presence (%)
D J F M A M J J A S O N D J F M A M J J A S
WoNo
WoN++
WoN+
W++No
W++N++
W++N+
W+No
W+N++
W+N+

**C**


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Yellow leaves (%)
D J F M A M J J A S O N D J F M A M J J A S
WoNo
WoN++
WoN+
W++No
W++N++
W++N+
W+No
W+N++
W+N+

**D**


90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Fruit prresence (%)
D J F M A M J J A S O N D J F M A M J J A S
WoNo
WoN++
WoN+
W++No
W++N++
W++N+
W+No
W+N++
W+N+

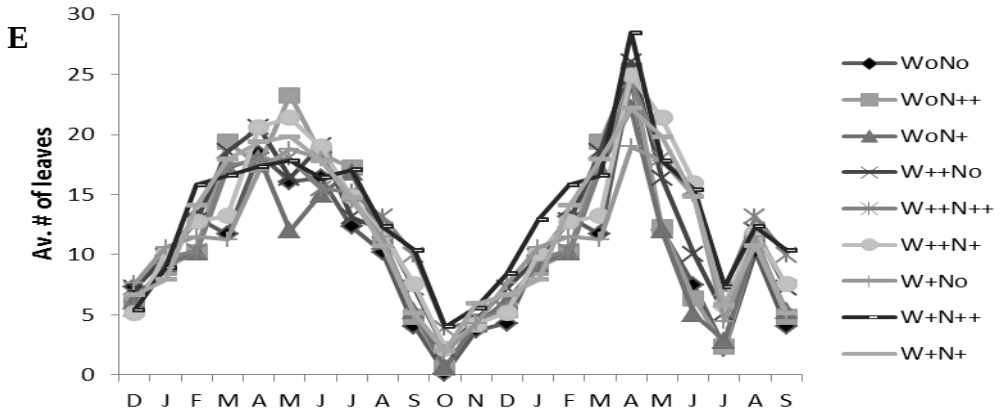



**Figure 2.2.** Changes in phenological stages of resprouting trees as a result of water and nutrient additions to resprouting trees; A) bud presence, B) leaf presence, C) discoloured leaves, D) fruit presence and E) average number of leaves. The first letter in the coding refers to the water treatment while the second letter represents the nutrient treatment. Months shown represent a period from December 2010-September 2012.

At the end of the first growing season (December 2010 to March 2011), high water addition ($W_{++}$) had no significant effect on leaf bud initials when interacting with the nutrient additions in the two growing seasons. The percentage of leaf bud initials was highest when $W_{+}$ was interacting with $N_{++}$ ($F_{19.88}$=8.57; $p<0.05$). No water addition ($W_0$) had significant effects in increasing leaf presence with high nutrient addition ($W_0N_{++}$) ($F_{19.88}$=7.13; $p<0.05$). No water addition also had significant effects under low nutrient ($N_{+}$) additions ($F_{19.88}$=11.29; $p<0.05$) on leaf presence during the second growing season (November 2011-March 2012). Low water addition ($W_{+}$) had significant effects on leaf presence when interacting with $N_{++}$ in both the first growing season ($F_{19.88}$=12.31; $p<0.05$) and the second growing season ($F_{19.88}$=9.08; $p<0.05$), while $W_{++}$ had a significant effect on leaf presence when interacting with $N_{+}$ in the first growing season ($F_{19.88}$=16.81; $p<0.05$) and $N_{++}$ in the second growing season ($F_{19.88}$=11.81; $p<0.05$).

In the first growing season, the percentage of yellow leaves with no water addition were higher when there were no nutrient additions ($W_0N_0$) ($F_{19.88}$=6.33; $p<0.05$). The percentage of yellow leaves was at the lowest when $W_{+}$ was interacting with $N_{++}$ ($F_{19.88}$=7.34; $p<0.05$). The same trend was observed in the second growing season. Percentage fruit presence was also significantly higher when $W_{+}$ was interacting with both $N_{+}$ and $N_{++}$ in the second growing season ($F_{19.88}$=3.29; $p<0.05$) and ($F_{19.88}$=12.99; $p<0.05$). The number of leaves had a similar growth pattern, with $W_{+}N_{++}$ recording the highest leaf numbers in both growing seasons ($F_{19.88}$=10.71; $p<0.05$). There were no significant effects under the control water treatment

($W_0$) on fruit production and the average number of leaves produced at the different nutrient additions in both growing seasons during the study.

## 2.4 DISCUSSION

As hypothesized, water and nutrient additions caused a shift in the timing and duration of the phenological stages of coppicing trees. Adding water and nutrients resulted in higher leaf numbers and also caused leaf presence to extend later into each subsequent growing season, favouring growth and increasing the photosynthetically active period in supplemented trees. The effects of adding water and nutrients in the second growing season were not clear cut or as high as the first season response showed. Results also showed that a combination of high water and nutrient ($W_{++}N_{++}$) additions did not result in, for example, the highest fruit presence or the highest leaf presence in resprouting trees, as one would probably expect. Instead low water and high nutrient additions ($W_{+}N_{++}$ treatment) appeared to have the highest positive effect on the timing of different phenophases. The data (Fig. 2.2) indicate a close relationship in the timing and duration of phenological stages. For example, higher leaf bud initials during the dry season also translated to higher leaf presence as well as higher mean number of leaves for supplemented trees. Also, the $W_0N_0$ treatment had the lowest leaf presence during the dry season and this translated to the highest percentage of yellow leaves during the same period.

The timing of the different phenological stages followed seasonal variations, with changes in rainfall distribution strongly influencing the changes in the timing of phenological stages. Peak levels for leaf bud and leaf presence were obtained during the growing wet seasons (November-April) and maximum (100 %) leaf discolouration obtained in the dry dormant seasons (May-October). Bud presence dropped faster for trees that were not supplemented with either water or nutrients, while supplemented trees showed a slower decrease in bud presence towards the end of the first growing season (April 2011). The same trend was observed for leaf presence under both water and nutrient additions, with supplemented trees reaching low figures of 10 % in leaf presence and bud presence in the dry season compared to 0 % in trees that were not supplemented. Supplemented trees showed no increase in the date of leaf presence (leaf flush), showing a strong deterministic regrowth pattern. Leaf discolouration started occurring earlier for trees that were not supplemented with water and nutrients (45 % by March 2011) compared to trees supplemented with water and nutrients (10

% by March 2011). Trees that were not supplemented with either water or nutrients for this study were similar in terms of timing of phenophases to *T. sericea* in Hwange National Park, Zimbabwe (Childes, 1989). There, the proportion of leaf buds was shown to decrease as the wet season progressed for *Baikiaea plurijuga* (Harms) and *Guibourtia coleosperma* (Benth) with late dry season leaf flushing observed for *G. coleosperma* and *T. sericea* in Zimbabwe (Childes, 1989).

Fruit presence did not occur until almost two years following resprouting in supplemented trees. It was highest for $W_+N_{++}$ additions, while $W_0N_0$ trees did not produce any fruits. It is proposed that during the first year after resprouting, trees could not produce fruits because allocation of resources was more towards recovery and development of vegetative organs that were important for carbon assimilation than fruits. This is supported by higher leaf numbers in trees supplemented compared to unsupplemented trees. Resprouting trees would have used a lot of energy within that first year if fruits had been produced, as proposed by Bellingham and Sparrow (2000), Bond and Midgely (2001) and Clarke et al. (2012). In avoiding producing fruits, such a regrowth pattern instead initially focused resources more on growth in the process, rather than investing resources on producing expensive reproductive parts such as fruits and flowers. Possibly, there may always be enough stored carbon reserves to suggest that fruit production in resprouting trees after a period of more than a year is not limited by water and nutrient availability.

The interaction between the low water and high nutrient ($W_+N_{++}$) treatments had the highest leaf bud presence (20 %) at the beginning of the wet season months (September-October 2011), while control ($W_0N_0$) trees had 0 % during the same period. The same trend was observed for leaf presence with $W_+N_{++}$ additions recording highest leaf production at 30 % at the beginning of the wet season months (September-October) compared to 0 % for $W_0N_0$ trees. Higher leaf presence at the end of the dry season for supplemented trees signalled late dry season leaf flushing in this study, which was dependent on the reserves of water and nutrients. Late dry season leaf bud presence (about 20% between September and October 2011) caused higher leaf presence in supplemented trees as the dry season finished. This may have resulted in supplemented trees developing a strategy to make use of most of the nutrients available with the onset of the first rains and, therefore, assimilate as much carbon as possible.

Late dry season leaf presence meant that supplemented trees were ready to start photosynthesizing the moment conditions became suitable. Also, the timing of the phenophases can be explained by seasonality because in savannas, flushing and flowering occur in the warmer and rainy months, and also when days are longer (Childes, 1989). This is in contrast to the reduction in leaf production and survival that are more frequently observed in the dryer and colder months and when days are shorter (Childes, 1989). Although not measured in this study, increase in soil moisture (Borchert, 1994) has been suggested to increase tree water storage capacity (Broadhead et al., 2003). Therefore, with this in mind, increasing soil moisture levels through water addition for the current study may have increased tree water storage, allowing stored water to act as a buffer against low soil moisture levels in the dry season. Although not all trees store water equally well, such buffering activity may have consequently contributed to maintenance of higher leaf presence and higher mean leaf numbers in trees supplemented compared to unsupplemented trees. The buffering may have been an advantage in causing supplemented trees to flush leaves (record leaf presence) earlier (September 2011) and therefore to initiate photosynthesis earlier before the beginning of the growing season (October 2011) compared to $W_0N_0$ trees that had leaf flush later compared to supplemented trees. These results also imply that in extending bud presence and leaf presence into the early dry season, supplemented trees, such as $W_+N_{++}$ trees, extended their growing season further into the dry season compared to $W_0N_0$ treatment trees.

The higher number of leaves in supplemented trees (especially for the $W_+N_{++}$ treatment) into the dry season likely had implications on carbon assimilation. The extension of leaf presence and delay in leaf discolouration in supplemented trees means that trees may have been photosynthesizing well into the dry season and therefore accumulating more carbon compared to $W_0N_0$ trees, while also exploiting water pulses (Scholes and Walker, 1993). In an ecosystem where competition for food is high and resources for plant growth are limited, such early leaf flushing would be vital for goats and even grazers. New leaves can be a major source of food at a time when most herbivores struggle to fulfil their nutritional needs, especially at the end of the dry season. Therefore, this would ensure that herbivores are assured of a food source, because cattle have been shown to browse more than graze during the dry season (Katjiua and Ward, 2006a).

Chapin III (1991) suggested that plants adapted to low-resource environments tend to grow slowly, even when provided with an optimal supply and balance of resources previously lacking. He further stated that this slow growth reflects a low capacity of such plants to capture resources even under optimal conditions. Following this reasoning, it can be hypothesized that the addition of high nutrients and water in this current study did not yield expected results of, for example, increasing leaf numbers and fruit presence because resprouting trees were probably allocating more resources towards survival of existing organs, and also storage than towards furthering growth (Mooney and Gulmon, 1982). Similar results were found when an increase in soil moisture levels was shown to be correlated to shifting phenological patterns to either later in the dry season or later in the wet season (Borchert, 1994, Sheffield et al., 2003). An increase in leaf flushing was reported before the initial rains in *Melia volkensii* (Guerke) and *Croton megalocarpus* (Hutch) in Kenya (Broadhead et al., 2003); also shown in a savanna woodland dominated by Mimosaceae and Combretaceae trees (Shackleton, 1997, De Bie et al., 1998) and in the drought deciduous ecosystem of the Kalahari region in South Africa (Jolly and Running, 2004).

## 2.5 CONCLUSIONS

This study demonstrated that adding water and nutrients to coppicing trees increases leaf bud and leaf presence late in the wet season and early into the dry season. Although produced in low quantities, fruit presence was influenced more by nutrients than water addition. Unsupplemented trees changed leaf colour earlier and had very low leaf presence in the dry seasons. Water and nutrient addition had significant positive effects in reducing leaf discolouration while the impact of high water and high nutrient addition was not what was expected. Therefore, from the results and it may be expected that a savanna tree species such as *T. sericea* can adjust its phenology and adapt well to further rapid changes associated with climate change or fluctuations in the distribution of rainfall. Such information can be vital in establishing the competitive ability of *T. sericea* in a multiple-species ecosystem affected by environmental changes. Therefore, a longer period in which trees remain green implies that trees are assimilating carbon for a longer period of time. This has consequences on the growth rate and recovery of cut trees. Additional studies that can examine changes in temperature, rainfall and resprouting tree water status, and relate these to changes in phenological behaviour can add more knowledge to work already done in this study.

## CHAPTER 3

## EFFECTS OF WATER AND NUTRIENT ADDITION ON THE COPPICE RESPONSE OF CUT *Terminalia sericea*


## ABSTRACT

The ability of a woody plant to coppice and remain vigorous largely depends on the severity of the disturbance with reference to above-ground biomass, the availability of water and nutrients, and also on the availability and mobilization of resources above- and below-ground. In savannas, there is limited information about the role played by resource limitation on the recovery of cut trees. This study investigated the effects of water and nutrients supplementation on the coppice growth responses of resprouting cut trees in a semi-arid savanna in South Africa. Cut trees were exposed to different levels of water and nutrient (nitrogen and phosphorus) supplementation over a period of two years in a factorial experimental design. Adding water and nutrients significantly increased shoot diameter, shoot length, and resprouting ratio for the initial 12 months after cutting, with no significant effects on stem non-structural carbohydrate levels recorded. Such a response pattern suggests that initial growth of resprouting shoots may be strongly resource-limited in this system. In general, however, the strength of the effects of addition decreased after 12 months of addition. If practicing rotational tree harvesting, trees resprouting in resource-poor locations need a longer resting period to recover lost height and thickness after cutting.



*Key words*: Water, nutrients, resprouting, supplementing, replenishing, total non-structural carbohydrates

## 3.1 INTRODUCTION

Plants are subjected to various forms of disturbances and stresses that affect their growth, production and survival. As a result, coppicing (resprouting) has been proposed to be central to the survival and resilience of trees in disturbance-prone systems (Bellingham and Sparrow, 2000). Coppicing can be defined as the production of vegetative shoots at the base of the stem or sprouts arising from a stump (Hardesty, 1984, van Wyk and van Wyk, 1997, Laureysens et al., 2003). The result is the emergence of new shoots from the stump or roots. Coppicing has important implications for population dynamics and vegetation processes such as the rate of carbon assimilation and its duration. The active management of coppice has been suggested as one possible means of enhancing firewood production and species persistence in savanna ecosystems prone to disturbances, because little is known about the factors that shape and determine coppice response and ecosystem recovery (Shackleton, 1993, Shackleton, 1997, Hardesty and Box, 1988, Kozlowski, 2002, Neke et al., 2006, Kaschula et al., 2005a).

In the process of recovering lost biomass after a disturbance event and also ensuring sustainable production in a savanna ecosystem, interactions between climate, soil nutrient status, fire, human activity and herbivore pressure have the potential to limit the full recovery of a disturbed ecosystem (Hoffmann et al., 2002, Holdo et al., 2009). Thus there is a need to understand the implications of the use of ecosystem resources interacting with climatic factors, such as rainfall variation. This is because such factors influence edaphic properties such as soil moisture availability and therefore the recovery of cut trees through coppicing. An understanding of such interactions will have further management implications for the long-term productivity and sustainability of savanna woodlands as utilization and fluctuations in the amount of available moisture shape the recovery of trees (Neke, 2004, Neke et al., 2006, Pote et al., 2006).

An increase in soil nutrient and water availability affects tree regrowth through increasing growth rates after disturbances and determining allocation to storage in resprouting organs (Cruz et al., 2002, Sankaran et al., 2008). This is supported by Cruz et al. (2002) who suggest that resprout growth can be limited by the low amount of moisture during the early stages of regeneration after a disturbance. Water availability was shown to be positively correlated with regeneration after *Acacia tortilis* (Forssk) was exposed to a browsing event in Tunisia

(Noumi et al., 2010). At times, very high soil moisture conditions negatively impact tree regrowth. For instance, in North America, stomatal conductance of two poplar clones (*Populus tristis* Fisch and *P. balsamifera*) was reduced when stem cuttings were exposed to very high soil moisture conditions (flooding). Positive water effects on tree regrowth were also demonstrated when there were increased growth rates, greater number of resprouting shoots and higher shoot-lengths in resprouting *Populus tristis* Fisch and *P. balsamifera* supplemented with water compared to trees not supplemented (Dickmann et al., 1996).

Nutrients play a key role in replenishing depleted stored nutrient reserves of plants after a disturbance such as tree cutting (Bowen and Pate, 1992), and their interaction with moisture might affect coppice regrowth (Castell and Terradas, 1994). Since nitrogen (N) in the remaining plant parts may be used for reconstructing new tissue, adding more N through fertilizer application may also result in the excess of nitrogen being stored in roots for later use after a potential disturbance (El Omari et al., 2003, Kabeya and Sakai, 2005). This was demonstrated when fertilized resprouting *Erica australis* L. Com. Trees were found to grow faster and produce higher biomass than un-fertilized trees two years after fertilizer application in Spain (Cruz et al., 2002). Nutrient addition also increased both diameter and height of *Betula pendula* Roth. and willow (*Salix* spp.) stands in Finland (Hytonen and Kaunisto, 1999).

Although very high N levels may reduce growth through toxicity effects (Jaoudé et al., 2011), adequate nitrogen levels induce plant regrowth after a disturbance (Kabeya and Sakai, 2005). N supply results in higher concentrations of photosynthetic enzymes, which in turn cause a higher rate of photosynthesis in leaves (Chapin III, 1991). At the other extreme, high fertilizer application in a poplar short rotation plantation in Italy reduced soil respiration through reducing specific root respiration rate, root biomass, root biomass turnover and the quantity of decomposed aboveground litter fall in resprouting trees (Jaoudé et al., 2011). The same study also showed that high fertilizer application may lead to a reduction in mycorrhizal respiration or turnover of carbon inputs from root exudation and a reduction of microbial respiration associated with decomposition processes, reducing overall plant growth.

In savannas, resprouting is common (Bond and Midgley, 2001). It has been suggested that stored carbohydrate reserves and surviving meristems are the most important resources controlling resprouting after disturbances (Kabeya and Sakai, 2005, Bond and Midgley, 2001,

Bellingham and Sparrow, 2000). For example, higher levels of starch storage were found after fires in resprouting trees and seedlings in South-west Australian Epacridaceae and *Erica* species of the Cape Floristic Region (Bell and Ojeda, 1999, Bell et al., 1996). In *Quercus ilex* L. seedlings, resprouting was limited when seedlings were grown under N-limited conditions, even after accumulating high levels of total non-structural carbohydrates (TNC) (El Omari et al., 2003). TNC concentration in resprouting *Quercus crispula* Blume was positively correlated to resprouting shoot length and leaf number (Kabeya et al., 2003). Differences in soil nutrient levels also have an effect on the stored carbohydrate reserves. For instance, starch concentrations in roots of coppicing *Salix viminalis* L., were in trees that received higher levels of nitrogen compared to plants that received lower levels (Fircks and Sennerby-Forsse, 1998).

Surprisingly, little is known about the regeneration strategies of woody species in tropical and sub-tropical savannas (Neke, 2004, Pote et al., 2006) because most studies have focused on ecosystems that differ markedly from African savannas, such as temperate ecosystems (Wilson, 2002). Such ecosystems differ in terms of the seasonality and distribution of rainfall, tree population structure, moisture levels and tree densities. Most studies on tree responses have also been strongly focused on the effects of varying resource levels on seedlings growth and survival (Kraaij and Ward, 2006, Wilson and Witkowski, 1998, Scogings and Mopipi, 2008, Wendler and Millard, 1996, Druege et al., 2000, Cheng and Fuchigami, 2002), rather than mature and established trees. In savannas, there is a lack of information on how water and nutrient availability interact to influence a tree's regrowth and carbon storage capacity after cutting. Knowing such information would provide clues for understanding mechanisms underlying a tree's regrowth strategies after a disturbance. It is also important to understand water and nutrient effects on tree regrowth so as to evaluate how changes in resources may impact a community exposed to different disturbance types and fluctuations in resource availability.

This study was carried out to investigate how water and nutrients interact to influence tree regrowth as well as the TNC storage capacity after cutting. The following question was asked: how do the varying levels in water and nutrient levels influence the coppice response and stem stored TNC reserves of cut trees? It was hypothesized that supplementing resprouting trees with water and nutrients would increase coppice response and would also result in higher TNC levels in supplemented trees compared with unsupplemented trees.

## 3.2 METHODS

### 3.2.1 Study site

The study site is described in detail in Chapter 1.

### 3.2.2 Study species

The study species is described in detail in Chapter 1.

### 3.2.3 Experimental design

The experimental design for this experiment is explained in detail in Chapter 2.

### 3.2.4 Morphological measurements

From each resprouting stump, the following variables were measured per stump on a monthly basis:

(i) total number of shoots, (ii) resprout shoot diameter and (iii) resprout shoot length. For (ii) and (iii), the leader shoot showing the greatest length was selected and marked using strings.

Shoot production was calculated as the number of shoots produced per unit area of stump basal area. The tree's original stump diameter was measured at the beginning of the experiment and used together with resprout shoot diameter to calculate the resprout shoot diameter as a ratio of the original tree's stump diameter. This was termed the resprout ratio.

### 3.2.5 Total non-structural carbohydrate (TNC) sampling and determination

All trees exposed to treatments as illustrated in Fig. 2.1 (Chapter 2) were sampled for stem TNC levels twice during the course of the study:

i. After a year of treatment application and at the end of the beginning of the wet season (September 2011), and

ii. After 18 months of treatment application and at the end of the wet season (April 2012).

Trees were sampled using an increment borer (4.3 mm diameter) to extract two 3 cm-long wood cores from the stumps. Stem cores were taken about 10 cm above ground because the most evident effects of vegetation removal are evident in roots and lower parts of the stem (Garcia et al., 2001). Before storing the cores in airtight plastic bottles, the outer tree bark was immediately removed from cores after sampling. The core samples were then bottled and placed inside a freezer. Drying of samples was done at 65 $^{0}$C for two days and then samples ground using a coffee grinder before finer grinding through a 40-mesh Wiley Mill screen in the Mack lab at the University of Florida, USA. It was assumed that constant weight was reached during the two day drying period. A composite sample was obtained after grinding.

TNC was the determined using the anthrone method described by Edwards et al. (2011) on a dry weight basis. Ground samples were washed four times with hot ethanol to extract soluble sugars, and the supernatant was stored for sugar determination, later. The remaining solid residue was washed twice with 52 % perchloric acid to solubilize and extract the starch. The starch solution was reacted with a mixture of anthrone and hydrochloric acid to hydrolyse the starch to glucose. Absorption at 620 nm was determined using a spectrophotometer (Edwards et al., 2011), and absorbances were regressed against readings from a set of standard solutions of glucose. A correction factor of 0.9 was used to convert glucose equivalents to starch. Total non-structural carbohydrates measured in this study were the sum of the soluble fraction (glucose and sucrose) and the insoluble fraction (starch).

### 3.2.6 Confounding effects of browsing

Due to the presence of antelope at the study site, the possible effects of browsing on the response of trees after cutting were very high. The proportion of shoots that were browsed was estimated by counting the total number of shoots resprouting per stump at the time of recording morphological changes. The total number of shoots browsed was also counted. The browse proportion was then calculated as the number of browsed shoots relative to the total number of shoots resprouting per stump, and expressed as a percentage. The browse proportion was compared across all the treatments for the duration of the study.

### 3.2.7 Statistical analyses

The data were partitioned into two 12-month time intervals to test for the effects of water and nutrient additions on harvested trees using linear mixed models implemented in SAS with proc GLM. The September 2010-September 2011 interval represented the end of the initial 12 months while the September 2011-September 2012 interval represented the second 12 month period. Tree responses were compared across treatments for each 12 month interval using Tukey's *post hoc* test to compare means among treatments at $\alpha<0.05$. To control for the influence of site on the monitored tree responses, site was included in the analysis as a random effect. When significant water by nutrient interactions were observed, indicating non-additivity, simple effects were evaluated on the effects of water additions for each nutrient level, and vice-versa. Where necessary, data were log-transformed to fit assumptions of normality.

## 3.3 RESULTS

### 3.3.1 Interactive effects on the coppice response

The initial analysis on the data showed that site had a significant effect on the response of trees to resource addition. Results presented here were obtained after controlling for the influence of site on the response of trees. A year after cutting, under no nutrient addition ($N_0$), shoot production was significantly lower when water was highest ($W_{++}N_0$), but highest when water was low ($W_{+}N_0$) and control ($W_0N_0$). No significant differences were observed two years after trees were cut (Fig. 3.1A). Under no water addition ($W_0$), shoot production was highest under double ($W_0N_{++}$) and no ($W_0N_0$) nutrient additions and lowest under low nutrient additions ($W_0N_{+}$) in September 2011. For shoot diameter in September 2011 under no nutrient addition, it was highest under high water addition ($W_{++}N_0$) and lowest at low water ($W_{+}N_0$) and no water levels ($W_0N_0$). For no water addition, shoot diameter was significantly higher in both nutrient addition levels (*i.e.*, $W_0N_{+}$ and $W_0N_{++}$).

In the second year after cutting, under no nutrient addition, shoot diameter was significantly higher when water was double ($W_{++}N_0$). Under no nutrient addition in September 2011, shoot length was significantly higher when water was highest ($W_{++}N_0$), while there were no significant differences in September 2012. Under no water addition, shoot length was

significantly higher at low nutrient addition ($W_0N_+$), while no significant differences in shoot length in September 2012. In September 2011 under no nutrient additions, resprout ratio was significantly higher when water addition was highest ($W_{++}N_0$), with the same trend observed in September 2012. Under no water additions in September 2011, resprout ratio was lowest when there were no nutrient additions ($W_0N_0$), while in September 2012 resprout ratio was highest when nutrient levels were highest ($W_0N_{++}$) (Fig. 3.1D).

In September 2011, low water and low nutrient addition ($W_+N_+$) and no water and high nutrient addition ($W_0N_{++}$) recorded the highest shoot production (Fig. 3.1A), while there were no significant differences in September 2012. Shoot diameter was highly significant under the $W_+N_+$ and $W_{++}N_+$ (Fig. 3.1B) in September 2011, while the lowest shoot diameter values were recorded in the $W_+N_0$ in September 2012. Shoot length was highest in the $W_{++}N_{++}$ treatment after 12 months, while there were no significant differences between $W_{++}N_{++}$ and $W_{++}N_+$ at 24 months (Fig. 3.1C). Resprout ratio was highest in the $W_{++}N_{++}$ and $W_+N_{++}$ treatments after 12 months, while the $W_0N_0$ and $W_+N_0$ had the lowest resprouting ratio after 24 months.

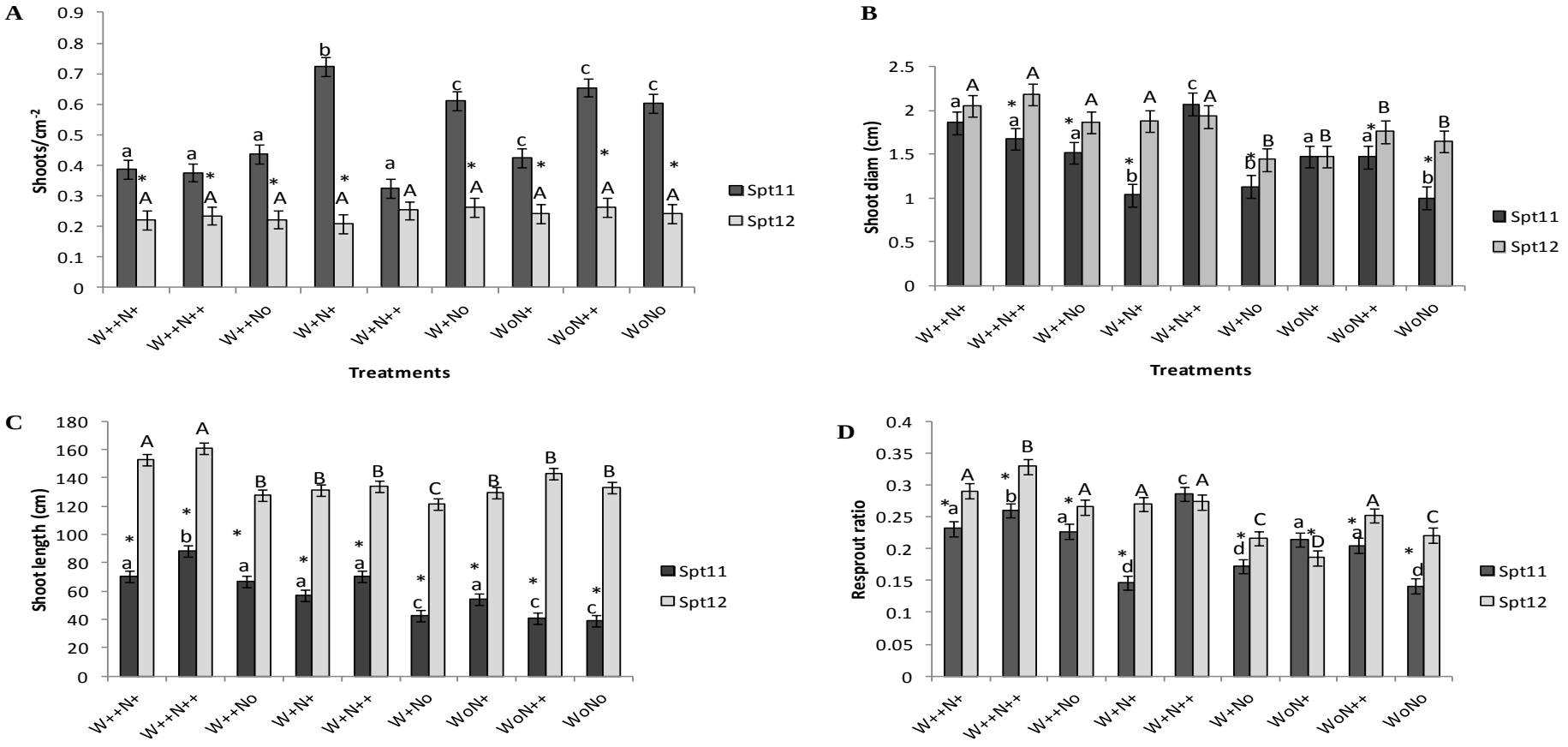
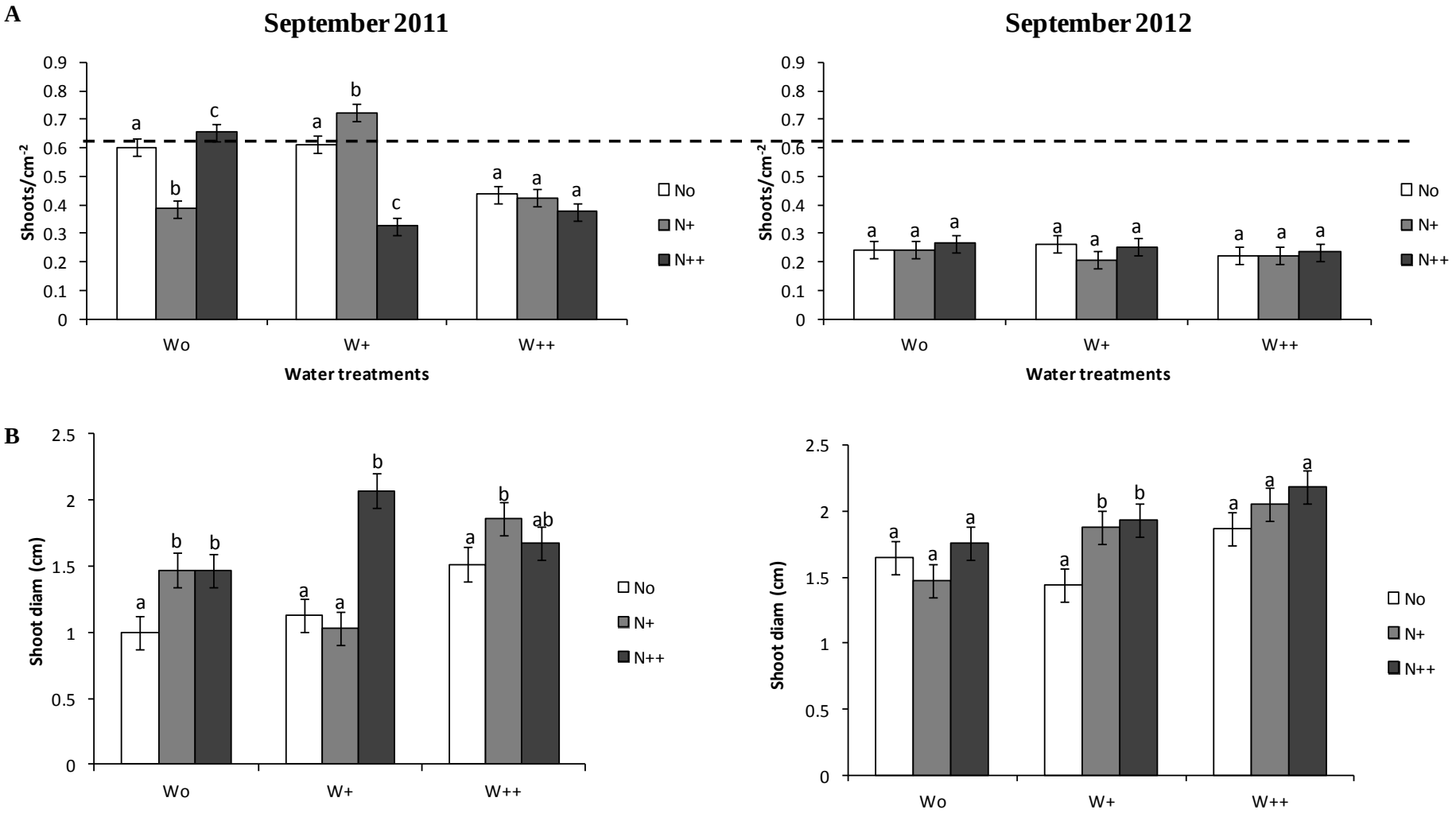



**Figure 3.1.** Effects of water and nutrient addition on A) shoot production, B) shoot diameter, C) shoot length and D) resprout ratio between September 2011 and September 2012. The small letters compare treatment effects across Sept. 2011 while the block letters compare effects across Sept. 2012. The asterisks indicate treatment differences between the two time points (September 2011 and September 2012).

### 3.3.2 Effects of water and nutrient additions on coppice response

In September 2011, 12 months after trees were cut, in the no water addition, shoot production was significantly higher in the high nutrient addition treatment ($W_0N_{++}$) than the other nutrient treatments, while in the low water addition treatment ($W_+$) shoot production was lowest under high nutrient addition ($W_+N_{++}$) (Fig. 3.2A). There were no significant differences in shoot production in the $W_{++}$ treatment in September 2011. The second year after cutting (September 2012), there were no significant differences in shoot production in all water treatment levels. A year after trees were cut, under no water addition, there were no significant differences between $W_0N_+$ and $W_0N_{++}$ for shoot diameter, with $W_0N_0$ recording the lowest shoot diameter. For the $W_+$ treatment, shoot diameter was highest under the $W_+N_{++}$, with significantly lower shoot diameter recorded for the $W_+N_0$ and $W_+N_+$. For the $W_{++}$ treatment, $W_{++}N_+$ had significantly higher shoot diameter than $W_{++}N_0$, although this value was not significantly higher than diameter under the $W_{++}N_{++}$. The second year after cutting, there were no significant differences in shoot diameter in the $W_0$ and $W_{++}$ treatments, while in the $W_+$ treatment, $W_+N_+$ and $W_+N_{++}$ recorded the higher shoot diameter than $W_+N_0$ (Fig. 3.2B).

A year after cutting, under no water addition, shoot length was highest under no nutrient addition ($W_0N_0$); in both the $W_+$ and $W_{++}$ treatments, shoot length was lowest at the high nutrient addition level ($W_+N_{++}$). The second year after cutting, under no water addition, shoot length was highest under high nutrient addition ($W_0N_{++}$), while under $W_+$ and $W_{++}$, shoot length was lowest under no nutrient additions ($W_+N_0$ and $W_{++}N_0$). A year after cutting, resprout ratio was significantly lowest for $W_0N_0$, and highest under high nutrient additions with both low and high water additions. In September 2012 under no water addition, resprout ratio was lowest for $W_0N_+$. Under the $W_{++}$ water treatment, resprout ratio was highest under high nutrient addition ($W_{++}N_{++}$) (Fig. 3.2D).


A
September 2011
September 2012
Shoots/cm-2
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
b
c
a
b
c
a
a
a
a
a
a
a
a
a
Wo
W+
W++
Water treatments
No
N+
N++
B
Shoot diam (cm)
2.5
2
1.5
1
0.5
0
a
b
b
a
a
b
a
b
ab
a
a
a
b
b
a
a
a
Wo
W+
W++
No
N+
N++

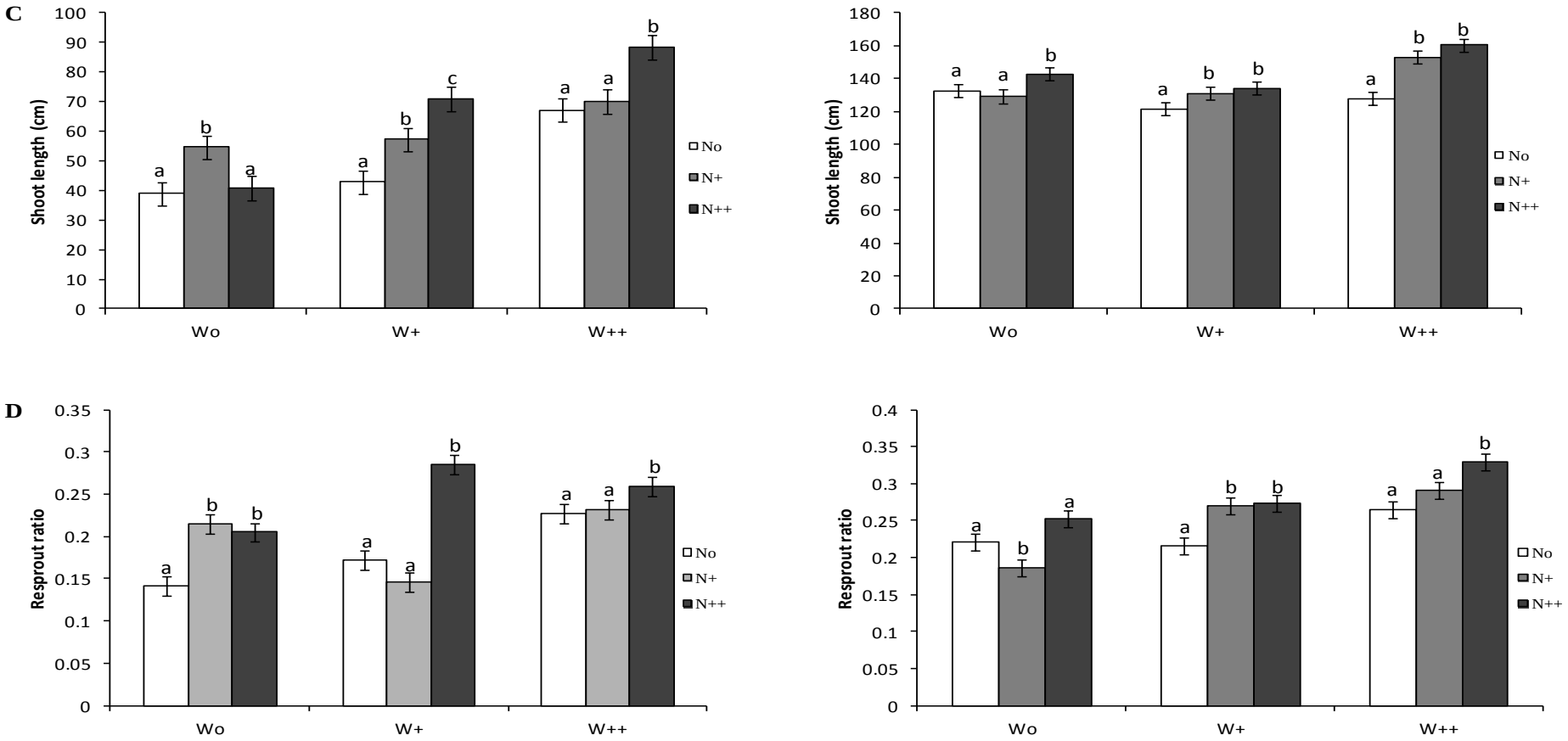



**Figure 3.2**. The effect of water and nutrient addition on A) shoot production (calculated as number of shoots per unit area of original stump circumference), B) shoot diameter, C) shoot length and D) resprout ratio between September 2011 and September 2012. Bars with different letters indicate significant differences within a water treatment. The dashed line in A indicates the drop in shoot production across treatments and between the two time points (September 2011 and September 2012).

### 3.3.3 Effect of water and nutrient additions on stem TNC levels

Supplementing cut trees with water and nutrients had no significant effect on stem TNC concentration for both time points (September 2011 and April 2012) (Table 3.1). Uncut trees recorded significantly higher TNC levels compared to unsupplemented trees ($W_0N_0$) in September 2011.

**Table 3.1**. Changes in TNC (mg $g^{-1}$ DW) levels between September 2011 and April 2012 as a function of water and nutrient additions. Sample means are represented with standard deviations. Letters are for treatment comparisons within each time-point. Different letters indicate significant differences within one time point.

| | Treatment | September 2011 | April 2012 |
|---|---|---|---|
| Interactive | $W_0N_0$ | $52.37^{a}$ (10.8) | $38.01^{a}$ (11.9) |
| | $W_0N_{++}$ | $51.96^{a}$ (13.5) | $24.79^{a}$ (10.7) |
| | $W_0N_{+}$ | $60.71^{ab}$ (16.2) | $34.44^{a}$ (12.5) |
| | $W_{++}N_0$ | $68.62^{ab}$ (13.7) | $38.96^{a}$ (7.8) |
| | $W_{++}N_{++}$ | $65.00^{ab}$ (13.8) | $46.54^{a}$ (17.4) |
| | $W_{++}N_{+}$ | $65.77^{ab}$ (39.2) | $29.2^{a}$ (17.2) |
| | $W_{+}N_0$ | $63.80^{ab}$ (19.3) | $30.88^{a}$ (21.8) |
| | $W_{+}N_{++}$ | $66.67^{ab}$ (10.1) | $43.6^{a}$ (19.9) |
| | $W_{+}N_{+}$ | $58.16^{ab}$ (12.9) | $44.88^{a}$ (19.6) |
| | Non-harvested* | $74.48^{b}$ (24.3) | $43.09^{a}$ (14.4) |

* Non-harvested refers to trees that were not cut and not supplemented with either water or nutrients at the time of sampling.

### 3.3.4 Confounding effects: browsing

Browsing (percent of shoots browsed per stump) on resprouting trees was widespread in both growing seasons during the study, although it was lower in the second compared to the first (Fig. 3.3). There were no significant differences ($F_{10.259}$= 1.57, p=0.167) in browsing proportion across all treatments during the study.

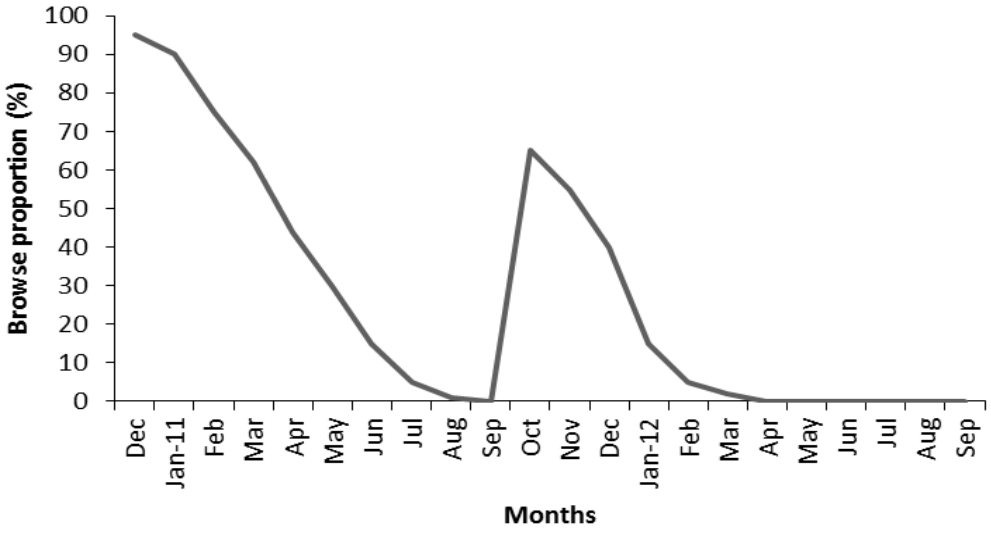



**Figure 3.3.** The changes in browsing proportion on resprouting trees supplemented with water and nutrients from December 2010-September 2012.

## 3.4 DISCUSSION

This study set out to investigate the effects of adding different levels of water and nutrients on the coppice response and replenishment of starch storage levels of cut *T. sericea* trees. It was hypothesized that adding water and nutrients to cut trees will increase the coppice response and stem TNC levels. While water and nutrient addition had no significant effects on shoot production, the addition, as hypothesized, resulted in increases in resprout shoot diameter and shoot length, although not always significantly different from unsupplemented trees. Contrary to the hypothesis, adding water and nutrients had no significant effect on stem TNC levels at both time-points, September 2011 and April 2012.

### 3.4.1 Effects of water and nutrients on coppice response of cut trees

High additions of water and nutrients to cut trees had a significant effect on shoot production after 12 (but not after 24) months. When interacting with nutrient addition, increasing water levels appeared to limit shoot production after 12 months, with $W_{++}N_{++}$ trees having significantly lower shoot production compared to $W_0N_0$ trees. There were significant differences among treatments in 2012. The differences in the response of trees to resource additions can possibly be attributed to the higher amount of rainfall received in the 2012 rainfall season compared to the 2011 season. The higher rainfall received may have contributed to treatment effects being non-measurable in 2012.

To explain tree responses to water treatments after 12 months, the relationship between shoot production and resprout shoot length can be used to establish a shift in coppicing strategy for supplemented trees. A weak significant negative correlation ($p<0.05$, $r= -0.13376$, results not shown) for the $W_{++}N_{++}$ treatment implies that trees may have been investing resources in maintaining fewer shoots that were both thicker and longer. This is further supported by that average shoot diameter and average shoot length were almost double compared to $W_0N_0$ treatment trees. In comparison, trees from the control treatment ($W_0N_0$) invested in many shoots that were thinner and shorter. Alternatively, this pattern could also be interpreted as generally the speeding up of the resprouting process because resprouting trees start off with many small shoots and, over time, tend to invest in fewer, larger shoots. Therefore, the effect of water and nutrients could have been to speed up the rate at which this shift in allocation happens. Similar results were found when shoot production increased by 23 % after water and nutrient addition is *Pinus taeda* L. (Albaugh et al., 2004). Similar nutrient addition effects have been reported when there was an increase in biomass and above ground shoot production in *P. taeda* L., *P. elliottii* and *Liquidambar styraciflua* L. (Cobb et al., 2008, Albaugh et al., 2004) and also in *Populus deltoids* Bartr. and *Planatus occidentalis* L. (Coyle and Coleman, 2005).

The average shoot length and shoot diameter for trees supplemented with water and nutrients were significantly higher between September 2011 and September 2012. The highest shoot diameter was in the $W_{++}N_{++}$ treatment after 12 and 24 months of addition, with shoot length following a similar trend. Under high soil moisture conditions, there is a general increase in sprouting vigour leading to the transfer and supply of growth promoters such as auxins, cytokinins and gibberellins (Ferm and Kauppi, 1990). This is not the case when there is very low soil moisture (Liu and Dickmann, 1996). Consequently for this current study, adding water may have led to an overall increase in cell division and resprouting shoots exhibiting stronger apical dominance resulting in higher average shoot diameters and average shoot lengths compared to $W_0N_0$ trees.

It has been proposed that fertilizer addition increases foliar N concentrations as well as chlorophyll levels, leading to increased photosynthetic efficiency (Scott et al., 2004). Therefore, nutrient additions in this current study may have increased photosynthetic enzyme levels and stomatal conductance resulting in an increase in carbon assimilation, as suggested by Ewers et al. (1999). Nutrient additions possibly resulted in increased leaf area (Ewers et

al., 1999), increasing the surface area for elevated photosynthetic activity in the process. This may have contributed to an increase in shoot elongation and shoot thickness. Fertilizer application, together with coppicing ability of resprouting trees, has been shown to increase fine root biomass (Dickmann et al., 1996, Jaoudé et al., 2011). Such an increase improves the absorption capacity of resprouting trees, leading to improved growth rates. Using this line of thinking, it can be proposed that water and nutrient addition in this study might have activated microbial activity associated with decomposition processes (Scott et al., 2004).

Tree diameter and height has been demonstrated to increase in trees as a result of nutrient addition (Coyle and Coleman, 2005, Castell and Terradas, 1994, Cobb et al., 2008, Dickmann et al., 1996). Results from this current study are similar to work by Osman and AboHassan (2010), when shoot production and resprout shoot length increased after the addition of N and P to *Rhizophora mangle* L. (Lovelock et al., 2004). In addition, current findings are also supported by results from the addition of nitrogen to thinned *P. taeda* that increased productivity, stand biomass as well as diameter and length (Sayer et al., 2004). However, results from this study are in contrast with work on *Arbutus unedo* Carl when there were no differences between fertilized and non-fertilized tree resprouts in relative height growth rate (Castell and Terradas, 1994). Also, irrigation did not influence any resprouting response in *Planatus occidentalis* L. and *P. taeda* (Coyle et al., 2008).

An overall reduction in the number of shoots for all treatments at the beginning of the wet season in September 2012 implies that there was self-thinning. Between September 2011 and September 2012, there was over 50 % reduction in the number of shoots in all treatments. While self-thinning could be viewed as a way of reducing high respiration demands associated with high leaf material, this growth pattern was observed even on supplemented trees. While self-thinning is more likely to be controlled by whether a tree has enough resources to attempt to grow into a tall adult tree, findings from this study could possibly mean that resource availability does not necessarily control self-thinning, *i.e.*, self-thinning may, in fact, be controlled within the trees, and not by environmental factors.

The growth patterns of supplemented and unsupplemented trees were different, with fewer, thicker and longer shoots for supplemented trees compared to unsupplemented trees which had many, thin and shorter shoots. While biomass production was not measured at the end of this study, biomass production might have been the same at the end of the experiment. This

point is supported by a value which indicates biomass production (results not shown) that was calculated as the product of the number of shoots produced and the shoot length of each monitored shoot. This value indicated no significant differences (results not shown) across treatments. This suggests that even with differing growth patterns, allocation towards biomass production might have been the same across all treatments in this study.

### 3.4.2 Effect of water and nutrients on stem TNC levels

Adding water and nutrients had no significant effect on stem TNC levels at both time points. This was surprising given that an increase in soil moisture and nutrient levels through resource additions extended leaf survival early into the dry season (Chapter 2), thereby extending the period of photosynthesis for trees supplemented. Such an extension of the period of photosynthesis would have, as one would assume, allowed maintenance of greater leaf area, and hence higher carbon assimilation, in trees supplemented. This would have been in comparison to unsupplemented trees which had leaf survival that only lasted towards the end of the growing season, thereby photosynthesizing for a shorter period. Given this, the expectation was that these phenological shifts in the dry season (September 2011) for supplemented trees would extend the photosynthetically active period to enable supplemented trees to not have to rely on stored reserves for regrowth compared to unsupplemented trees. Since TNC concentrations in tree tissues are considered a measure of carbon storage or a demand for growth (Druege et al., 2000, Kabeya and Sakai, 2005, Sakai and Sakai, 1998), the lack of significant effects the addition of water and nutrients had may indicate that the carbon demand in resprouting trees, even for supplemented trees which had a longer period to photosynthesize, was exceeding the supply from photosynthesis alone, as stored TNC were mobilized for growth. Resprouting trees appear to continuously draw from stored reserves.

Findings from this study are different to work on *Quercus crispula* Blume, where root TNC levels were higher after resource addition (Kabeya and Sakai, 2005). Similar to findings from this study, other studies also found that N additions had no effect on carbohydrate reserves in beech (*Fugus sylvatica* L.) (Pahlsson, 1992), while it had little effect on starch levels for Chrysanthemum cuttings (Druege et al., 2000).

Browsing was high during the wet season beginning in December 2010. Browse proportion was lower during the second growing season of the study (from October 2011). This can be

attributed to resprout shoots escaping the browsable height limit, making shoots inaccessible for browsing. Browsing proportion was the same across all treatment. This implies that while browsing may have influenced shoot length and possibly the number of shoots produced as well as total biomass produced, the influence was evenly spread across all the treatments and therefore did not unduly influence the relative differences in the variables measured between treatments.

Water and nutrients were supplemented through addition immediately adjacent to the tree stump. Water addition may have facilitated nutrient uptake, enhancing the ability of fine roots to absorb most of the nutrients added. The mean annual rainfall in the study area (650mm per annum) lies between the upper and lower limits of the study species range. Considering that *T. sericea* adapts well to droughts (Griffiths, 1959), the rainfall in the area is intermediate when compared to the lower limit of the species range. For a tree species adapted to growing in a resource-poor environment, this may mean that the weaker effects of water addition in the second season may have been a result of the study species' allocation of resources towards storage, instead of growth, as suggested by Witkowski et al. (1990). Such allocation may help explain the low effectiveness of high water addition on coppice regrowth during the second season of growth.

## 3.5 CONCLUSION

This study demonstrated that resprouting is water- and nutrient limited in cut trees, and that resource addition does not replenish the stem carbon storage. In particular, there were significant effects of adding nutrients and water on average shoot diameter, shoot length. The results suggest that water is limiting for resprout shoot diameter, length of resprouting plants, but not for shoot production and the stem storage levels. Results from this study thus support the hypothesis that supplementing cut trees with water and nutrients increases coppice growth, but this effect holds primarily only for the first growing season after cutting, with the effect declining over time. Results also suggest that even though a tree supplemented with water and nutrients may end up photosynthesizing for a longer period compared to an unsupplemented tree, this does not necessarily change the tree's reliance on stored carbon reserves for regrowth early in the growing season. Total number of shoots produced displays clear self-thinning and it is interesting to note that water and nutrient additions do not impact this self-thinning. This suggests that it light related or is not plastic with resource availability.

Future research could focus on how adding water and nutrients changes the balance of TNC in roots and stems, and not only the stem TNC as covered in this current study. Cutting of trees at shorter intervals for *e.g.* firewood can be done in environments that have higher water and nutrient levels, because a quicker recovery of lost biomass is expected in resource rich environments compared to resource poor environments.

## CHAPTER 4

## THE COPPICE RESPONSE OF RESPROUTING *Terminalia sericea* TREES IS NEGATIVELY INFLUENCED BY BROWSING


## ABSTRACT

Herbivory, interacting with human activities such as tree felling, can change the structure of the vegetation by reducing tree growth or even increasing tree mortality when pressure is too high on saplings. There is limited information about the effects of herbivory on coppicing trees, with available data reflecting on mature trees and seedlings. In this regard, the effect of subjecting resprouting *Terminalia sericea* trees to a five month period of browsing before excluding browsing, on the coppice response was studied in a semi-arid savanna in South Africa. As trees were regrowing, the coppice response of browsed was then compared with that of trees not browsed. Shoot production was initially higher for trees that were exposed to a period of browsing, but this effect diminished with time. Resprout shoot diameter, shoot length and resprout ratio remained higher through-out the study for trees not exposed to browsing. Leaf stomatal conductance and leaf increment were initially higher for trees browsed, with no significant differences observed as the wet season progressed. Foliar nitrogen and phosphorus were higher for trees subjected to browsing. After disturbances, such tree responses suggest that exposing resprouting trees to browsing initially induces compensatory response in order to recover but this growth reduces as the growing season progresses. Despite an increase an initial increase in shoot production, individual shoot growth is significantly reduced in browsed trees compared to unbrowsed trees.



*Key words*: herbivory, stomatal conductance, resprouting, recovery, disturbances, defoliation

## 4.1 INTRODUCTION

The structure of savanna ecosystems is influenced by climate, soil nutrient status, fire, direct human activities such as tree cutting and indirect activities, such livestock grazing and browsing (Holdo et al., 2009, Hoffmann et al., 2002, Scholes and Walker, 1993, Kennedy and Potgieter, 2003). The indirect human activities determine vegetation composition through strongly influencing the regeneration success of woody species (Wassie et al., 2009, Rendón-Carmona et al., 2009). Since most savanna trees are deciduous, browsing of leaves mostly occurs during the growing season, while twig-biting is especially common during the late dry season or when there is a drought (Rooke et al., 2004). Such browsing contributes significantly towards limiting the recovery of woodlands, through reducing new shoot growth after a disturbance or reducing the survival of germinating seedlings early in the growing season (Scholes and Archer, 1997). Browsing also influences tree structural dimensions through browsing on shoot tips and on lateral shoots, thus reducing vertical growth and foliage density (Pepin et al., 2006). This effect was demonstrated when browsed *Acacia tortilis* (Forssk) trees recorded significantly smaller trunk diameter and tree height compared to unbrowsed trees in Tunisia (Noumi et al., 2010). Wilkinson and Neilsen (1995) in Tasmania showed that severe simulated browsing strongly reduces seedling survival in *Eucalyptus nitens* (Deane et Maiden) and *Eucalyptus regnans* (F. Muell) by 49% and 20% respectively.

The responses of plants to browsing or any other disturbance depend on the genetics of the plants, the frequency of disturbance events, the plant development stage at the time of the disturbance, the specific plant parts browsed, burnt or cut and the prevailing conditions at the time of the disturbance (Bergstrom, 1992, Coley et al., 1985). For conservation purposes, it is important to understand tree responses to disturbances such as herbivory. It is especially important in stressful ecosystems such as savannas where tree growth is negatively impacted by environmental stresses and frequent disturbances (Covelo and Gallardo, 2002). To reduce the effects of herbivory, plants may respond through tolerance, compensation, or induced defense. Compensation is increased plant growth after loss of tissue to herbivores (Gadd et al., 2001, Lehtila and Syrjanen, 1995, Fornara and Du Toit, 2007). Compensatory growth is most likely to occur when resources such as water and nutrients are not limiting, so that plants are able to recover after disturbances (van der Meijden et al., 1988, Lehtila and Syrjanen, 1995, Scogings and Mopipi, 2008).

Several physiological changes are known to occur following browsing or after a form of partial defoliation. These include increases in maximum rates of photosynthesis, increases in photosynthetic capacity per unit leaf area and changes in patterns of carbon allocation in the remaining plant parts (Reich et al., 1993, McGraw et al., 1990). Since plants must maintain movement of water between the soil and leaves (Hetherington and Woodward, 2003), it has been proposed that the control of stomata opening is important in order to balance the trade-off between the amount of carbon assimilated and the amount of water transpired (Beer et al., 2009). Herbivory may also indirectly affect carbon gain by altering traits associated with photosynthetic ability, such as leaf diffusive conductance to water vapour and carbon dioxide (Reich et al., 1993). After defoliation, high stomatal conductance has been proposed to increase photosynthetic rates (Reich et al., 2009, Ayres et al., 2004).

The removal of foliar material reduces radial growth during the current and the next growing seasons in plants (Lavigne et al., 2001). This may result in an increase in leaf nitrogen, related to an elevation in leaf photosynthetic capacity because of the role played by nitrogen rich compounds in carbon dioxide fixation (Reich et al., 2009, Lavigne et al., 2001). Moderate shoot removal increases the growth rate of the remaining or resprouting shoots because of enhanced photosynthetic rates in the foliage (Danell et al., 1994, Lavigne et al., 2001). Shoot removal has also been demonstrated to result in the production of fewer but longer shoots that have larger leaves (Danell et al., 1994, Bergstrom et al., 2000, Hrabar et al., 2009, Du Toit, 1990, Lavigne et al., 2001). In some cases, increases in the frequency of defoliation and severe defoliation have been shown to significantly reduce the growth rate of resprouting trees. For example, defoliation reduced stem height and diameter increment in *Eucalyptus globulis* Labill (Pinkard et al., 2007); and also in *T. sericea* when browsing decreased leaf area, leaf mass and number of resprouting shoots (Katjiua and Ward, 2006a). In other cases though, effects of defoliation are not significant as shown when goat browsing had no significant effects on resprout shoot length in *Acacia karroo* Hayne (Scogings and Macanda, 2005).

A plant may also respond to herbivory pressure by altering the carbon/nutrient ratio, which in turn results in changes in the levels and types of chemical and physical defenses (Coley and Barone, 1996, Mauricio, 2000, Katjiua and Ward, 2006a). Since photosynthesis provides the building materials and energy that support growth, there may possibly be a trade-off, in some cases, between growth and defense because processes related to growth and defense require

similar resources, such as nitrogen (Tang et al., 2009). Severe leaf removal tends to lead to regrowth with smaller shoots and leaves and in some cases can result in either increased or decreased defence (Bryant et al., 1992, Gadd et al., 2001, Rooke and Bergstrom, 2007). Such responses were reported when simulated browsing increased condensed tannin levels for *T. sericea* (Katjiua and Ward, 2006a) and also in *Acacia karroo* Hayne exposed to severe goat browsing (Scogings and Macanda, 2005).

Since soils and plants form the template on which communities and ecosystems are assembled, interpreting the factors that determine plant regrowth and re-establishment is central for our understanding of ecosystem utilization and sustainability (Mwavu and Witkowski, 2008, Nzunda et al., 2008, Neke, 2004). Knowing how disturbances such as herbivory shape savanna structure and composition is critical for predicting future changes in tree cover and for formulating management policies (Holdo, 2007, Holdo, 2005). Such knowledge is also important for estimating the full consequences of defoliation on tree performance, regrowth and resource allocation (Kaitaniemi et al., 1999). Also, knowing how resprouting trees allocate resources towards shoot numbers and length is critical because when trees are resprouting, they are within the browse zone. Therefore, their response to browsing might determine how quickly they grow out of the browse zone.

This study investigated two possible response strategies of cut trees exposed to a period of browsing; 1) an initial quick response in terms of *e.g.*, shoot production after exposure to herbivory *i.e.*, compensatory response, or 2) that there are residual or legacy effects of herbivory on resprouting and plant physiology after the removal of browsing. The main objective was to investigate the effects of exposing resprouting trees to browsing on the coppice response of *T. sericea*. The question asked was: how does exposing cut *T. sericea* to a period of browsing influence its coppice response? It was hypothesized that exposing cut trees to browsing will decrease coppice response because the cutting will have stimulated an initial, quick response. A further disturbance in the form of browsing is suggested to likely result in trees reducing coppice response relative to the quick, initial response and possibly allocating nitrogen towards either photosynthesis or defence.

## 4.2 METHODS

### 4.2.1 Study site

Details for the study site are described in Chapter 1.

### 4.2.2 Study species

The study species is described in detail in Chapter 1.

### 4.2.3 Experimental design

An experiment was set-up in September 2011 to determine the effects of browsing on coppice regrowth of cut *T. sericea*. The experiment consisted of pairs of plots, one for each experimental treatment (described below). Each pair represented a block, and there were three replicates (sites). Each plot had 15 trees, with plot size ranging between 100 $m^2$ and 169 $m^2$, bringing the total number of trees to 90. All trees in plots were standardized based on stump diameter range of between 5 and 9 cm. Single-stemmed trees were selected based on initial tree stump diameter; which was standardized (from 5-9 cm) such that the size of the original stem was used as a covariate to control its effects on coppice response. In cases where single-stemmed trees could not be used, multi-stemmed trees of a combined diameter ranging between 5 and 9 cm were used. Stems in this diameter range were considered medium-sized and were chosen because it has been suggested that larger stems take a shorter time to respond to a cutting event, positively influencing initial coppice growth through having a larger size of the residual root system (Shackleton, 1997). Treatments were applied as follows;

i. On a set of plots in each site, trees were immediately fenced (using 2 mm diamond shaped wire fence) after cutting to prevent browsing by antelope on resprouting coppice shoots (referred to as 'unbrowsed').
ii. On the other set of plots, trees were not fenced for a period of five months from September 2011. This period allowed for exposure to browsing. Trees were then fenced after that five month period of browsing (referred to as 'browsed' from here

onwards) to exclude browsing. Browsers in this experiment included impala, kudu and waterbuck.

All trees were cut in September 2011 using a chain-saw. Trees were cut at a height of approximately 25 cm from the ground. Since research has shown that the production of resprouting shoots increases with cutting height (Shackleton, 1997, Khan and Tripathi, 1986, Ibrahima et al., 2007, Kaschula et al., 2005b), the height used in this study was kept constant to minimize its effects on resprouting. Monitoring of trees for morphological changes started in February 2012, after fencing the last set of plots and lasted for 12 months.

### 4.2.4 Morphology measurements

The following variables were measured per stump monthly;

(i) total number of shoots resprouting, (ii) resprout shoot diameter (iii) resprout shoot length. For (ii) and (iii), the shoot showing the greatest length was selected and marked using string for monitoring.

Shoot production was calculated as the number of shoots produced per unit area of stump basal area. The tree's original stump diameter was measured at the beginning of the experiment and used together with resprout shoot diameter to calculate the resprout shoot diameter as a ratio of the original tree's stump diameter. This was termed the resprout ratio.

Towards the end of the dry season, and immediately after leaf flush in September 2012, two leaves growing on the monitored shoot were randomly selected and marked. Ten trees per treatment were monitored. Leaves of the same size were used for these measurements in order to minimize the effect of age influencing the results. On the two leaves the following measurements were carried out twice every week in the morning, between 07:00 and 10:00 am for a period of about a month. An average of the two measurements for leaf level stomatal conductance and change in leaf length was calculated;

i. Leaf level stomatal conductance using a Leaf Porometer (Model SC-1, Decagon Devices), and
ii. Change in leaf length along the axis length of the leaf using a ruler (termed leaf extension).

### 4.2.5 Foliar analysis

Immediately after fencing in February 2012, leaf samples were collected from both sets of plots *i.e.*, from browsed and unbrowsed trees. Leaves collected were oven dried at 60 $^0$C for 48 hours and then ground using the Wiley Mill. Leaf samples were taken to the University of Florida Laboratory for carbon (C), nitrogen (N) and phosphorus (P) concentration analyses in the two treatments. Total C and N were measured using a Costech ECS 4010 Elemental Analyzer (Valencia, CA, USA), while P was measured using the modified single solution method described by Murphy and Riley (1962).

### 4.2.6 Browse proportion

The number of shoots browsed per tree in the plots subjected to browsing after cutting was counted after fencing in February 2012. Browse proportion was calculated by expressing the total number of shoots browsed as a proportion of total number of shoots produced, and then converted to a percent (%) value. Browse proportion for the browsed plots trees ranged between 85-95 % for all the trees in February 2012.

### 4.2.7 Statistical analyses

All data for comparing the effect of fencing on coppice response and foliar chemical properties were analysed using ANOVA with Tukey's *post hoc* used to compare means between treatments at $\alpha<0.05$. To control for the influence of site by site variation on the monitored tree responses, site was included in the analysis as a random effect for the mixed model analysis. Where necessary, data were log-transformed to fit assumptions of normality. A repeated measures ANOVA was used to test for significance treatment effects. The leaf extension was calculated as the logarithm change in leaf length relative to time between late September and early November 2012.

## 4.3 RESULTS

### 4.3.1 Morphological properties

Exposing harvested *T. sericea* trees to browsing had a significant positive effect on resprout shoot production after five months of browsing ($F_{23.66}$=43.84; $p<0.05$). Shoot production (number of shoots produced) was initially significantly higher (February 2012) in the browsed treatment than in the unbrowsed, but this significant difference diminished to reach no differences after April (Fig. 4.1A). Preventing browsing had significant effects on resprout shoot diameter ($F_{23.66}$=58.13; $p<0.05$) (Fig. 4.1B), resprout shoot length ($F_{23.66}$=87.97; $p<0.05$) (Fig. 4.1C) and resprout ratio ($F_{23.66}$=39.18; $p<0.05$) (Fig. 4.1D) throughout the study respectively.

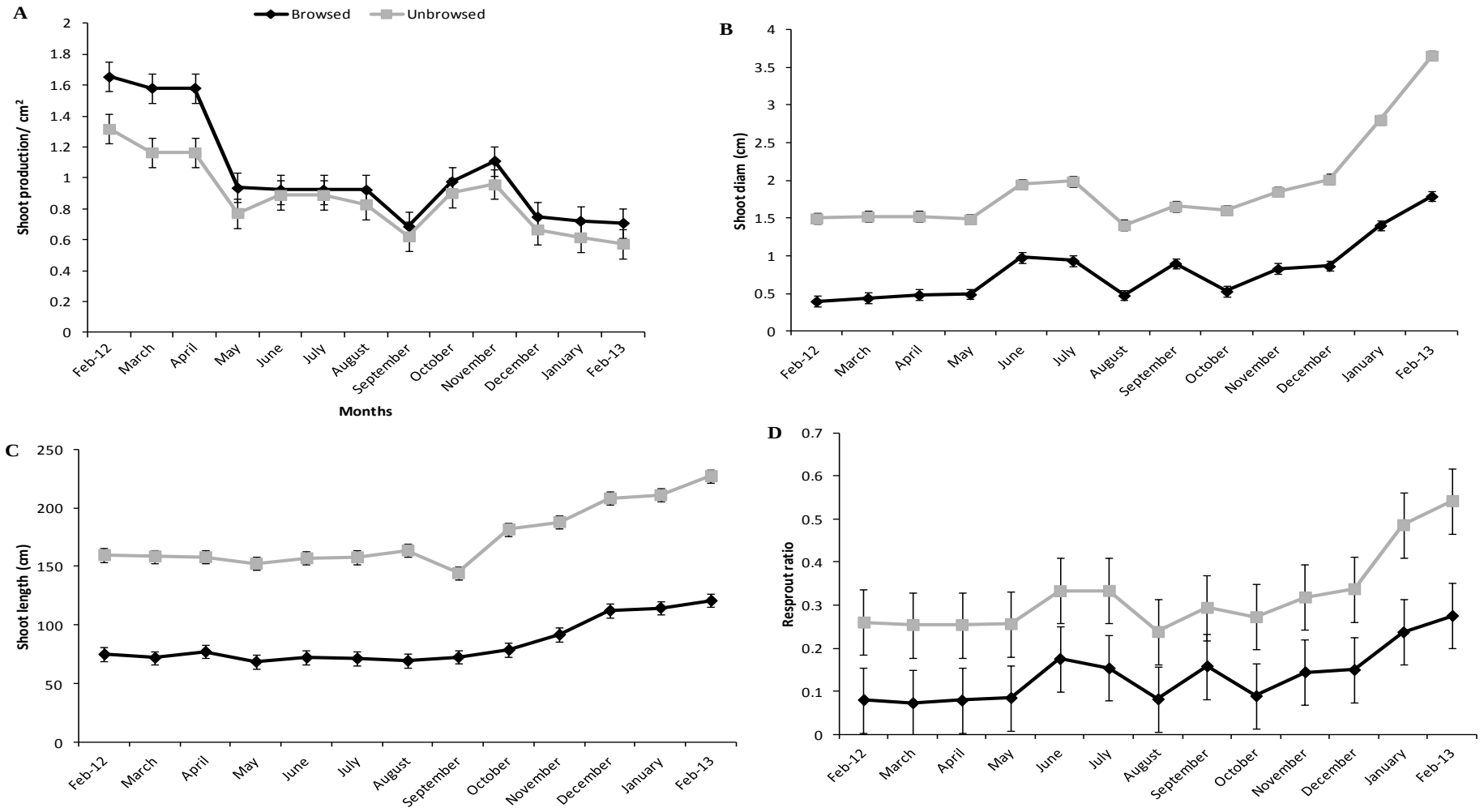



**Figure 4.1.** The changes in A) shoot production (calculated as number of shoots per unit area of circumference), B) shoot diameter, C) shoot length and D) resprout ratio (with standard error bars) of cut trees subjected to a five month period of browsing. All the data points represent the monitoring period after fencing. Means were used for plotting the graphs except for resprouting vigour calculated as a ratio between shoot diameter and original stump diameter.

### 4.3.2 Foliar properties

*4.3.2.1 Growth properties*

Trees exposed to a five month browsing period after cutting (browsed) initially had significantly higher leaf increment compared to unbrowsed trees ($F_{23.66}$=53.64; $p<0.05$), with leaf relative growth rate similar as the wet growing season progressed (Fig. 4.2A). Exposing cut trees to browsing had a significant effect on stomatal conductance, with browsed trees recording significantly higher leaf conductance compared to trees not exposed to browsing ($F_{23.66}$=114.61; $p<0.05$), while leaf conductance levels were the same at the end of the experiment and as the wet season progressed (November 2012) (Fig. 4.2B).

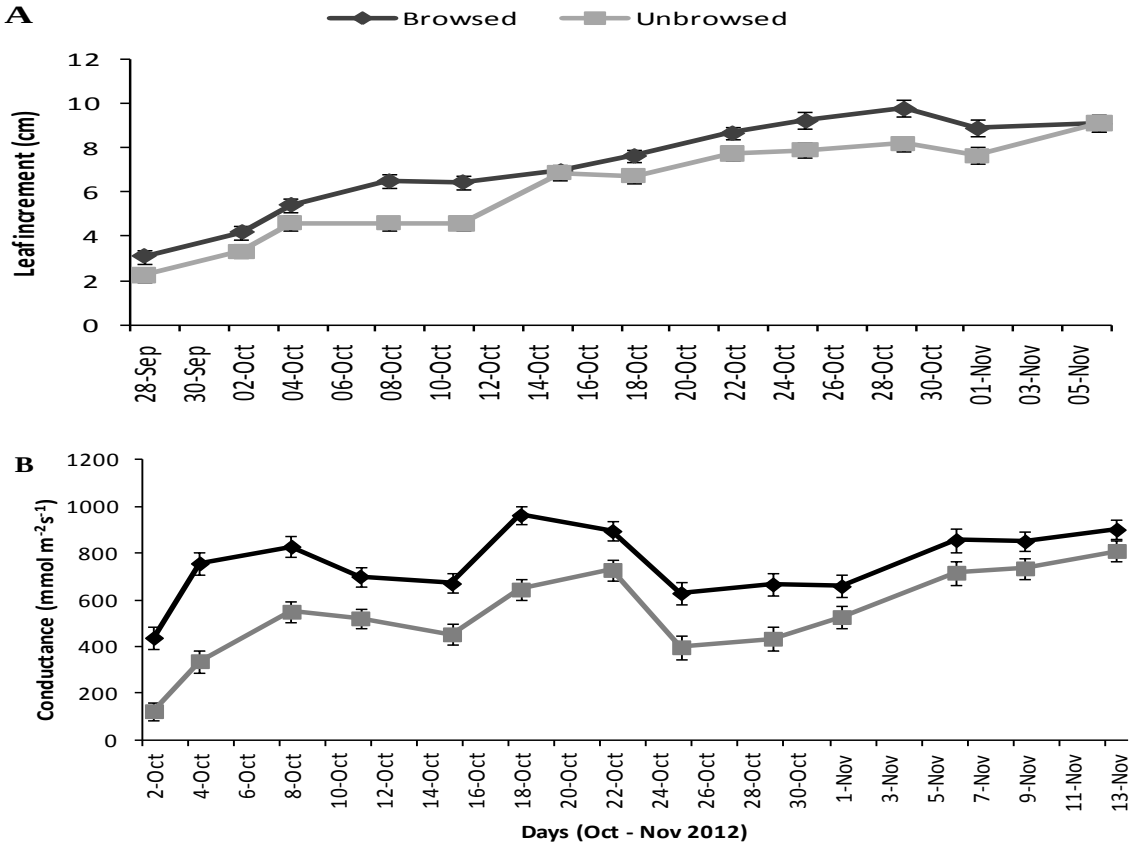



**Figure 4.2**. A) increment and B) stomatal conductance of leaves for browsed and unbrowsed trees (with standard error bars). The data represented are from early in the 2012 growing season (September-November 2012).

*4.3.2.2 Changes in foliar chemical properties*

Exposing cut trees to browsing had no effect on foliar C but resulted in an increase in foliar N and P (Fig 4.3).

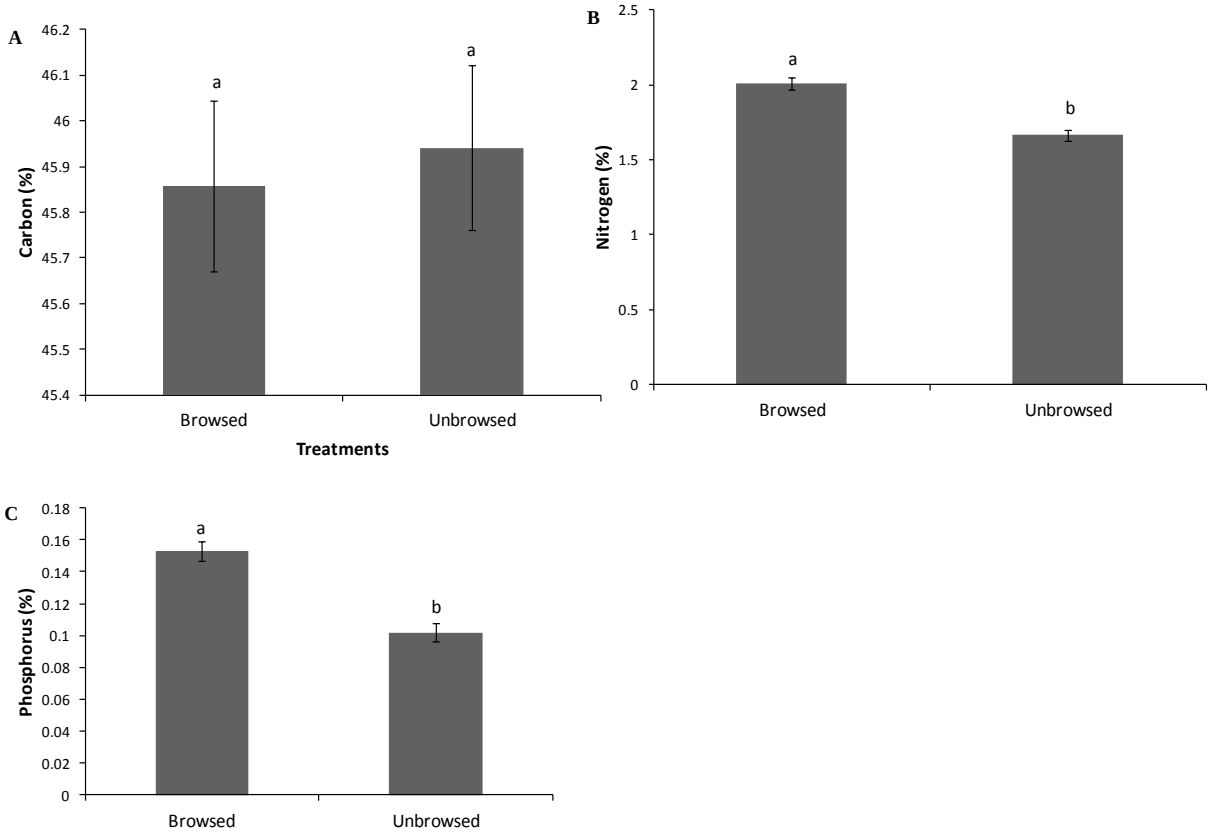



**Figure 4.3.** Mean leaf levels (%) of A) carbon, B) nitrogen and C) phosphorus due to exposing resprouting harvested trees to browsing for a period of five months. Bars with different letters represent significant differences.

## 4.4 DISCUSSION

This study was carried out to demonstrate the effects of exposing previously cut resprouting *T. sericea* trees to browsing on coppice response and to also determine how previously browsed trees respond to the exclusion of browsers. It was hypothesized that browsing on coppicing trees will result in an initial quick response after exposure to herbivory, although still reducing individual shoot growth. This hypothesis was confirmed when the shoot diameter and shoot length for browsed trees were significantly lower compared to unbrowsed trees during the study. Leaf C levels remained the same for both treatments, with leaf N and P for browsed trees significantly higher compared to N and P for unbrowsed trees in February 2012. The browsing proportion calculated showed that browsing was generally high before

fencing. For the first three months after excluding browsing (March-May 2012), the shoots production was significantly higher for browsed trees than unbrowsed trees. However, the differences in the shoot production between the two treatments decreased from April 2012, and were similar from then onwards.

### 4.4.1 Effects on morphological responses

Exposing resprouting trees to browsing stimulated an initial significant increase in shoot production compared to unbrowsed trees. This may be because growing tips were being browsed, thus apical dominance suppressed; leading to more meristem buds being activated. Shoots for the browsed plots were shorter and thinner compared to the unbrowsed plots, meaning shoots probably maximised leaf area at the expense of height gain. Shoot diameter and shoot length values for browsed trees were nearly half those of unbrowsed trees for entire duration of the study. Browsing of resprouting trees was both on lateral shoots and leader shoots. This had detrimental effects on tree resprouting as well as trees reaching pre-disturbance height levels because trees could not escape that height interval within which trees could be reached and browsed. This is supported by Palmer and Truscott (2003) who propose that if the leading shoot is continuously browsed, the replacement leader shoot will not be as long as the original shoot. The authors also proposed that the time taken to escape the critical disturbance height is increased if a tree is continuously exposed to browsing.

When browsed, apical dominance was reduced, which resulted in more shoots in browsed trees, but the individual shoots were on average younger (*i.e.* shorter and thinner) or older but with reduced length and width growth following loss of the shoot tip.. The initial increase in shoot production for the browsed trees may have been an adaptive form of response to promote tolerance because increasing the number of resprouting shoots possibly ensured that browsing did not exhaust shoot numbers. However, any subsequent browsing event would still reduce the leaf area but due to high shoot numbers, the impact of browsing would be minimized. This is in comparison to unbrowsed trees which had fewer shoots. Although not calculated for this study browsed trees may have shown an initial form of compensatory response by investing more in the production of a higher number of shoots that were both thinner and shorter compared to unbrowsed trees, which had fewer shoots which were thicker and longer. This can be viewed as a form of defence mechanism to help restrict the amount that herbivores can eat, or to create a cage-like structure so that the older outer shoots protect

the younger non-lignified shoots in the centre of the resprouting tree (Archibald and Bond, 2003). Similar results were found by Fornara and Du Toit (2007) on *Acacia nigrescens* Miller, while Cooper et al. (2003) found no significant differences between browsed and unbrowsed *Acacia schaffneri* Herm., *Acacia greggii* Gray and *Prosopis glandulosa* Torr.

Browsed *T. sericea* underwent substantial physiological adjustments in response to herbivory by the antelope. Such adjustments largely compensated for the loss of leaf area and photosynthetic capacity in the previous season. These included higher stomatal conductance and leaf extension compared to unbrowsed trees at the beginning of the first growing season after browsing as proposed by Hetherington and Woodward (2003). Although not measured in this current study, net carbon assimilation in leaves has been shown in previous studies to be strongly correlated to increased stomatal conductance (Ayres et al., 2004, Morrison and Reekie, 1995).

Measurements for the current study were carried out in the wet season i.e. under non-restricting water availability in soil. Therefore, it is proposed that browsed trees exhibited a trade-off of water loss (through higher stomatal conductance) for carbon gain (though enhanced photosynthetic capacity). This was a demonstration of opportunistic and quick growth during short periods of water availability as proposed by Hetherington and Woodward (2003). In the study area characterized by low soil moisture levels (Shackleton, 1997, Shackleton and Shackleton, 2000), this trade off between water loss and carbon gain would be most feasible in the wet season in browsed trees. High leaf water loss during the dry season would increase tree susceptibility to drought stress and tugor loss.

Results from the current study are similar to what Fornara and Du Toit (2007) found when clipping experiments resulted in higher number of shoots produced for *Acacia nigrescens* miller in the Kruger National Park (South Africa). Results from this study are different from those of Perevolotsky and Haimov (1992) who found that *Phillyrea latifolia* L. in Israel increased in both height and diameter when tree cutting was followed by browsing. There were also no significant differences in resprout responses in Spain when *Atriplex halimus* L. was browsed by sheep and goats (Valderrhbano et al., 1996). Browsing by mountain hare also did not influence any height or diameter change in Scots pine (*Pinus sylvestris* L.) but instead showed similar findings to this study, with trees which had new and old browsing recording a significant increase in the numbers of shoots produced per tree (Rao et al., 2003).

Exposing cut resprouting *Ericascoparia* L. and *E. Australis* L. to red deer and free ranging cattle did not result in significant differences in biomass production between browsed and unbrowsed trees (Paula and Ojeda, 2011). However, height of oak tree saplings was shown to decrease after browsing events by red and roe deer (Palmer et al., 2004), while balsam fir and paper birch seedlings were significantly taller in fenced areas than in unfenced areas every year after cutting and browsing by white-tailed deer (Casabon and Pothier, 2007). Simulated leaf and shoot herbivory of *Acacia drepanolobium* Harms ex Y. Sjostedtin Kenya was shown to increase shoot production (Gadd et al., 2001). Similar to this current study, Reich et al. (1993) recorded higher stomatal leaf conductance in 4-year old *Pinus resinosa* Ait seedlings in the spring of the year following defoliation, but not at the end of that summer.

Total number of shoots produced in both treatments declined with time, especially as the dry season progressed. This may have been due to self-thinning and shoot die-back. While self-thinning could be viewed as a way of reducing high respiration demands associated with high leaf material, this growth pattern was observed even during the wet season (November 2012-February 2013), when water availability was not limiting. This could mean that resource availability does not control self-thinning, *i.e.*, self-thinning is controlled within the trees and not by environmental factors. Instead, self-thinning is driven by the need, at some point, to switch towards a resource allocation strategy aimed at height gain.

### 4.4.2 Effects on foliar chemical properties

Leaves from unbrowsed trees had lower levels of nitrogen compared to leaves from browsed trees. Leaf nitrogen levels were about 20 % higher in browsed trees compared to unbrowsed trees. There are three possible explanations for the observed increase in leaf N for browsed trees, although with a lower C/N ratio (results not shown). The first one is that leaves from browsed trees may have been younger than those on unbrowsed trees. Younger leaves typically have higher N levels than older leaves. The second possible reason is that browsed trees increased investment by leaves in defence strategies such as alkaloids. High levels of polyhydroxyalkaloids have been found in *T. sericea* (Eloff et al., 2008, Katjiua and Ward, 2006a). Therefore, the implication of this may be that browsed trees investing in defence strategies were avoiding physical damage. While using nitrogen in defence strategies may have been beneficial during that time, this strategy may have reduced growth, as evidenced by the lower resprout diameter and shoot length compared to unbrowsed trees.

An alternative possible explanation for higher N in browsed trees is that proposed by Rooke and Bergstrom (2007). These authors suggested that a high leaf N level in *Combretum apiculatum* Sonder may imply that leaves growing after successive disturbances should be more palatable to herbivores because of young age and owing to lower levels of defensive compounds such as alkaloids. If alkaloids are highly concentrated, nitrogen levels are, in turn, decreased in leaves. High foliar N levels in this study are unlikely to have resulted in high levels of alkaloids because Mooney and Gulmon (1982) and Kudo (1996) have proposed that leaf chemical properties such as low foliar N are expected to reduce herbivory. Instead, the high foliar N in this study may have increased palatability of leaves instead. As a result of the large amount of leaf organic N present in the chloroplasts, higher leaf N levels are associated with higher rates of maximum photosynthesis, transpiration rates and an increase in metabolic processes within a plant (Poorter and Evans, 1998, Turnbull et al., 2007, Lavigne et al., 2001). It is proposed that higher foliar N, coupled with leaf stomatal conductance, in browsed trees resulted in compensatory photosynthesis early in the growing season as suggested by Senock et al. (1991), Nowak and Caldwell (1984), and Heichel and Turner (1983).

Similar results were found when leaves from heavily browsed *Acacia nigresens* Miller, were shown to have higher levels of N and P compared to leaves from unbrowsed trees (Du Toit, 1990). Short-term responses to above ground branch removal in *C. apiculatum* showed that over the season, leaf N levels were higher on severely defoliated trees compared to trees not defoliated (Rooke and Bergstrom, 2007). Simulated clipping of six Cerrado Neotropical savanna tree species also resulted in at least 1.4 times higher leaf N levels in cut compared to uncut trees (Mundim et al., 2012). Similar results were also found when *Fagus sylvatica* L. responded to herbivory by producing larger leaves with higher leaf N content and higher leaf stomatal conductance for trees exposed to previous season defoliation compared to trees not exposed to defoliation (Ayres et al., 2004, Reich et al., 1993). However, there were no significant differences in leaf stomatal conductance between *Acer saccharum* Marsh leaves exposed to insect defoliation and those not exposed to (Ellsworth et al., 1994).

With the differences observed in resprout shoot length between the unbrowsed and browsed trees, it can be assumed that a resprouting tree may reach heights as high as two meters within a two year period. This way, a tree escapes the height reachable by browsers and fire within a shorter period, compared to when it is exposed to another disturbance. Although this

study measured leaf nitrogen changes due to browsing, further research needs to be done on how nitrogen levels change in storage organs such as roots, shoots and stems of resprouting browsed trees compared to resprouting trees not exposed to any browsing event. Considering the extent of the effect of insect herbivory on plant growth and regeneration (Carson and Root, 1999, Howe and Jander, 2008, Maron, 1998), this study assumed that the degree of the effects of insect herbivory on all trees in this experiment was similar.

## 4.5 CONCLUSION

This study was designed to investigate the role herbivores play in shaping plant regrowth. In supporting the hypothesis for the study, results suggest that exposing cut trees to a period of browsing, indeed, influenced tree coppicing through reducing shoot length, shoot diameter and resprout ratio. Browsed trees exhibited initial compensatory response through higher shoot production, but this decreased with time. In communal savanna rangelands, a tree stand may resprout after a harvesting event, but exposure to continuous browsing will limit a stand from re-establishing. Therefore, browsing on resprouting trees should be kept minimal because of its negative effects on shoot growth. Alternatively trees can be cut at a height that is not accessible to browsers, so that height recovery is quicker.

## CHAPTER 5

## THE EFFECTS OF REPEATED CUTTING ON COPPICE RESPONSE OF *Terminalia sericea*


## ABSTRACT

Multiple cuttings of the same trees are likely to result in changes in resprouting vigour and a possible decline in tree species abundance, especially in disturbance-prone environments such as savannas with fluctuating seasonal rainfall availability. The effects of subjecting *Terminalia sericea* trees to one, two and multiple (eight) cutting events on coppice response were investigated in a savanna woodland of South Africa. Resprout shoot diameter and shoot length were lower in trees exposed to a high number of cutting events compared to trees exposed to one cutting event. Increasing the number of cutting events significantly reduced stem total non-structural carbohydrate levels in trees, indicating a depletion of stored reserves. Foliar carbon remained largely the same, while leaf nitrogen and phosphorus concentration increased significantly with each cutting event. Results indicate that trees cut once had not replenished depleted reserves even after a period of 18 months during which time no cutting took place. Sustainable utilization of this tree species must allow for at least more than 18 months of undisturbed growth between harvests to allow for the replenishing of reserves.



*Key words*: repeated cutting, harvesting, stored reserves, total non-structural carbohydrates, depleted, replenishment.

## 5.1 INTRODUCTION

The cutting of trees for rural livelihoods is both extensive and intensive in the savannas of Africa (Shackelton et al., 2004, Shackleton et al., 2004, Shackleton, 1993, Twine et al., 2003, Pote et al., 2006, Neke et al., 2006, Shackleton et al., 2007). While trees have the capacity to regrow after a cutting event, there has been concern about the sustainability of these cutting levels. This is because in communal areas, many stems are cut in an unplanned manner and without implementing activities that promote natural regeneration, such as rotational cutting cycles (Rendón-Carmona et al., 2009, Mwavu and Witkowski, 2008). Where there are no regulations, people utilize the opportunity they get to repeatedly cut trees. This results in over-utilisation and a reduction in the regrowth capacity of trees (Rendón-Carmona et al., 2009). There is much concern about the sustainability of intensive cutting of trees for firewood purposes in communal areas (Twine et al., 2003, Kaschula et al., 2005a, Neke et al., 2006, Shackelton et al., 2004). Cumulative over-harvesting in these areas has contributed to degraded woodlands and thus diminished the availability of wood as a source of energy.

Intensive cutting of a plant severely depletes stored carbon reserves and potentially reduces the growth of a plant. Although at times intensive cutting can induce a fast response through refoliation (Reichardt et al., 1991, Bryant et al., 1983), it breaks apical dominance through removal of terminal meristems and reduces reproduction (Rooke and Bergstrom, 2007). The effect of continued shoot removal on total non-structural carbohydrates and regrowth of trees is poorly understood (Carpenter et al., 2008, Luostarinen and Kauppi, 2005), especially in semi-arid, nutrient poor savannas. In addition, the question of the role played by reserve carbohydrates in regrowth of intensively harvested communal woody species remains unclear, and therefore merits attention considering that some studies have motivated for trees mobilizing stored nitrogen for use in regrowth instead of stored carbohydrates (Druege et al., 2000, El Omari et al., 2003, Wendler et al., 1995, Millard and Proe, 1992).

Cutting of trees results in the reduction of photosynthetic material, as well as photosynthetic capacity and translocation of previously fixed carbon. Losses of carbon and nitrogen are exacerbated by herbivory (Richards, 1993, Kosola et al., 2001). When branches and leaves have been removed during cutting, trees survive for long periods of time in a stunted non-reproductive state by repeatedly resprouting from surviving below-ground storage structures (Bond and Midgley, 2001). Since the availability of stored reserves is central to the

vegetative regeneration after a cutting event, trees will respond through allocating resources to growth or defence strategies (Rooke and Bergstrom, 2007). This allocation of resources is determined by various factors which include; the availability of water, nutrients and sunlight during and after the disturbance; and the extent of the severity of damage on the plant caused by the disturbance (Katjiua and Ward, 2006a).

After a severe disturbance event, lower availability of water and nutrients may reduce regrowth, while increasing the allocation towards defence (Katjiua and Ward, 2006a, Luostarinen and Kauppi, 2005). The frequency of damage, interacting with plant evolutionary characteristics has led to the evolution of chemical (compounds such as tannins) and mechanical (thorns or spines) defences which reduce the level of damage during and after disturbance (Bryant et al., 1983). Both defence strategies - the change in nutritional status of leaves and the plant's ability to increase spines or thorns - have been associated with influencing the ability of a plant to survive and to withstand damage, since both potentially reduce disturbance pressure (Casotti and Bradley, 1991).

For plants, it is a biological advantage to have a readily available source of energy after a disturbance (Fornara and Du Toit, 2007). This is because vegetative parts need to be maintained to initiate establishment of new photosynthetic surface for shoot recovery (Bowen and Pate, 1993, Luostarinen and Kauppi, 2005, Kozlowski, 2002). Some woody plants store enough carbohydrate reserves in stumps and roots to meet more than one resprouting event following a disturbance (Carpenter et al., 2008, Luostarinen and Kauppi, 2005). To recover after a browsing event which removes leaf material, a plant needs viable meristems and carbon reserves, at least until new shoots become functional and can photosynthesize (Kabeya and Sakai, 2005). To recover after a disturbance, resprouting trees also rely on stored carbohydrate reserves to support growth and respiration until a tree recovers enough leaf area for carbon assimilation to meet growth demands (Chapin III et al., 1990, Bond and Midgley, 2001).

When photosynthetically efficient, a resprouting plant can reach peak growth and then allocate carbon towards storage. Van der Heyden and Stock (1996) showed that after branch cutting, regrowth of the shrub *Osteospermum sinuatum* Norl was dependent on stored reserve carbon and this reliance shifted to photosynthates produced by new and remaining leaves. Similar findings have been shown by Canadell and Lopez-Soria (1998) when multiple

clippings on *Erica arborea* L. and *Arbutus unedo* L. resulted in large amount of total non-structural reserves being mobilized. The allocation of reserves to storage carries a cost trade-off between continued growth and reproduction (Bond and Midgley, 2001). Bowen and Pate (1993) found that production of *Stirlingia latifolia* R. Br. decreased due to successive harvests, with root starch reserves higher for plants that were burnt once and allowed to recover compared to trees that were burnt and clipped. Shoot production was lower in frequently cut *Gliricidia sepium* (Jacq) compared to less frequently cut trees (Erdmann et al., 1993). Also, repeated clipping of the western *Eucalyptus kochii* Maiden resulted in eventual death of the tree, with TNC reserves shown to be higher for trees not cut compared to trees recovering from a single cut (Wildly and Pate, 2002).

The process of replenishing carbohydrate reserves is largely dependent on trees striking the balance in being able to photosynthesize efficiently, grow sufficiently and then being able to have excess carbon for storage; all of this being dependent on soil moisture content and soil nutrient status (Cruz et al., 2003). However, little is known about the factors that control the reserve content of a plant, how much of the reserve is utilized after a disturbance such as a harvest (Cruz et al., 2003), and the changes in the recovery of nutrients such as nitrogen and carbon lost during a disturbance. These factors have significant implications for the sustainable use of savannas subjected to intensive wood harvesting.

The objective of this study was to investigate how repeated cutting of trees affects their ability to regenerate and changes the concentration of stem stored reserves as well as foliar carbon (C), nitrogen (N) and phosphorus (P). The following questions were asked: (1) How does exposing *T. sericea* to multiple cutting events affect its coppice response? (2) How does exposing *T. sericea* to different cutting regimes influence the level of TNC in the stem wood?, and (3) How do foliar C, N and P levels differ as a result of exposing trees to repeated cutting? It was hypothesized that repeated cutting will negatively affect resprouting at the end of the two year cutting period, while also significantly reducing stem total non structural carbohydrates and increasing foliar N and P.

## 5.2 METHODS

### 5.2.1 Study site

Details describing the study site are in Chapter 1.

### 5.2.2 Study species

The study species is described in detail in Chapter 1.

### 5.2.3 Experimental design

A completely randomized experiment with three treatments replicated in three sites, was established in September 2010 to determine the effects of repeated cutting on the coppice response of cut trees. Ten trees were selected per treatment plot, numbering a total of 90 trees for the experiment. Single-stemmed trees were selected based on initial tree stump diameter; which was standardized (from 5-9 cm) to control its effects on coppice response. In cases where single-stemmed trees could not be used, multi-stemmed trees of a combined diameter ranging between 5 and 9 cm were used. Stems of such diameter range were considered medium-sized and were chosen because it has been suggested that larger stems take a shorter time to respond to a cutting event, positively influencing initial coppice growth through having a larger size of the residual root system (Shackleton, 1997).

Trees were exposed to three cutting regimes over a two year period. In the absence of data on cutting frequency in communal lands, a harvest interval of three months was selected. Treatments began in September 2010 to September 2012 as follows;

(a) Cut once over the two year period in September 2012, from hence forth termed cutting regime **a** (CRa);
(b) Cut twice over the two year period in September 2010 and in September 2011, cutting regime **b** (CRb), and
(c) Cut in three-month cycles over the two year period beginning in September 2010 and ending in September 2012, resulting in eight successive cutting events, cutting regime **c** (CRc).

For the first cut under each regime, trees were cut at a height of approximately 25 cm from the ground. Since research has shown that the production of resprouting shoots increases with cutting height (Shackleton, 1997, Khan and Tripathi, 1986, Ibrahima et al., 2007, Kaschula et al., 2005b), the height used in this study was kept constant to minimize its effects on resprouting. Successive harvests for CRb and CRc were done through removing all resprouting shoots from the stumps.

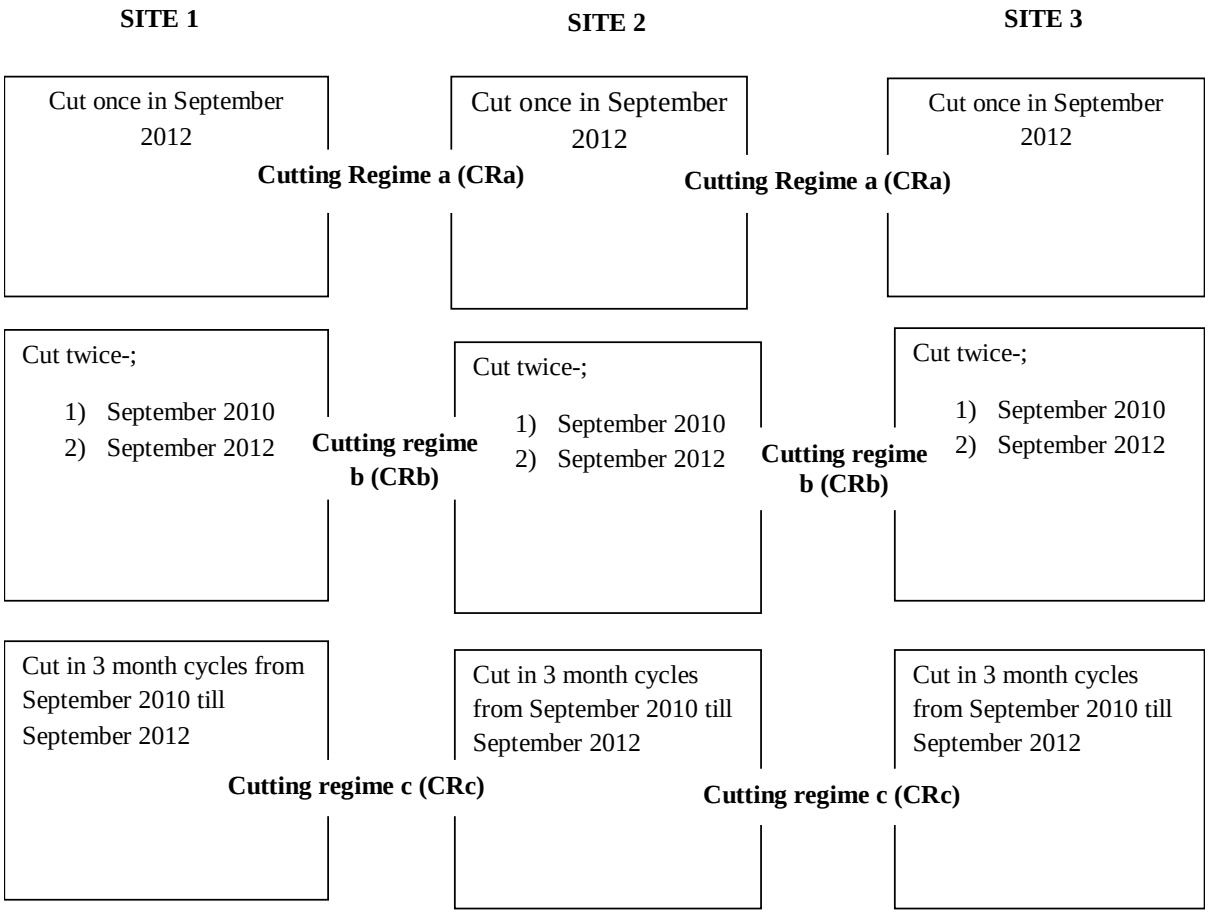



**Figure 5.2** The diagrammatic representation of the treatments in the study in three sites showing the three treatments.

### 5.2.4 Morphology measurements

Monitoring of trees for morphological changes started at the end of October 2012 and ended at the end February 2013 because trees in CRb were being used in other experiments. For each resprouting stump, the following variables were measured monthly;

(i) total number of shoots resprouting, (ii) number of leaves per monitored shoot, (iii) shoot length and (iv) shoot diameter. For (ii), (iii) and (iv) the leader shoot was selected and marked for monitoring.

Shoot production was calculated as the number of shoots produced per unit area of stump basal area.

### 5.2.5 Chemical analyses of the above ground components

*5.2.5.1 Above-ground storage analysis*

Total non-structural carbohydrates (TNC) were determined for all experimental trees using wood cores, each 3 cm long with a diameter of 4.3 mm. Since measurements were made before the end of the experiment, samples were collected from the following;

i) Uncut = not cut,
ii) Cut once = trees cut once and
iii) Cut 6-times = cut six times

Two cores were extracted per cut tree stump using an increment borer, at the end of the 2012 growing season in April. This means stem samples were collected when CRc trees had been cut six times, CRb trees had been cut once and CRa trees had not been cut at the time of sample collection. Stem cores were taken 10 cm above ground because the most marked effects of vegetation removal are evident in roots and lower parts of the stem (Garcia et al., 2001). Before storing the cores in airtight plastic bottles, the outer tree bark was immediately removed from cores after sampling. The core samples were then bottled and placed inside a freezer. Drying of samples was done at 65 $^{0}$C for two days and then samples ground using a coffee grinder before finer grinding through a 40-mesh Wiley mill screen, in the Mack lab at

the University of Florida, USA. It was assumed that constant weight was reached during the two day drying period. A composite sample was obtained after grinding.

Samples were then determined for TNC using the anthrone method described by Edwards et al. (2011) on dry weight basis. Ground samples were washed four times with hot ethanol to extract soluble sugars, and the supernatant was saved for sugar determination. The remaining solid residue was washed two times with 52 % perchloric acid to solubilize and extract the starch. The starch solution was reacted with a mixture of anthrone and hydrochloric acid to hydrolyse the starch to glucose. Absorption at 620 nm was determined using a spectrophotometer (Edwards et al., 2011), and absorbances were regressed against readings from a set of standard solutions of glucose. A correction factor of 0.9 was used to convert glucose equivalents to starch. Total non-structural carbohydrates measured in this study were the sum of the soluble fraction (glucose and sucrose) and the insoluble fraction (starch).

*5.2.5.2 Foliar analysis*

For C, N and P levels, leaf samples were collected from uncut trees and trees cut six times at the end of the 18-month sampling period. Leaves were collected a month after leaf flushing at the beginning of each growing season during the study (October 2010 and 2011), during what was termed the 'peak' of each growing season during the study (January 2011, 2012) and at the end of each growing season during the study (April 2011, 2012). There were no leaf collections in both dry seasons during the study because trees were shedding leaves during that period (i.e. between July and September). Leaves collected were oven dried at 60 $^{0}$C for 48 hours and then ground using the Wiley mill. Leaf samples from a total of six harvests (a period of 18 months) were taken to the University of Florida Laboratory for carbon, nitrogen and phosphorus concentration analysis as influenced by the different cutting regimes. Total carbon and nitrogen were measured using a Costech ECS 4010 Elemental Analyzer (Valencia, CA, USA), while phosphorus was measured using the modified single solution method described by Murphy and Riley (1962).

### 5.2.6 Statistical analyses

All data were analyzed using analysis of variance to test the effects of repeatedly cutting *T. sericea* on coppice response, total non-structural carbohydrates, C, N and P levels. Tukey's

mean comparison at $p<0.05$ was used for mean comparisons. Where necessary, data were log-transformed to fit assumptions of normality. All significance levels were defined at $p<0.05$.

## 5.3 RESULTS

### 5.3.1 Effects on coppice response

Exposing *T. sericea* to different cutting regimes had significant effects on the coppice response of resprouting trees. Shoot production was significantly higher in repeatedly cut trees (CRc) through-out the monitoring period compared to the other treatments. In some instances, e.g. in November 2012 and February 2013, differences between trees cut once (CRa) and trees cut twice (CRb) in shoot production were not significant. For number of leaves produced, there were no significant differences between CRa and CRb trees from October 2012 to January 2013, while CRa and CRb trees had significantly higher mean leaf numbers compared to CRc trees in February 2013 (Fig. 5.1B). Resprout shoot length and shoot diameter for CRa and CRb trees (Fig. 5.1C and D) were significantly higher than those for CRc trees throughout the study, while CRb trees recorded higher resprout shoot length and shoot diameter than CRc trees from November 2012 onwards.

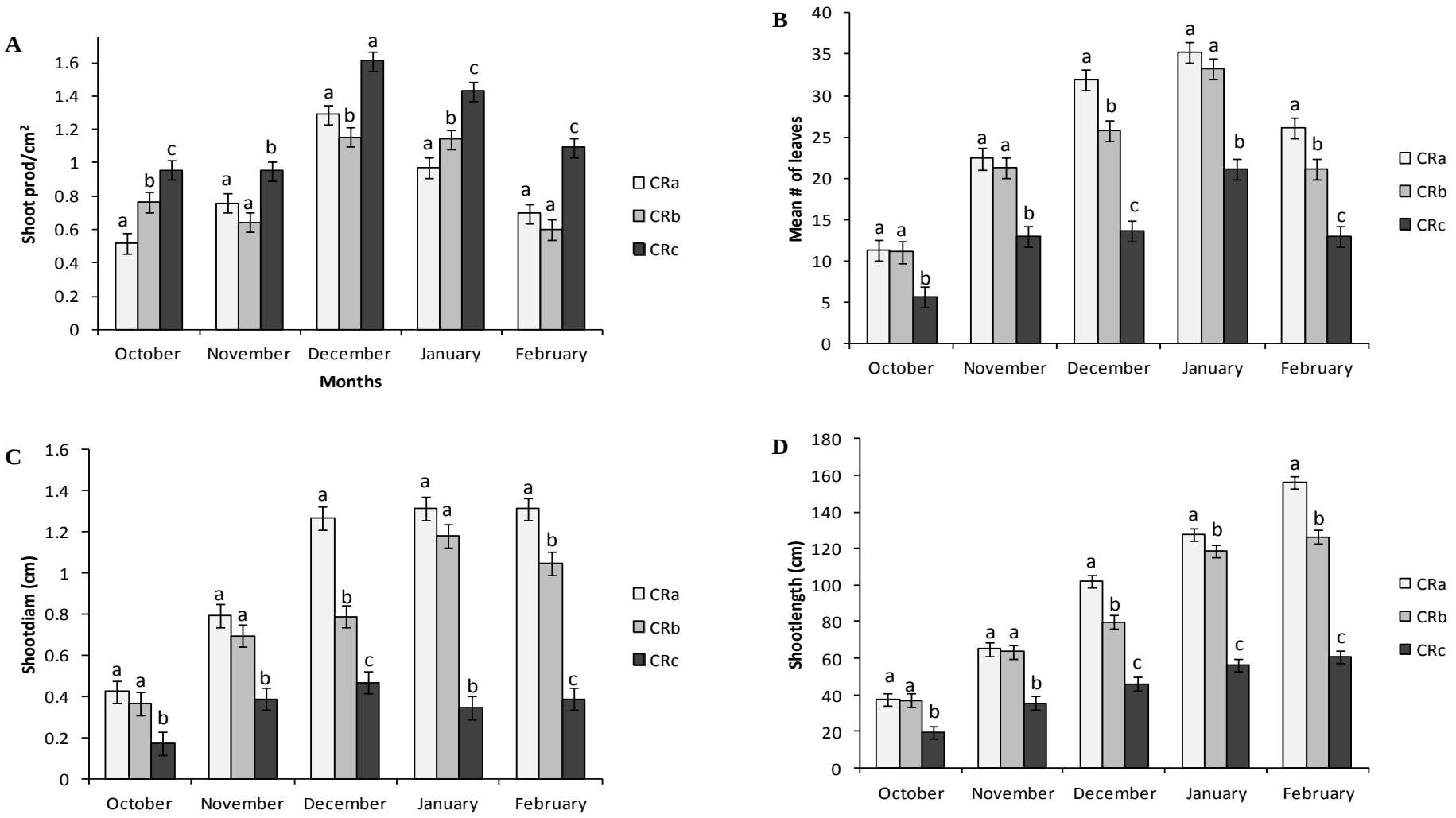



**Figure 5.3.** The monthly effects of exposing *T. sericea* to different cutting regimes on A) shoot production, B) mean number of leaves, C) resprout shoot diameter and D) resprout shoot length from October 2012 to February 2013. Means within a month having different letters are significantly different (CRa = cut once, CRb = cut twice, CRc = cut eight times).

### 5.3.2 Effects on total non-structural carbohydrates (TNC)

Exposing *T. sericea* to different cutting regimes had a significant effect on TNC levels, with levels declining significantly with an increase in the cutting frequency (Fig. 5.2). TNC levels from trees cut six times at the time of sampling were three times less than uncut trees, while levels in trees cut once were half the levels in uncut trees (Fig. 5.2).

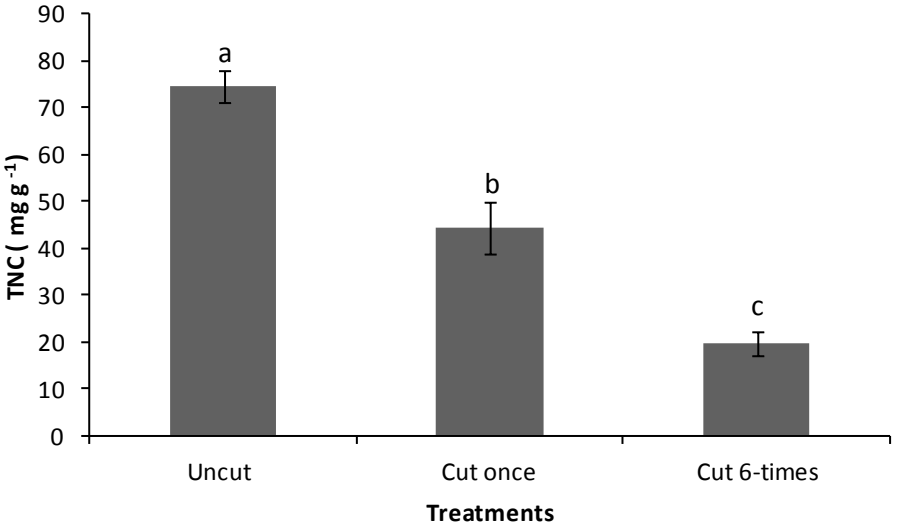



**Figure 5.4.** Mean (dry weight) total non-structural carbohydrates (TNC) in three harvesting regimes. Bars with different letters indicate significant differences at $p<0.05$ (Uncut = not cut, Cut once = trees cut once, Cut 6-times = cut six times at time of sampling) .

### 5.3.3 Effects on foliar C, N and P levels (%)

From October 2010 to April 2012, exposing *T. sericea* to six cutting cycles had a significant positive effect on nitrogen and phosphorus levels. Nitrogen levels for repeatedly cut trees significantly increased between October 2010 and April 2012, at the same time being significantly higher compared to uncut trees (Table 5.1). Carbon levels remained largely the same for both cutting regimes from October 2010 to April 2012, with significant decreases in January 2011, while remaining the same as uncut trees through-out the harvesting months. Phosphorus levels significantly increased between October 2010 and April 2012, with leaves from repeatedly cut trees recording higher phosphorus levels compared to trees not cut during the respective months (Table 5.1).

**Table 5.1**. Mean nitrogen, carbon and phosphorus concentrations (%) of Cut 6-times and Uncut trees, (s.d. = standard deviation). Uncut = not cut, Cut 6 times = cut six times in 18 months. Means with different small letters indicate significant differences between repeatedly cut (Cut 6-times) and uncut trees in the same month, while block letters indicate significant effects within a treatment. Different letters show significant differences at $p<0.05$.

| | Cut date | Cut 6 times | Uncut |
|---|---|---|---|
| Nitrogen % | October 2010 | 1.27 $^{A, a}$ (0.12) | 1.17 $^{A, a}$ (0.04) |
| | January 2011 | 1.87 $^{B, a}$ (0.27) | 1.46 $^{B, b}$ (0.19) |
| | April 2011 | 1.81 $^{A, a}$ (0.22) | 1.30 $^{B, b}$ (0.21) |
| | October 2011 | 1.82 $^{B, a}$ (0.22) | 1.48 $^{B, b}$ (0.09) |
| | January 2012 | 1.92 $^{B, a}$ (0.28) | 1.54 $^{B, b}$ (0.40) |
| | April 2012 | 2.44 $^{C, a}$ (0.22) | 1.80 $^{C, b}$ (0.29) |
| Carbon % | October 2010 | 46.61 $^{A, a}$ (1.02) | 45.86 $^{A, a}$ (1.58) |
| | January 2011 | 43.81 $^{B, a}$ (3.00) | 47.63 $^{B, b}$ (3.85) |
| | April 2011 | 45.09 $^{A, a}$ (2.24) | 45.95 $^{A, a}$ (0.82) |
| | October 2011 | 45.35 $^{A, a}$ (1.05) | 46.31 $^{A, a}$ (1.07) |
| | January 2012 | 46.45 $^{A, a}$ (0.69) | 45.72 $^{A, a}$ (0.75) |
| | April 2012 | 45.57 $^{A, a}$ (1.52) | 45.93 $^{A, a}$ (1.04) |
| Phosphorus % | October 2010 | 0.12 $^{A, a}$ (0.03) | 0.08 $^{A, a}$ (0.02) |
| | January 2011 | 0.13 $^{A, a}$ (0.03) | 0.08 $^{A, a}$ (0.03) |
| | April 2011 | 0.11 $^{A, a}$ (0.05) | 0.08 $^{A, a}$ (0.02) |
| | October 2011 | 0.21 $^{B, a}$ (0.08) | 0.10 $^{B, a}$ (0.02) |
| | January 2012 | 0.24 $^{B, a}$ (0.04) | 0.10 $^{B, a}$ (0.05) |
| | April 2012 | 0.27 $^{B, a}$ (0.03) | 0.20 $^{B, a}$ (0.04) |

## 5.4 DISCUSSION

Among reserves needed and utilized by trees such as nitrogen reserves (El Omari et al., 2003), non-structural carbohydrates represent a tree's capital reserve and source for growth and recovery after damage or after a period of dormancy (Li et al., 2002, Bond and Midgley, 2001). Stored carbohydrate reserves have been suggested to act as a buffer for insufficient photosynthetic activity that occurs due to loss of leaf material after cutting (Li et al., 2002), with an emphasis on starch which is said to be the most important reserve capacity in trees (Kozlowski, 1992). This study was designed to investigate the effects of different tree cutting regimes on the regrowth of trees and stem reserves.

### 5.4.1 Effects on coppice response

Exposing *T. sericea* to eight cutting cycles over a 24-month period significantly reduced the number of leaves, resprout shoot diameter and shoot length per monitored resprout shoot. Shoot production for trees cut once was almost double that of repeatedly cut trees by the end of February 2013, while there were no significant differences between trees cut once and those cut twice in months such as November 2012 and February 2013. The high shoot production, but with fewer leaves for the repeatedly cut trees may be seen as a response to ensure an increase in the surface area for photosynthesis. This would have increased carbon assimilation for use in either growth or replenishment of stored reserves. High shoot production in repeatedly cut trees may have also been a result of higher reserve mobilization late in the dry season and early into the growing season as suggested by Wildy and Pate (2002), Cruz and Moreno (2001). Trees cut once had significantly higher resprout shoot diameter, shoot length and mean number of leaves than repeatedly cut trees, but these were not always significantly different from trees cut twice. For instance, there were no significant differences in shoot production produced between the two treatments between November 2012 and February 2013.

Stored TNC reserves are the most important source of carbon that aid and support growth and recovery of a plant after a disturbance (Canadell and Lopez-Soria, 1998, Chapin III et al., 1990, Van der Heyden and Stock, 1996). Early growth of shoots is associated with the mobilization of previously accumulated reserves of either nutrients or starch (Latt et al., 2000, Garcia et al., 2001, Canadell and Lopez-Soria, 1998). The similarities in the response of trees cut once and trees cut twice can be explained with reference to fluctuations in stored carbohydrate reserves, because trees mobilize reserve carbohydrates to rebuild photosynthetic tissue after cutting. Trees cut twice were first cut in 2010, and left undisturbed until the second cut in 2012. During this two year resprouting period, trees cut twice restored TNC reserves that were utilized after the first cut in September 2010. Although restored reserves in trees cut twice may not have reached pre-cut levels, this restoration enabled TNC reserves that could be utilized to exhibit coppice response similar to trees cut once, as reflected in the results.

Repeatedly cut trees had the lowest coppice response when considering the other response variables in this study other than shoot production. Given the period between cutting events (three months), the resprouting response as well as the TNC levels in repeatedly cut trees, it is proposed that cutting trees often, *i.e.*, without enough recovery time, progressively depletes TNC reserves. This is mainly because insufficient time for TNC replenishment between successive cutting events would be short (Latt et al., 2000). For this study, the three month period between the cutting events was probably not enough recovery time for trees to regrow and establish new photosynthetic mass, because that will have enabled trees to grow and restore some of the carbohydrate reserves utilized.

After a disturbance, net photosynthesis has been suggested to increase through elevated leaf N levels in newly produced foliage after a disturbance (Tschaplinski and Blake, 1989, Bryant et al., 1983, Bryant et al., 1992). This way, a tree grows and hastens the replenishment of stored reserves. Although net photosynthesis was not measured in this study, high foliage nitrogen levels for repeatedly cut trees help support this suggestion, as explained in the foliar response section. Trees in this study resprouted during the wettest period of the year in the region (Neke, 2004, Shackleton, 1997). When this point is considered, the fact that abundant resources such as high soil moisture levels may have contributed to an increased response in terms of high resprout shoot production for repeatedly cut trees cannot be totally dismissed. For example, previous studies, *e.g.*, Latt et al. (2000), have shown an increase in the replenishment of TNC reserves and biomass production in the wet season.

### 5.4.2 Effects on stem TNC levels

Exposing trees to repeated cutting events (trees cut six times) significantly reduced stem TNC levels compared to uncut trees and trees exposed to one cutting event. After 18 months of regrowth or recovery, trees cut once had not restored TNC levels to reach those of uncut trees. The expectation was that after more than a year of regrowth, TNC levels for trees cut once would have reached those of uncut trees. These ideas are supported by Bowen and Pate (1993), who suggested that TNC reserve levels initially decrease after a cutting event because of the initiation of shoot recovery. Bowen and Pate (1993) went on to propose that the reserve levels are expected to increase only after shoot biomass has reached similar levels to that before cutting. Based on these propositions, it can be assumed that trees cut once did not recover enough photosynthetic mass to enable recovery and restoration of depleted carbon

reserves to pre-cut levels. On the other hand, considering the coppice response results, the fact that trees cut twice also restored carbohydrate reserves within the 2-year recovery period should be taken into account. This is because the coppice response of trees cut once were similar to trees cut twice, indicating the possible implication that trees cut once may have restored some of depleted reserves.

Compared to trees cut once trees, exposing trees to two and eight cutting events created a decrease in the TNC sink and source activity, with trees cut once maintaining photosynthesis as their source of carbon. Repeatedly cut trees, on the other hand, shifted their source of carbon to stored reserves because cutting trees on three month cycles reduced sink activity, increasing the reliance on stored carbon for facilitating regrowth. Also, trees cut once had significantly higher TNC levels compared to repeatedly trees because there was a regrowth period of more than a year for trees cut once. During that period trees cut once had the opportunity to balance the TNC sink and source activity that was shifted after cutting.

The results imply that when trees are cut once, a higher quantity of TNC reserves are mobilized for regrowth compared to a situation whereby trees are cut six times. For trees to fully replenish reserves to reach pre-harvesting levels, a period of more than 18 months is required. Results from the study agree with other studies in which TNC reserves in woody plants have been shown to decrease as regrowth occurred after cutting, burning and defoliation (Miyanishi and Ellman, 1986, Bowen and Pate, 1993, Canadell and Lopez-Soria, 1998, Landhausser and Lieffers, 2002, Schutz et al., 2009, McPherson and Williams, 1998, Luostarinen and Kauppi, 2005). TNC concentrations were also highest in trees cut less frequently compared to trees harvested more frequently in *Gliricidia sepium* (Jacq.) Walp trees (Garcia et al., 2001), in *Salix nigra* (Carpenter et al., 2008) and also in *Populus maximowiczii* (Henry) (Tschaplinski and Blake, 1995).

### 5.4.3 Effects on foliar properties

After 18 months since trees were cut, subjecting trees to repeated cutting significantly increased leaf N and P levels compared to uncut trees. During that period leaf N and P levels doubled, although with a lower C/N ratio (results not shown), compared to uncut trees. Although leaf carbon dropped significantly between October 2010 and January 2011, it remained largely the same from then to April 2012. Leaf samples from the treatments may

have been different in terms of age, leading to younger leaves in repeatedly cut trees having higher N levels. Nevertheless, an increase in leaf N can also be explained by two other possible mechanisms. The first reason may have been due to increased investment by leaves in defence strategies such as alkaloids (Eloff et al., 2008, Onoda et al., 2004). For a Combretaceae tree species in southern Africa such as the study species, *T. sericea*, polyhydroxyalkaloids have been found in high levels (Eloff et al., 2008, Katjiua and Ward, 2006a).

An alternative explanation for higher N in repeatedly cut trees is that proposed by Rooke and Bergstrom (2007). They suggested that a high leaf N level in *Combretum apiculatum* Sonder may imply that leaves growing after successive disturbances are younger and should be more palatable to herbivores owing to lower levels of alkaloids. If alkaloids are highly concentrated, N levels are, in turn, decreased in leaves. High foliar N levels in this study are unlikely to have resulted in high levels of alkaloids because Mooney and Gulmon (1982) and Kudo (1996) have proposed that leaf chemical properties such as low foliar N are expected to reduce herbivory. Instead, the high foliar N in this study may have increased palatability of leaves instead. As a result of the large amount of foliar organic N present in the chloroplasts, higher leaf N levels are associated with higher rates of maximum photosynthesis, transpiration rates and an increase in metabolic processes within a plant (Poorter and Evans, 1998, Turnbull et al., 2007, Lavigne et al., 2001). A higher TNC reserve demand for regrowth in repeatedly cut trees in the current study may have led to C stress, thereby reducing the production of alkaloids, making the leaves more palatable. Higher leaf N and P levels are associated with higher rates of maximum photosynthesis because of the large amount of leaf organic N in RUBISCO present in the chloroplasts (Poorter and Evans, 1998, Parry et al., 2008).

Short-term responses to above ground branch removal in *Combretum apiculatum* Sonder showed that over the season, leaf N levels were higher on severely defoliated trees compared to trees not defoliated (Rooke and Bergstrom, 2007). Leaf N levels were higher for *Cardiopetalum callophylum* (Annonaceae) and *Maprounea guianensis* (Euphorbiaceae) trees clipped monthly compared to trees clipped after every three months (Mundim et al., 2012). There were also higher leaf N levels on heavily browsed *Acacia nigrecsens,* Miller, compared to lightly browsed trees (Fornara and Du Toit, 2007).

Sampling for TNC concentration was done once at the end of the growing season in April 2012. It is acknowledged that TNC concentrations may have fluctuated seasonally due to changes in water, nutrient and light availability. Foliar sampling for C, N and P was done mainly during early growing season and late into the growing season. Foliar chemical changes were expected to be influenced by seasonal changes. Although increasing as the growing season progressed, leaf N, C and P were not significantly affected by seasonal changes, especially because leaf senescence prevented sampling during the dry seasons of the study. Growing season sampling for this study was representative because for example, Fornara and du Toit (2007) found that leaf N levels for *A. nigrescens* in the Kruger National Park, South Africa, were highest during the peak of the growing season (November) due to heavy browsing.

Since trees were sampled for TNC after six cutting events, it would be interesting to follow how the TNC levels change as the cutting cycles are increased to more than six because it has been proposed that mortality in trees eventually occurs if the reserves are sufficiently depleted through trees being repeatedly clipped (Cruz et al., 2003, Miyanishi and Ellman, 1986, Wildly and Pate, 2002). Trees cut once were allowed a regrowth and recovery time of about 18 months to replenish reserves to reach similar or pre-harvest levels. After that period, trees cut once had replenished some of the reserves. It would also be interesting to determine how much longer trees cut once need to fully replenish reserves to reach pre-harvesting levels.

## 5.5 CONCLUSION

In supporting the hypothesis for this study, results show that subjecting trees to multiple cutting events significantly decreases the coppice response in terms of resprout shoot diameter and shoot length. The TNC levels in repeatedly cut trees were significantly lower when compared to trees exposed to fewer cutting cycles. Repeatedly cut trees utilized TNC reserves after every cutting event, depleting stored reserves and contributing to reduced coppice response. Increases in N and P in repeatedly cut trees were probably associated with high levels of photosynthesis in the new and younger leaves. In light of this, a form of cutting or harvesting technique should be in place that allows for sustainable regeneration of the study species. The threshold of number of cutting events a tree can tolerate should also be established, as this has a direct effect on the coppice growth and survival of the tree.

Additional research is needed to compare the effects of multiple cutting cycles on the changes in TNC reserve levels between the stem wood and roots since some studies suggest that depletion starts with stem wood reserve levels before root levels are depleted.

# CHAPTER 6

# THE COPPICING OF A SAVANNA TREE SPECIES (*Terminalia sericea*) IN RELATION TO RESOURCE MANIPULATION AND DISTURBANCE

This concluding chapter sets out to:

- Present the findings of the study within conceptual framework.
- Discuss the study's contribution to an understanding of factors affecting resprouting in savannas, with particular emphasis on resource availability and tree cutting.
- Discuss potential management implications of the study, considering predicted changes in climate as well as the role played by important savanna determinants such as herbivores.

## 6.1 The conceptual framework

Centered on coppice regrowth, the framework developed in this study considers the resource drivers (water and nutrient availability) and the disturbance drivers (repeated cutting and repeated browsing) that affect the coppice regrowth of a cut tree (Fig. 6.1). When considering the effect of the resource drivers and also based on the results, the framework implies that water has greater effects on coppice growth than nutrients (Fig. 6.1). This is because on its own, water is important for cell expansion, cell division, while it is also a medium for metabolic processes and reactions such as photosynthesis and respiration (Chapin III, 1991, Chapin III et al., 1993, Abe et al., 2003, Chaves et al., 2003). The greater effect of water availability on tree resprouting is also through its effects on making nutrients available in solution. Through water, nutrients (e.g. nitrogen) are available to influence processes such as photosynthesis and cell enlargement, and are also important for water uptake, tissue growth and loss (Chapin III, 1991).

According to the framework, the internal factors are affected by the external drivers (Fig. 6.1). This level of interaction has direct consequences for the coppice response of trees to disturbances and resource availability. In this case, repeated cutting of resprouting shoots affects coppice regrowth through its effects on decreasing stored TNC reserves after each cutting event. In the same manner, browsing on leaves and shoot tips affects coppice regrowth through decreasing the amount of available photosynthetic tissue.

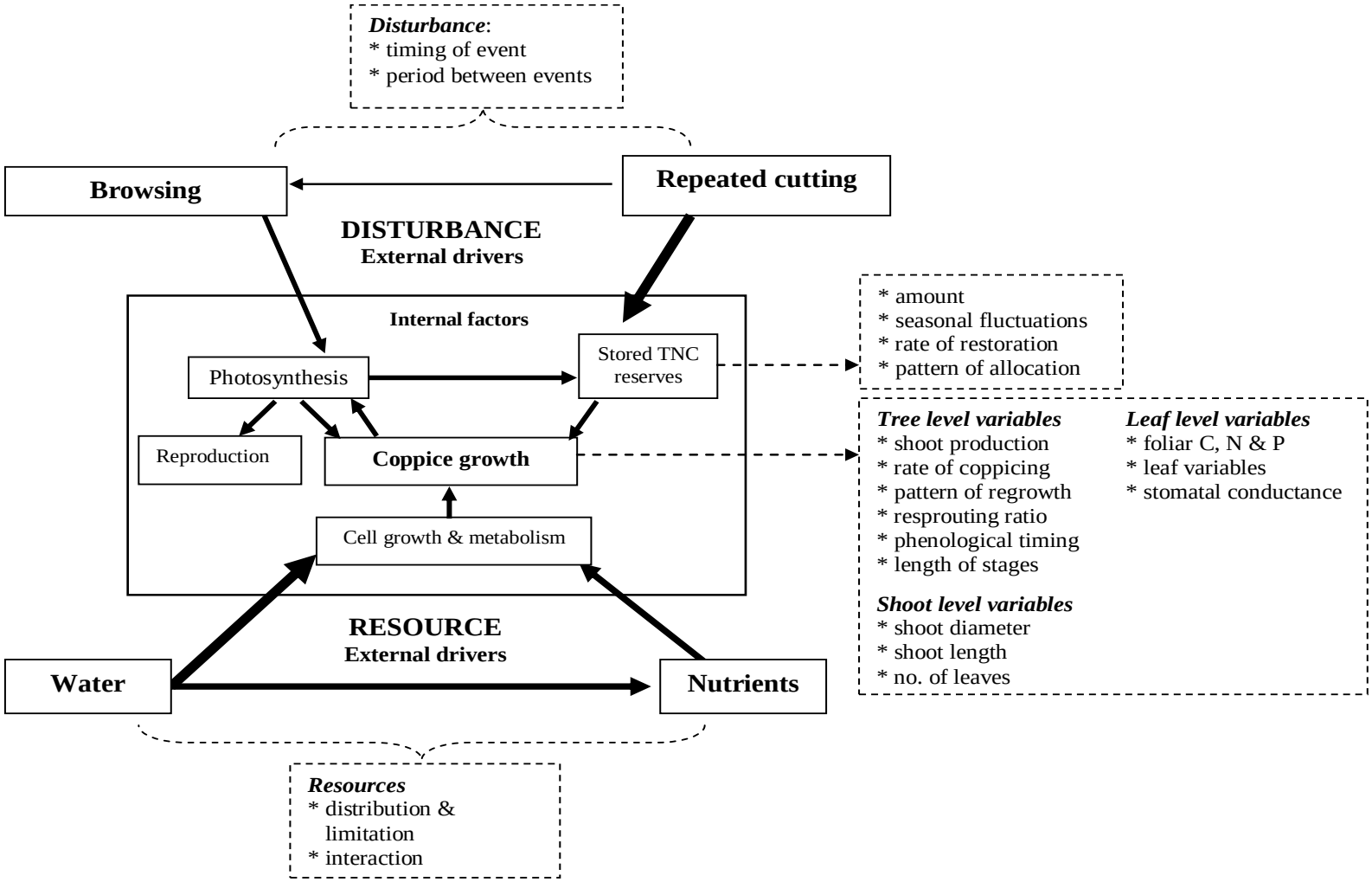



**Figure 6.1.** The expanded conceptual framework of the elements brought together in the discussion. The thickness of the arrows indicates the factor's significance and impact on tree regrowth. The dashed arrows and dashed boxes expand on respective factors and drivers considered in this study.

The low photosynthetic tissue translates to decreased carbon assimilation, which would result in reduced coppice regrowth. It has been proposed that the growth allocation pattern of trees falls into two categories with (i) an allocation of photosynthetic assimilates more towards plant height and (ii) an allocation more towards the production of lateral branches and foliar growth (Hara et al., 1991). However, from the conceptual framework and as shown by significantly higher resprout shoot length and shoot diameter in supplemented compared to unsupplemented trees, it is proposed that when the resource drivers are not limiting, the study species adopts both patterns and allocates photosynthetic assimilates towards the construction of shoot height, shoot thickness and foliage production, but not shoot production. These growth patterns have implications for increasing carbon assimilation. Also, such allocation patterns towards quicker height recovery can be an advantage in a disturbance prone ecosystem through ensuring quicker escape from fire and browsing. This would be in contrast to growth and allocation patterns under low resources, which may have allocation of resources towards the production of lateral branches. In such cases, the probability of escape from the fire and browsing heights is reduced.

The results from this study conform to the conceptual framework that was developed for the study (Fig. 6.1), with evidence of this provided by higher leaf presence in trees supplemented with water and nutrients compared to trees not supplemented. In this case, water influenced the tree level variables by increasing leaf presence and reducing the quantity of yellow leaves in supplemented trees compared to unsupplemented trees. It is acknowledged that the framework does not explicitly show the pathway played by nutrients in the timing of phenological stages, but the role of nutrients is appreciated through elements such as nitrogen being building blocks and also influencing processes such as photosynthesis (Chapin III, 1991).

For the disturbance drivers, the greater effect of repeated cutting compared to repeated browsing of resprouting trees is observed through the changes in storage TNC levels as well as the effects of browsing on photosynthesis (Fig. 6.1). Repeated cutting events remove all growing biomass; while repeated browsing events limit but do not totally deplete the entire photosynthetic surface. Therefore, with reference to the internal factors on the conceptual framework, the source-sink carbon relationship in

browsed trees is not as severely affected compared to repeatedly cut trees. The remaining leaf biomass continues to photosynthesize, instead of drawing on stored reserves for energy. This means that browsed trees rely on stored TNC reserves to a lesser extent compared to repeatedly cut trees.

With no leaves remaining on tree stumps, repeatedly cut trees draw all of the energy from stored TNC reserves i.e. stored TNC reserves become the main source of carbon for the production of new shoots and new leaves. Therefore, as leaves grow in repeatedly cut trees, the energy obtained is shared between replenishing TNC reserves and development of shoots with more leaves compared to carbon gained in browsed trees which can go directly towards growth. This leads to, for instance, lower overall coppice regrowth in repeatedly cut trees compared to repeatedly browsed trees (Fig. 6.1). In other words, browsed trees have a 'platform' to build regrowth from through the remaining shoots on the tree. This is comparison to repeatedly cut trees that do not have a 'platform' to regrow and rely solely on stored TNC reserves.

## 6.2 Discussion of ecological findings and additional insights

### 6.2.1 The importance of coppicing

Resprouting is a key strategy for plants faced with unavoidable disturbances such as fire and browsing, that cause high aboveground biomass losses (Vesk, 2006). Resprouting is as a result of a combination of the plant's inherent abilities together with environmental factors that shape growth and ecosystem structure (Vesk et al., 2004). Much of what is known about resprouting trees comes from the forestry research on plantation tree species (Shen et al., 2011, Del Tredici, 2001). A broader study of resprouting in trees has been recommended as a means of understanding plant traits, functions and ecosystem recovery (Clarke et al., 2012, Shen et al., 2011, Bond and Midgley, 2003).

Although ecologists have begun to document and explore the evolutionary implications of resprouting (Bellingham and Sparrow, 2000, Bond and Midgley, 2001, Midgley et al., 2010, Gignoux et al., 2009, Clarke et al., 2013, Clarke et al.,

2010, Lamont et al., 2011), the forestry literature provides limited information concerning the role played by resprouting in ecosystems that have experienced different disturbances, such as intensive fires, over-browsing and intensive cutting. Among other factors, resprouting varies depending on the tree species, type of disturbance and its intensity, as well as environmental conditions during or after a disturbance (Bond and Midgley, 2001, Bellingham and Sparrow, 2000, Del Tredici, 2001).

Generally, at community level, the importance of resprouting decreases as resource availability increases, such as an increase in rainfall amounts, such that re-seeding becomes the main pathway for tree recovery, assuming that trees are exposed to similar disturbance regimes (Lévesque et al., 2011). This suggests that vegetative regeneration is the dominant recovery strategy under resource-limited environments compared to non-resource limited conditions. However, the degree to which sprouts contribute to recovery of a tree stand or species depends on environmental conditions interacting with resprout shoot production, shoot survival and their growth rate relative to that of surrounding vegetation (Rijks et al., 1998). Tree responses to disturbances depend on the adaptive traits to different disturbance types. While abiotic constraints such as rainfall and soil fertility greatly influence the rate of biomass recovery (Calvo et al., 2005, Clarke et al., 2012), successful resprouting depends on stored resources (Bellingham and Sparrow, 2000, Bond and Midgley, 2001), or on the ability of new leaf growth to generate energy through photosynthesis (Sakai and Sakai, 1998).

### 6.2.2 Coppicing in relation to resource limitation

In the study, it was demonstrated that increasing nutrient and water availability to cut trees increases the resprouting of cut trees in terms of shoot diameter and shoot length during the first year of addition. These effects decreased into the second year of treatment. Although still significant, the effects were not as marked as in the first year. Higher rainfall in the second year of the study may have ameliorated the effect of water supplementation. Another possible line of thinking is that trees that are adapted to low water and nutrient availability exhibit a low degree of response (i.e. phenotypic plasticity) even when there is an increase in resource availability. In this sense, it is

plausible that when there was a constant increase of resources through adding water and nutrients in this study, with reference to the second year relative to previous resource growth conditions, trees readily exploited these resources and stored them without changing much in their growth allocation patterns. Such an opinion has also been suggested by Chapin III (1991) and Witkowski et al. (1990).

Increasing nutrient levels had a significant positive effect on shoot length and shoot diameter, with intermediate nutrient levels increasing shoot production. This indicates that water and nutrients were synergistic in increasing shoot length and shoot diameter, but not for shoot production. Although the conceptual framework shows the contribution of water, it does not explicitly show that water has no significant effects on shoot production for the study species. Instead, water appears to be limiting for shoot length and shoot diameter, thus conforming to the conceptual framework. Hara et al. (1991) proposed that tree diameter growth patterns are highly correlated with foliar growth patterns. Therefore, similarly, the high shoot diameter of supplemented trees could have resulted from higher leaf numbers. High leaf numbers could also have influenced an elevation of photosynthesis rates, as proposed by Dickmann et al. (1996).Such positive effects of adding water and nutrients are not unique to this study. Similar results have been documented on resprouting after an increase in resource availability in *Pinus taeda* L. in West Gulf Coastal Plain site in Louisiana (Sayer et al., 2004), in *Populus deltoids* Bartr. and *Planatus occidentalis* L. in a predominately Blanton sand and loamy subsoil in the Carolina Sand Hill (USA) (Coyle and Coleman, 2005).

Importantly though and in line with the conceptual framework, tree response patterns followed the seasonal limitation of water, with highest response recorded during the wet season in the study region (between November and March). This response was also evident for the phenological response of cut trees, trees exposed to browsing as well as trees exposed to the different cutting regimes. Other studies have proposed that such differences in growth may be due to an increase in growth efficiency as a result of an increase in resource availability (Albaugh et al., 2004, Dickmann et al., 1996).

Biomass production was not measured in this study because the focus of the research was mainly to demonstrate the effects of resource availability and disturbances on regrowth strategies, and not the total production after resource additions and disturbances. Nevertheless, Etienne (1989) reported that dry matter yield and biomass production in trees is dependent on leader shoot length and diameter growth patterns.

Trees supplemented with resources recorded higher leaf presence before trees unsupplemented *i.e.*, leaf presence late in the dry season, and also after unsupplemented trees had dropped leaves *i.e.* later in the wet season. This would have meant, as one would expect, that supplemented trees utilized less stored TNC reserves for leaf production early in the growing season, because leaf presence in supplemented trees did not drop to reach the zero that was reached by unsupplemented trees. Therefore, adding water and nutrients would have been expected to facilitate non-relocation of stored reserves, contributing to higher stored TNC levels in supplemented compared to unsupplemented trees. This was not the case for supplemented trees, indicating that even supplemented trees require as much TNC reserves for early and late season growth as unsupplemented trees. Supplemented and unsupplemented trees were utilizing stored carbon reserves for growth similarly, because carbon gain from photosynthesis, even for supplemented trees, may have been too low to support growth. As a consequence of utilizing stored reserves for regrowth, supplemented and unsupplemented trees recorded similar levels of stem TNC levels.

Deciduousness is a feature of trees within savanna ecosystems across the world, with pronounced seasonal reductions in leaf presence as the dry season progresses (Williams et al., 1997, Reich and Borchert, 1984). In this study, the shedding of more leaves as the dry season approached, to balance transpirational area with water availability, can be viewed as an adaptation to low soil moisture conditions in the dry season. It can also be viewed beneficially, in a fire-prone disturbance ecosystem, as this would reduce the impacts of regular dry season fires, because fire intensity increases as the dry season progresses in savannas (Williams et al., 1997).

Supplemented trees also had higher leaf numbers and the change in leaf colour from the normal silvery grey to yellow was also delayed towards the end of the growing season for supplemented trees compared to trees not supplemented. The implication may be that trees supplemented were photosynthesizing by the time the rainfall period started, thus prolonging the effective growing season for these trees. This is in comparison to unsupplemented trees, which initiated leaf production just before the beginning of the rainfall period. This is because supplemented trees maintained the green leaves for a longer period and the carbon gained during this period was probably used for growth.

There has been considerable debate about the role played by water and temperature in timing phenological stages (Archibald and Scholes, 2007, Childes, 1989, Higgins et al., 2011). Several authors have argued against the view that the timing of phenological stages in trees is under the primary control of environmental factors (Wang et al., 1992, Reich and Borchert, 1984, Reich and Borchert, 1982, Reich, 1995, Borchert, 1994). Although steps have been taken to prove this point, it is still acknowledged that whole-plant mechanisms are modified by environmental conditions (Reich, 1995, Wang et al., 1992).

While the role of temperature in initializing leaf presence cannot be totally dismissed, Archibald and Scholes (2007) and Kutsch et al. (2008) propose that in ecosystems with pronounced rainfall seasonality and water limitation, the response of trees to temperature may be secondary compared to the response to water changes. On the other hand, Higgins et al. (2011) suggest that a strategy that pre-empts rainfall, such as leaf presence in this study, must rely on a cue other than the availability of rainfall. This cue has been proposed to be temperature (Sekhwela and Yates, 2007, Higgins et al., 2011, Archibald and Scholes, 2007). However, in this study, temperature was consistent across all treatments. Although it is acknowledged that some trees are more driven by water and others by temperature, it is proposed that in this study for example, the timing of leaf presence (which can be also viewed as leaf flush) is controlled within the whole plant via stem rehydration during the late dry season as suggested by Reich and Borchert (1984) and Williams et al. (1997). From the conceptual framework, the results demonstrate the significant role played by water in determining phenological stages such as the timing of leaf presence.

Rossatto et al. (2009) argue that early flushing may be a strategy to avoid nutrient losses by pre-empting insect phenology, thereby reducing exposure to herbivory at a critical phase in leaf development. However, this is highly unlikely in the study area where larger browsers, such as antelope, are likely to target late dry season flushing. The low production of fruits and flowers for resprouting supplemented trees in favour of investment in growth during the first year after cutting may also be considered as an adaptive response in this study. Trees were still recovering from the cutting event during the first year and could not allocate resources for producing fruits and flowers. This is because of the high costs in terms of allocation of resources associated with producing reproductive organs such as flowers in disturbance prone ecosystems (Clarke et al., 2012, Bond and Midgley, 2001, Bellingham and Sparrow, 2000). Therefore, supplemented *T. sericea* trees were trading the production of reproductive organs in place of persistence as suggested by Bond and Midgely (2001). Although the conceptual framework indicates the contribution of reproduction on coppice growth, it does not show that there was no fruit production during the first year after cutting, but instead may imply that reproduction occurs even during the first year after cutting.

The close association between resprout tree phenology and climatic factors makes tree phenology vulnerable to extreme changes in climate, considering that temperature and rainfall are the main cues for changes in the timing of phenological patterns (Sekhwela and Yates, 2007). For example, Bond and Midgely (2012) suggest that trees recovering after disturbances are most sensitive to elevated carbon dioxide levels. Such sensitivity will have implications on the resprouting tree's water use efficiency, photosynthetic rates, light and nutrient use efficiency (Bond and Midgley, 2012, Drake et al., 1997). Elevated carbon dioxide levels due to low levels of transpiration can enhance woody plant expansion over grasses through an increase in water use efficiency (Polley et al., 1997). This has indirect effects on increasing soil moisture levels, favouring phenology stages and trees that promote carbon assimilation and, therefore, tree recovery through the utilization of stored carbon (Bond and Midgley, 2012).

The timing of phenological stages can be important economically with reference to livestock that depend on late dry season leaf flush for browsing. Therefore, the close

association between phenology and climate changes may have either negative effects on the timing of late dry season leaf flushing, that would result in periods when the availability of browse becomes limiting. The association may also have positive effects in making browse available later in the dry season through late dry season flushing.

### 6.2.3 The effects of disturbances on coppicing

The study provided evidence that resprouting in terms of shoot diameter and shoot length of cut trees is reduced by browsing. Browsed trees had lower shoot diameter and shoot length compared to unbrowsed trees, while initially recording higher shoot production compared to unbrowsed trees. Although there were significant reductions in resprout shoot diameter and shoot length of browsed trees, the quick compensatory response through increasing shoot production can be viewed as a response to tolerate browsing, as reported by Rodgers et al. (1995). Such a response lessened the negative browsing effect on tree performance through increasing the probability of surviving shoots in the event of more browsing events. It is also proposed that increasing shoot production was a strategy by trees to increase the leaf material for photosynthesis.

In tolerant trees, it has been suggested that the rapid shoot production response of browsed trees through high shoot production is achieved through mobilizing stored carbohydrate reserves or through carbon gained from current photosynthesis (Paula and Ojeda, 2011). When trees were exposed to a period of browsing, there was a shift in resource status and availability, with the resulting loss of leaf material reducing carbon and nitrogen available for use in the tree (Lovett and Tobiessen, 1993, Kosola et al., 2001). The strategy developed when recovering lost biomass was to either use stored reserves or replace the lost reserves by new uptake, as suggested by Lovett and Tobiessen (1993). This may have been done through elevating the photosynthetic rates of existing leaves. Alternatively, trees could have adapted both strategies while recovering lost biomass. Although not measured in this study, browsed trees possibly utilized stored TNC reserves to support high shoot production. Therefore, high shoot numbers coupled with high leaf increment and stomatal conductance are evidence of mechanisms for increases in carbon gain for browsed trees compared to unbrowsed trees.

Foliar chemical composition influences a range of plant and ecosystem processes that include the regulation of herbivory through producing defensive chemicals and an increase in photosynthesis that enhances carbon gain (Chu et al., 1996). Keeping in mind that the soil in the study area is low in water and nutrient status (Neke, 2004, Shackleton, 1997), it has been proposed that plants adapted to low resource environments are characterized by a substantial allocation towards traits that limit herbivory (Bryant et al., 1983, Coley et al., 1985). Such traits include an increase in nitrogen production associated with defensive nitrogen rich alkaloids. These traits are important because of the low potential of plants in these environments to compensate for herbivory through growth (Bryant et al., 1983, Coley et al., 1985). While this may be the case, high foliar nitrogen levels in this study are unlikely to have resulted in nitrogen-rich alkaloids because Mooney and Gulmon (1982) and Kudo (1996) have proposed that leaf chemical properties such as low foliar nitrogen are expected to reduce herbivory. Instead, the high foliar nitrogen in this study may have increased palatability of leaves as proposed by Rooke and Bergstrom (2007).

High foliar nitrogen coupled with higher stomatal conductance, as evidenced for browsed trees in this study, supports the idea of increased photosynthetic rates in previously defoliated trees relative to non-defoliated trees, as suggested by Heichel and Turner (1983), Fay et al. (1993), Karlsson (1985) and Chapin (1987). Such an increase in photosynthetic rates can be termed compensatory photosynthesis (Senock et al., 1991, Nowak and Caldwell, 1984, Heichel and Turner, 1983). Therefore, through compensatory photosynthesis, browsed leaves in this study were able to partially alleviate the negative effects of browsing. Similar results have been reported by Heichel and Turner (1983) on *Acer rubrum* L. and Lovett and Tobiessen (1993) on *Quercus rubra* L.

The stomatal conductance and leaf increment for browsed trees were initially significantly higher compared to unbrowsed trees, but were not significantly different approximately a month into the growing season. It was observed that browsed trees were producing newer and younger leaves after the first flush in October 2012. Young leaves generally show high photosynthetic efficiency compared to older leaves (Damascos et al., 2008, Clarke et al., 2012, Nowak and Caldwell, 1984). Therefore, non-significant differences were observed because the stomatal conductance and the

rate of leaf increment for older monitored leaves had reduced compared to the newer and younger leaves.

Through cutting and then exposing resprouting trees to a five month period of browsing, this experiment combined two key determinants (herbivory and human activities) that shape ecosystem structure in a communal savanna. Therefore, the design simulated what would happen in a communal land, although not similar browsing intensity. The effects of herbivory were demonstrated in an area with a lower density of browsers when compared to a communal area. Therefore, it is stated with confidence that an increase in browser density would have higher negative effects on coppice growth compared to what was observed in this study. Livestock, especially goats, browse on new resprouting shoots. Evidence of this was provided when, during the dry season, there was low grass cover available for grazing and cattle and goats browsed on early pre-rain leaf flush of *T. sericea* (Katjiua and Ward, 2006b). Results from this study conform to the conceptual framework because browsed trees have the photosynthetic 'platform' to fix carbon compared to repeatedly cut trees. Repeatedly browsed trees also rely less on stored TNC reserves for regrowth compared to repeatedly cut trees. This contributes to repeated browsing having less severe impacts on coppice regrowth compared to repeated cutting.

The response of resprouting trees depends on the intensity and frequency of successive disturbances as these reduce the resources that fund regrowth (Clarke et al., 2012). Tree response is also dependant on the constraints of rainfall and soil nutrient status (Clarke et al., 2012, Bond and Midgley, 2001). Therefore, the differences in tree response determine the chances of recovery, relative abundance and species composition in an ecosystem (Paula and Ojeda, 2006, Canadell and Lopez-Soria, 1998). Repeated tree cutting in this study had a significant effect on tree regrowth and stem stored reserves. *T. sericea* trees exposed to eight cutting events had higher shoot production compared to trees exposed to one and two cutting events respectively.

Repeatedly cut trees were exhibiting a quick compensatory response to cutting by elevating shoot production compared to trees cut once. Also, as shown for trees that were browsed, such a strategy was important for survival and maintenance of actively

photosynthesizing material in case of another cutting event. As also reported for trees exposed to a period of browsing, higher foliar N levels were also found in repeatedly cut trees. While the leaf samples collected on browsed trees may have been younger, resulting in higher N (Onoda et al., 2004) compared to older leaves from unbrowsed trees , it can be speculated that the implications for higher foliar N found in browsed trees are the same as for repeatedly cut trees in terms of elevating photosynthetic rates.

The number of cutting events had a significant effect on stem TNC levels, with trees exposed to eight cutting events recording the lowest TNC concentration compared to trees exposed to one and two cutting events respectively. Low TNC reserves in trees repeatedly cut were a possible result of the lack of photosynthesizing tissue (i.e. low source activity) after each successive cutting event. The reason for this is because stored TNC reserves act as a buffer for insufficient source activity lost after foliage removal and are a tree's capital for growth during such periods (Li et al., 2002). After each cutting cycle, there was an exhaustion of stored reserves because reserves were facilitating resprouting as well as the removal of photosynthetically active material, leading to trees relying on stored reserves for growth and maintenance.

Trees exposed to eight cutting events produced the lowest leaf numbers compared to trees exposed to one cutting event, which provided evidence to support this suggestion. Other studies have reported similar results in *Miconia albicans* Triana and *Clidemia sericea* D. Don (Miyanishi and Ellman, 1986), in *Gliricidia sepium* Jacq. and in *G. sepium* and *Leucaena leucocephala* Lam. (Latt et al., 2000). Numerous studies on fire have shown that resprouting capacity is reduced under short fire intervals (Cruz et al., 2003, Paula and Ojeda, 2011).

Reduced vigour of resprouting trees has been related to the increase in disturbance frequency because of the difficulty in rebuilding or maintaining stored energy reserves in storage organs between consecutive disturbances (Bellingham and Sparrow, 2000). This suggests that the recovery period between disturbances is of importance in trees growing in disturbance prone ecosystems. Results from this study support the conceptual framework because repeated cutting of trees leaves no photosynthetic material for fixing carbon compared to repeated browsing. Repeated cutting also

increases the reliance of trees on stored TNC reserves because trees may eventually loose photosynthetic capacity if repeatedly cut. The reliance on TNC reserves also increases if the period between successive cutting events is short. This contributes to the greater effects of repeated cutting on coppice regrowth compared to repeated browsing.

It has been suggested that if there is not enough time between successive cutting events, the carbohydrate reserves will not replenished (Bell et al., 1996, Canadell and Lopez-Soria, 1998). With this idea, it can be proposed that the 3-month recovery time between successive cutting events was not enough to build the stored reserves utilized after cutting. Such a short recovery time between successive cutting events may not be sustainable in the long-term, because repeatedly cut trees required more than the 3-month recovery time for this study. For example, in two tropical savanna shrubs (*Miconia albicans* Triana and *Clidemia sericea* D. Don), a replenishment period of more than a year for starch was required (Miyanishi and Ellman, 1986), while a year was insufficient in *Betula pubescens* Ehrh (Johansson, 1992).

### 6.3 The height of resprouting shoots: browsing, cutting and coppicing nexus

While tree monitoring lasted for just over a year for trees exposed to browsing, and five months for trees repeatedly cut, two possible resprouting patterns can be proposed based on the results. Unbrowsed trees were observed to produce fewer shoots with a lower number of leaves, but with a higher shoot diameter and shoot length. In contrast browsed trees produced a high number of thinner and shorter shoots with more leaves. Under the 'normal' or current resource conditions and no browsing disturbances (Fig. 6.2a), the resprouting of a tree is expected to follow a sigmoid-shaped pattern, with shoots gaining enough height to escape from the browsing or fire zone (Fig. 6.2X) to reach threshold levels. When browsing is introduced, trees are expected to take longer to escape from the critical height disturbance zone, owing to frequent browsing events on leader shoots (Fig. 6.2b).

When frequently browsed trees eventually escape from the disturbance zone, it is proposed that the initial height reduction of browsed resprouting shoots will likely result in trees with thin shoots that are tall and with higher foliage density. As

suggested by Archibald and Bond (2003)**,** this growth response on the scale of the whole tree restricts access by herbivores to the inside of the tree. This is in comparison to unbrowsed trees that would have even taller trees but with thicker shoots and reduced foliage. In both cases though, the regrowth patterns would be determined by an escape from the 'critical height disturbance zone' (i.e. the height of resprouting shoots accessible to herbivores, or another key disturbance in savannas-fire). In the event of an increase in water and nutrient availability, frequently browsed trees are proposed to escape the disturbance zone within a shorter period of time (Fig. 6.2c). This way, frequently browsed trees growing under resource abundant conditions would reach the threshold height quicker than frequently browsed trees in low resource conditions. This is because results from this study show a quicker height recovery for trees resprouting in resource abundant conditions.

For repeatedly cut trees resprouting under 'normal' or current conditions, there is no escape from the disturbance zone (Fig. 6.2e). This means that repeatedly cut trees will not reach the maximum height threshold. Therefore, repeatedly cut trees are prone to frequent fires and also offer a constant supply of browse for herbivores, since there is no escape from the disturbance zone. Such trees are stuck in a 'browse trap' (Staver et al., 2009), a bottleneck limiting tree growth such as the 'fire trap' suggested by Higgins et al. (2000). Assuming that disturbances such as fires are minimal, repeatedly cut trees resprouting under resource abundant conditions are proposed to recover tree height, which is lost after each successive cut, quicker than trees under 'normal' conditions (Fig. 6.2d). This may also imply that repeatedly cut trees in such conditions also escape the disturbance zone during the period before the next cutting event.

The variation in time between disturbances is greater for a natural disturbance (such as a browsing event) compared to a disturbance such as a cutting event. This implies that the probability of having a period of time long enough between browsing events for trees to escape the 'critical disturbance height' is greater for repeatedly browsed trees compared to repeatedly cut trees. In the long term, subjecting trees to repeat cutting may prove unsustainable because trees will not be able to escape the disturbance height. The eventual result may be over-utilization as trees do not receive enough time to replenish stored TNC reserves. Therefore, sustainable harvesting

practices that include rotational cutting cycles can be implemented so that trees can replenish stored TNC reserves.

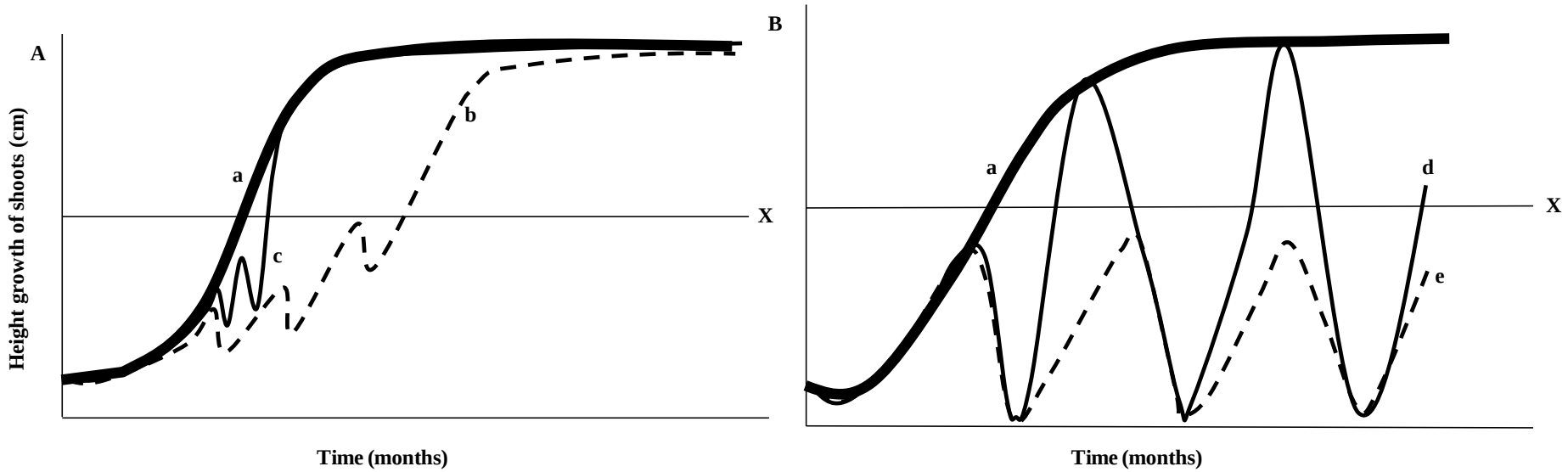



**Figure 6.2.** The height recovery of resprouting trees, A) resprouting in repeatedly browsed trees and B) resprouting in repeatedly cut trees. The dashed curved lines in both graphs represent a proposed recovery of height scenario with increased water and nutrient availability while the solid curved lines represent height escape under current water and nutrient conditions. Line X in both graphs represents the critical height disturbance zone. The thick solid line (a) represents regrowth of a tree under undisturbed conditions, with current resource conditions.

## 6.4 Knowledge contribution

### 6.4.1 Self thinning

Shoot numbers on the stumps significantly reduced with time. Rijks et al. (1998) argue that such a decrease in the number of sprouts per stump could either be random (e.g. insect herbivory or damage); or reflect the result of self-thinning that might correlate with nutrients and water. A result of self-thinning may also correlate with light, or indeed with a composite variable like growth rate or net C-balance of individual shoots, where shoots that are in deficit are likely to be shed. However, for this particular study, the possibility of competition for water or nutrients is dismissed because trees that received high water and nutrient addition also exhibited self-thinning. This study clearly demonstrated that even under resource-abundant scenarios, shoot thinning occurred. A possible explanation is that thinning is genetically determined, instead of being influenced primarily by external factors such as the availability of resources. Through self-thinning, the growth potential of resprouting trees is concentrated on fewer resprouting shoots. Reducing the shoot population can be viewed beneficially in fire prone ecosystems such as savannas because it reduces the fuel load and also allows one more rapid height gain of the remaining shoots (Skov et al., 2004).

### 6.4.2 The effect of water and nutrient supplementation

The research investigated the possible interactive effects of adding water and nutrients on the coppice regrowth of cut tree stumps. There is limited information about the effects of water and nutrient interactions on coppice regrowth in savanna trees. Most research in the past has focused on ecosystems different to savannas in terms of the seasonality of water distribution and also on trees different in terms of physiological growth characteristics compared to resprouting trees. Savanna studies have focussed more on seedlings establishment (Coyle and Coleman, 2005, Scogings and Mopipi, 2008, Wilson and Witkowski, 1998). There have also been studies on forest plantation trees (Coyle et al., 2008, Scott et al., 2004, Albaugh et al., 2004). Through demonstrating that water is limiting for shoot growth but not for number of shoots produced , this study provided new insights into the role of resource limitation on

coppicing. Results from this study suggest that savannas are resource limited for shoot growth characteristics, and the timing and duration of phenological stages as explained below. This has important implications for understanding carbon dioxide enrichment and its effects on resprouting trees. If resprouting trees are limited by other nutrients besides carbon, then perhaps predictions of bush encroachment under $CO_2$ enrichment are overblown.

With a number of studies proposing that either temperature or water availability play a pivotal role in controlling phenological changes (Archibald and Scholes, 2007, Childes, 1989, Chidumayo, 2001, Seghieri et al., 1995), this study offered an opportunity to test the role played by two of savannas' key determinants (water and nutrients) in controlling the timing of plant events such fruit production in an African savanna. Jenerette et al. (2010) also mention that the sensitivity of tree phenology to soil water fluctuations is not well understood. Also, most phenological studies have focused on mature trees. In this study, temperature was consistent across all treatments and the differences, in all likelihood, were as a result of varying water and nutrient levels. Through showing that an increase in water and nutrients extends the growing season well into the dry season, and also delays the yellowing of leaves, this study provided specific information about the role played by water and nutrients in prolonging the effective growing season of supplemented *T. sericea* trees, and not savanna trees in general.

### 6.4.3 Browsing effects

There is limited information about the response of resprouting trees to browsing. Most of the research has also focused on how seedlings or mature trees respond to either defoliation or simulated browsing. Through demonstrating that browsing produces an initial compensatory response in terms of photosynthesis and shoot production, while also reducing shoot diameter and shoot length, this study provided evidence of the negative effects of exposing resprouting trees to a certain period of browsing.

### 6.4.4 Repeated cutting effects

A tree can only tolerate disturbances/cutting cycles to a certain level (Landhausser and Lieffers, 2002). Therefore, a resprouting tree has to compromise between either replenishing depleted reserves or utilizing carbohydrates to grow and support existing plant parts (Schutz et al., 2009). Through exposing trees to different cutting regimes, this study demonstrated that the study species can be exposed to at least more than 6 cutting events, and maintain a certain level of resprouting capacity (as shown by higher shoot production in trees exposed to 8-cutting cycles). This study also demonstrated that cutting trees once has a bigger impact in terms of decreasing the stored TNC reserves compared to how cutting a tree 8-times decreases TNC. Knowing the threshold in terms of the effects of cutting on TNC reserves would be critical in savannas considering that these are disturbance prone ecosystems.

### 6.4.5 Browsing *vs* repeated cutting effects

This study did not explicitly compare the effects of subjecting trees to browsing and repeated cutting, but through subjecting resprouting trees to the different forms of disturbances, the study showed the level of effects of the disturbances on resprouting trees.

## 6.5 Management considerations and recommendations

The resprouting ability of a tree after a single or many cutting events allows a tree to persist, recover lost leaf area and height. It is considered an important component of plant life history (Bond and Midgley, 2001), with implications for recovery and sustainable utilization of trees. The capacity to regenerate is dependent not only on the resource availability, but also on the level of storage non-structural carbohydrates. Management implications and recommendations that can be drawn from this study include;

1. Although an increase in resource availability in the form of water and nutrients increased the thickness and length of resprouting shoots, such an increase did not result in an increase in shoot production, in terms of number of shoots. With

reference to low resource environments, high shoot production can be beneficial through increasing the photosynthetic tissue to capture light and fix high carbon levels. The recovery time of cut trees to the desired shoot size is shorter under high water and nutrients i.e. resprout shoots will exhibit quicker growth and reach maximum length and diameter within a shorter period compared to low water and nutrient conditions. This means that coppice regrowth can be harvested at shorter intervals under higher resource conditions.

2. An increase in resource availability will extend the period in which coppicing trees remain green. This has implications on the length of time resprouting trees are photosynthetically active because carbon gain will be higher for trees in higher water and nutrient conditions. Adding water and nutrients may be beneficial in increasing growth characteristics, although it might not necessarily increase biomass production. In other words, adding water and nutrients to cut trees may increase the regrowth of trees to reach pre-disturbance height in a shorter period of time, but such a growth pattern may not directly result in an increase in biomass production when cut trees receive water and nutrients.
3. An increase in the number of cutting cycles a tree is exposed to will deplete stem stored TNC reserves. The period between successive cutting events would be critical to replenishing stored TNC reserves. This can be viewed as the period of recovery (cutting interval) that resprouting trees are exposed to between successive disturbances. A low level of stored TNC reserves may decrease allocation patterns towards higher production and may eventually contribute towards mortality. In order to ensure sustainable utilization when cutting trees, it is recommended that the minimal threshold levels of stem stored carbohydrates should be established. This would be key in guiding ecologists and resource managers regarding the period of recovery between successive cutting events, or the number of cutting cycles a tree can tolerate before stored reserves are exhausted. When trees are cut at short intervals of three months for e.g. firewood, rotational cutting would be beneficial to allow trees a period to rebuild carbohydrate reserves. It is proposed that a rotational period or recovery time of at least more than six months should be given to trees so as to replenish part of stored reserve mobilized after the initial harvest.
4. Browsing on resprouting trees produces a compensatory growth response, with browsed trees recording higher shoot production compared to unbrowsed trees.

Since browsing significantly reduces resprouting vigour and height growth of resprouting shoots, it is recommended that browsing should be kept minimal in resprouting trees because escape from the browsing height is critical for resprouting trees (Jones et al., 2009). After escape from the 'browsing height', resprouting trees can regrow and possibly recover lost biomass if not exposed to further browsing events. Alternatively, it is recommended that trees can be cut at a greater height because resultant resprout shoots will regrow from a height that may not be accessible to some browsers, thereby limiting browsing effects.

## 6.6 Suggestions for future research arising from the study

- The experiments in this study involved grass removal around the individual resprouting tree stumps. This was done so as to remove competition with resprouting trees for resources. While this eliminated competition with grass or other vegetation, it did not allow for interactions between nutrient availability and the presence of competing vegetation such as grass on patterns of resprouting intensity, the nutrient capture during resprouting and the structure of the shoot population of each plant to be studied. Competition for resources cannot be dismissed in savanna ecosystems, where water and nutrients are considered limiting (Sankaran et al., 2008). In savanna ecosystems, the capacity of trees to capture and utilize nutrients may become a vital part in terms of resprouting ability in the context of climate change with, for example, more variable rainfall and nutrient deposition which may lead to steeper gradients in nutrient supply thus affecting the resprouting capacity of savanna trees. Thus the ability of resprouting savanna trees to capture available resources in the presence of varying competition levels should be considered as this may be important for savanna trees to remain persistent and to maintain current areas of distribution. In this case, competition with neighbouring nearest uncut or even cut trees can be considered. Comparisons can then be made between resprouting under uncut neighbouring trees vs. cut neighbouring trees.
- Although the rainfall figures during the study were almost the same with the long-term average monthly values, the month of February 2012 received very

high rainfall amounts. It is proposed that in such an event, the addition or supplementing values should be adjusted accordingly so as to match months that would have either received high amounts of rainfall or drought months during the wet or dry seasons.

- The standing biomass was not calculated in this study for the trees that received water and nutrient addition, and also for the trees that were exposed to a five month period of browsing. It is proposed that biomass production can be calculated at the end of such an experiment so as to compare treatment effects. Even with differing growth and allocation patterns, it is possible that the standing biomass ends up similar for the respective treatments.
- Water was applied directly to the tree stump, with the assumption that most of the water added was accessible to tree roots. Some of the main roots that spread out from the stump may not have accessed the water added. It is acknowledged that this approach may not have simulated rainfall events, but in justification of the approach used, a significant amount of water is funnelled down the tree trunk and deposited immediately at the base of the trunk during a rain storm.
- Exposing trees to browsing resulted in trees exhibiting a period of compensatory response through high shoot production, high leaf nitrogen and stomatal conductance. It would be interesting to investigate how such changes in foliar properties have an effect on the stored carbohydrate reserves considering the relationship between foliar nitrogen, photosynthesis and the changes in sink-source stored reserves (Coley and Barone, 1996, Bergstrom, 1992).
- This study tested the effects of adding water and nutrients, and the effects of repeated cutting on total carbohydrate reserves. Comparing the changes in stem and root stored reserves would be interesting as this would reflect the stored reserves utilized most and relied upon by resprouting plants.
- The study on the effects of repeated cutting sampled stored TNC reserves once during the study. Alternatively, stored TNC reserves can be sampled after every cut so as to track the changes in stored TNC reserves. The number of cutting cycles can also be increased so as to establish the maximum number of cutting events the study species can tolerate before mortality.

## 7. REFERENCES


**Abbot PG, Lowore JD. 1999**. Characteristics and management potential of some indigenous firewood species in Malawi. *Forest Ecology and Management*, **119**: 111-121.

**Abe H, Nakai T, Utsumi Y, Kagawa A. 2003**. Temporal water deficit and wood formation in *Cryptomeria japonica*. *Tree Physiology*, **23**: 859-863.

**Albaugh TJ, Lee Allen A, Dougherty PM, Johnesen KH. 2004**. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *Forest Ecology and Management*, **192**: 3-19.

**Allen JC. 1985**. Wood energy and preservation of woodlands in semi-arid developing countries; The case of Dodoma Region, Tanzania. *Journal of Development Economics*, **19**: 59-84.

**Amri E. 2011**. Germination of *Terminalia sericea* Buch. ex seeds: The effects of temperature regime, photoperiod, gibberellic acid and potassium nitrate. *International Journal of Applied Biology and Pharmaceutical Techonology*, **2**: 104-110.

**Archibald S, Bond WJ. 2003**. Growing tall vs growing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments. *Oikos*, **102**: 3-14.

**Archibald S, Bond WJ, Stock WD, Fairbanks DHK. 2005**. Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications* **15**: 96-109.

**Archibald S, Scholes RJ. 2007**. Leaf green-up in a semi-arid African savanna – separating tree and grass responses to environmental cues. *Journal of Vegetation Science*, **18**: 583-594.

**Avohou TH, Houehounha R, Glele-Kakai R, Assogbadjo AE, Sinsin B. 2011**. Firewood yield and profitability of a traditional *Daniellia oliveri* short-rotation coppice on fallow lands in Benin. *Biomass and Bioenergy*, **35**: 562-571.

**Ayres E, Heath J, Possell M, Black HIJ, Kerstiens G, Bardgett RD. 2004**. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. *Ecology Letters*, **7**: 469-479.

**Banda T, Schwartz MC, Caro T. 2006**. Woody vegetation structure and composition along a protection gradient in a miombo ecosystem of western Tanzania. *Forest Ecology and Management* **230**: 179-185.

**Baxter PWJ, Getz WM. 2005**. A model-framed evaluation of elephant effect on tree and fire dynamics in African savannas. *Ecological Applications*, **15**: 1331-1341.

**Beer C, Ciais P, Reichstein M, Baldocchi D, Law BE, Papale D, Soussana J-F, Amman C, Buchman N, Frank D, Gianelle D, Janssens IA, Knohl A, Kostner B, Moors E, Roupsard O, Verbeeck H, Vesala T, Williams CA, Wohlfahrt G. 2009**. Temporal and among-site variability of inherent water use efficiency at the ecosystem level. *Global Biogeochemical Cycles*, **23**: 1-13.

**Bell T, Ojeda F. 1999**. Underground starch storage in *Erica* species of the Cape Floristic Region-differences between seeders and resprouters. *New Phytology*, **144**: 143-152.

**Bell TL, Pate JS, Dixon KW. 1996**. Relationships between fire response, morphology, root anatomy and starch distribution in South-West Australian Epacridaceae. *Annals of Botany,* **77**: 357-364.
**Bellingham PJ, Sparrow AD. 2000**. Resprouting as a life history strategy in woody plant communities. *Oikos,* **89**: 409-416.
**Bergstrom R. 1992**. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science*, **3**: 315-324.
**Bergstrom R, Skarpe C, Danell K. 2000**. Plant responses and herbivory following simulated browsing and stem cutting of *Combretum apiculatum*. *Journal of Vegetation Science,* **11**: 409-414.
**Boivin-Chabot S, Margolis HA, Weber JC. 2004**. Variation in coppice-shoot growth among provenances of *Calycophyllum spruceanum* Benth. in the Peruvian Amazon Basin. *Forest Ecology and Management,* **198**: 249-260.
**Bond WJ, Midgley GF. 2012**. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Roral Society B,* **367**: 601-612.
**Bond WJ, Midgley JJ. 2001**. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution,* **16**: 45-51.
**Bond WJ, Midgley JJ. 2003**. The evolutionary ecology of sprouting in woody plants. *International Journal for Plant Science,* **164**: 103-114.
**Bond WJ, Woodward FI, Midgley GF. 2005**. The global distribution of ecosystems in a world without fire. *New Phytologist,* **165**: 525-538.
**Borchert R. 1994**. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology,* **75**: 1437-1449.
**Bowen BJ, Pate JS. 1992**. The sigificance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifoliaI* R. Br. (Proteaceae). *Annals of Botany,* **72**: 7-16.
**Bowen BJ, Pate JS. 1993**. The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifoliaI* R. Br. (Proteaceae). *Annals of Botany,* **72**: 7-16.
**Broadhead JS, Ong CK, Black CR. 2003**. Tree phenology and water availability in semi-arid agroforestry systems. *Forest Ecology and Management,* **180**: 61-73.
**Brudvig LA, Asbjornsen H. 2008**. Patterns of oak regeneration in a Midwestern savanna restoration experiment. *Forest Ecology and Management,* **255**: 3019-3025.
**Bryant JP, Chapin III FS, Klein DR. 1983**. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos,* **40**: 357-368.
**Bryant JP, Reichardt PB, Clausen TP. 1992**. Chemically mediated interactions between woody plants and browsing mammals. *Journal of Range Management,* **45**: 18-24.
**Calvo L, Tarrega R, Luis E, Valbuena L, Marcos E. 2005**. Recovery after experimental cutting and burning in three shrub communities with different dominant species. *Plant Ecology,* **180**: 175-185.
**Canadell J, Lopez-Soria L. 1998**. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology,* **12**: 31-38.
**Cardoso FCG, Marques R, Botosso PC, Marques MCM. 2012**. Stem growth and phenology of two tropical trees in contrasting soil conditions. *Plant Soil,* **354**: 269-281.

**Carpenter LT, Pezeshki SR, Shields Jr FD. 2008**. Responses of nonstructural carbohydrates to shoot removal and soil moisture treatments in *Salix nigra*. *Trees,* **22**: 737-748.
**Carr JD. 1994**. *The propagation and cultivation of indigenous trees and shrubs on the Highveld*, Johannesburg, Sandton Nature Conservation Society and the Tree Society of Southern Africa.
**Carson WP, Root RB. 1999**. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia,* **121**: 260-272.
**Casabon C, Pothier D. 2007**. Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec. *Forest Ecology and Management,* **253**: 112-119.
**Casotti G, Bradley JS. 1991**. Leaf nitrogen and its effects on the rate of herbivory on selected eucalypts in the jarrah forest. *Forest Ecology and Management,* **41**: 161-177.
**Castell C, Terradas J. 1994**. Effects of water and nutrient availability on water relations, gas exchange and growth rate of mature plants and resprouts of *Arbutus unedo* L. *Annals of Botany,* **73**: 595-602.
**Chapin III FS. 1991**. Integrated responses of plants to stress. *Bioscience,* **41**: 29-36.
**Chapin III FS, Schulze E, Mooney HA. 1990**. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics,* **21**: 423-447.
**Chapin III SF, Autumn K, Pugnaire F. 1993**. Evolution of suites of traits in response to environmental stress. *The American Naturalist,* **142**: 78-92.
**Chapin III SF, Bloom AJ, Field CB, Waring RH. 1987**. Plant responses to multiple environmental factors. *BioScience,* **37**: 49-57.
**Chaves MM, Maroco JP, Pereira JS. 2003**. Understanding plant responses to drought-from genes to whole plant. *Functional Plant Biology,* **30**: 239-264.
**Cheng L, Fuchigami LH. 2002**. Growth of young apple trees in relation to reserve nitrogen and carbohydrates. *Tree Physiology,* **22**: 1297-1303.
**Chiariello N, Roughgarden J. 1984**. Storage allocation in seasonal races of an annual plant: Optimal versus actual allocation. *Ecology,* **65**: 1290-1301.
**Chidumayo EN. 2001**. Climate and phenology of savanna vegetation in Southern Africa. *Journal of Vegetation Science,* **12**: 347-354.
**Childes SL. 1989**. Phenology of nine common woody species in semi-arid, deciduous Kalahari Sand vegetation. *Vegetation,* **79**: 151-163.
**Chirwa PW, Syampungani S, Geldenhuys CJ. 2008**. The ecology and management of the Miombo woodlands for sustainable livelihoods in southern Africa: the case for non-timber forest products. *Southern Forests: a Journal of Forest Science,* **70**: 237-245.
**Chmielewski FM, Rötzer T. 2001**. Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology,* **108**: 101-112.
**Chu CC, Field CB, Mooney HA. 1996**. Effects of CO2 and nutrient enrichment on tissue quality of two California annuals. *Oecologia,* **107**: 433-440.
**Clarke PJ, Lawes MJ, Midgley JJ. 2010**. Resprouting as a key functional trait in woody plants – challenges to developing new organizing principles. *New Phytologist,* **188**: 651-654.
**Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2012**. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist,* **1**: 1-17.

**Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013**. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist,* **197**: 19-35.

**Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD. 2007**. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution,* **22**: 357-365.

**Coates-Palgrave M. 2002.** Trees of Southern Africa. In: Coates-Palgrave K ed. *Trees of Central Africa.* Cape Town, Struik Publishers.

**Cobb WR, Will RE, Daniels RF, Jacobson MA. 2008**. Aboveground biomass and nitrogen in four short-rotation woody crop species growing with different water and nutrient availabilities. *Forest Ecology and Management,* **255**: 4032-4039.

**Coley PD, Barone JA. 1996**. Herbivory and plant defenses in Tropical forests. *Annual Review of Ecology and Systematics,* **27**: 305-335.

**Coley PD, Bryant JP, Chapin III FS. 1985**. Resource availability and plant antiherbivore defense. *Science,* **230**: 895-906.

**Cooper SM, Owens MK, Spalinger DE, Ginnett TF. 2003**. The architecture of shrubs after defoliation and the subsequent feeding behavior of browsers. *Oikos,* **100**: 387-393.

**Covelo F, Gallardo A. 2002**. Effect of pine harvesting on leaf nutrient dynamics in young oak trees at NW Spain. *Forest Ecology and Management,* **167**: 161-172.

**Coyle DR, Coleman MD. 2005**. Forest production responses to irrigation and fertilization are not explained by shifts in allocation. *Forest Ecology and Management,* **208**: 137-152.

**Coyle DR, Coleman MD, Aubrey DP. 2008**. Above- and below-ground biomass accumulation, production, and distribution of sweetgum and loblolly pine grown with irrigation and fertilization. *Canadian Journal of Forest Research,* **38**: 1335-1348.

**Craine JM, Balantyne F, Peel M, Zambatis N, Morrow C, Stock WD. 2009**. Grazing and landscape controls on nitrogen availability across 330 South African savanna sites. *Austral Ecology,* **34**: 731-740.

**Craine JM, Morrow C, Stock WD. 2008**. Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytologist,* **179**: 829-836.

**Crawley MJ. 1983**. *Herbivory: The dynamics of animal-plant interactions,* London, Blackwell.

**Crook C, Clapp RA. 1998**. Is market - oriented forest conservation a contradiction in terms? *Environmental Conservation,* **25**: 131.

**Cruz A, Moreno JM. 2001**. Seasonal course of total non structural carbohydrates in the lignotuberous mediterranean type shrub *Erica australis*. *Oecologia,* **128**: 343-350.

**Cruz A, Perez B, Moreno JM. 2003**. Plant stored reserves do not drive resprouting of the lignotuberous shrub *Erica australis*. *New Phytologist,* **157**: 251-261.

**Cruz A, Perez B, Quintana JR, Moreno JM. 2002**. Resprouting in the Mediterranean-type shrub *Erica australis* afffected by soil resource availability. *Journal of Vegetation Science,* **13**: 641-650.

**da Silva CEM, Goncalves JFD, Feldpausch TR. 2008**. Water-use efficiency of tree species following calcium and phosphorus application on an abandoned

pasture, central Amazonia, Brazil. *Environmental and Experimental Botany*, **64**: 189-195.

**Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D. 2000**. Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, **10**: 449-469.

**Damascos MA, Barthélémy D, Ezcurra C, Martínez P, Brion C. 2008**. Plant phenology, shoot growth, and branching pattern in *Mulinum spinosum* (Apiaceae), a cushion shrub of the arid Patagonian steppe of Argentina. *Journal of Arid Environments*, **72**: 1977-1988.

**Danell K, Bergström R, Edenius L. 1994**. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Journal of Mammalogy*, **75**: 833-844.

**De Bie S, Ketner P, Paasse M, Geerling C. 1998**. Woody plant phenology in the West Africa savanna. *Journal of Biogeography* **25**: 883-900.

**Del Tredici P. 2001**. Sprouting in temperate trees: A morphological and ecological review. *The Botanical Review*, **67**: 121-140.

**Dickmann DI, Nguyen PV, Pregitzer KS. 1996**. Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. *Forest Ecology and Management*, **80**: 163-174.

**Drake BG, Gonzàlez-Meler MA, Long SP. 1997**. More efficient plants: a consequence of rising atmospheric CO2?. *Annual review of plant biology*, **48**: 609-639.

**Dreyer LL, Esler KJ, Zietsman J. 2006**. Flowering phenology of South African *Oxalis*-possible indicator of climate change? *South African Journal of Botany*, **72**: 150 - 156.

**Druege U, Zerche S, Kadner R, Ernst M. 2000**. Relation between nitrogen status, carbohydrate distribution and subsequent rooting of Chrysanthemum cuttings as affected by pre-harvest nitrogen supply and cold-storage. *Annals of Botany*, **85**: 687-701.

**Du Toit JT. 1990**. Regrwoth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology*, **71**: 149-154.

**Edwards EJ, Downie AF, Clingeleffer PR. 2011**. A simple microplate assay to quantify non-structural carbohydrates of Grapevine tissues. *American Journal of Enology and Viticulture*, **62**: 133-137.

**Eggleton M, Zegada-Lizarazu W, Ephrath J, Berliner P. 2007**. The effect of brackish water irrigation on the above- and below-ground development of pollarded *Acacia saligna* shrubs in an arid environment. *Plant Soil*, **299**: 141–152.

**El Omari B, Aranda X, Verdaguer D, Pascual G, Fleck I. 2003**. Resource remobilization in *Quercus ilex* L. resprouts. *Plant and Soil*, **252**: 349-357.

**Ellsworth DS, Tyree MT, Parker BL, Skinner M. 1994**. Photosynthesis and water-use efficiency of sugar maple (*Acer saccharum*) in relation to pear thrips defoliation. *Tree Physiology*, **14**: 619-632.

**Eloff JN, Katerere DR, McGaw LJ. 2008**. The biological activity and chemistry of the southern African Combretaceae. *Journal of Ethnopharmacology*, **119**: 686-699.

**Erdmann TK, Nair PKR, Kang BT. 1993**. Effects of cutting frequency and cutting height on reserve carbohydrates in *Gliricidia sepium* (Jacq.) Walp. *Forest Ecology and Management*, **57**: 45-60.

**Eriksen SEH, Watson HK. 2009**. The dynamic context of southern African savannas: investigating emerging threats and opportunities to sustainability. *Environmental Science & Policy,* **12**: 5-22.
**Etienne M. 1989**. Non destructive methods for evaluating shrub biomass: a review. *Acta Ecologica* **10**: 115-128.
**Ewers BE, Oren R, Albaugh TJ, Dougherty PM. 1999**. Carry-over effects of water and nutrient supply on water use of Pinus taeda. *Ecological Applications,* **9**: 513-525.
**Fay PA, Hartnett DC, Knapp AK. 1993**. Increased photosynthesis and water potentials in *Silphium integrifolium* galled by cynipid wasps. *Oecologia,* **93**: 114-120.
**Fenner M. 1998**. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics,* **1**: 78-91.
**Fensham RJ, Fairfax RJ, Archer SR. 2005**. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology,* **93**: 596-606.
**Ferm A, Kauppi A. 1990**. Coppicing as a means for increasing hardwood biomass production. *Biomass,* **22**: 107-121.
**Fernando S, Marina F, Sonia M, Alfonso E. 2008**. Effects of simulated herbivory on photosynthesis and N resorption efficiency in *Quercus pyrenaica* Willd. saplings. *Trees,* **22**: 785-793.
**Fircks YV, Sennerby-Forsse L. 1998**. Seasonal fluctuations of starch in root and stem tissues of coppiced *Salix viminalis* plants grown under two nitrogen regimes. *Tree Physiology,* **18**: 243-249.
**Fornara DA, Du Toit JT. 2007**. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology,* **88**: 200-209.
**Forrester D, Bauhus J, Connell M. 2003**. Competition in thinned Silvertop Ash (*Eucalyptus sieberi* L. Johnson) stands from early coppice growth. *Forest Ecology and Management,* **174**: 459-475.
**Franklin JF, Forman TT. 1987**. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology,* **1**: 5-18.
**Fuller RJ, Warren MS. 1990**. *Coppiced woodlands: their management for wildlife.*, Britain, Joint Nature Conservation Committee.
**Gadd ME, Young TP, Palmer TM. 2001**. Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *OIKOS,* **92**: 515-521.
**Garcia H, Nygren P, Desfontaines L. 2001**. Dynamics of nonstructural carbohydrates and biomass yield in a fodder legume tree at different harvest intensities. *Tree Physiology,* **21**: 523-531.
**Gaugris JY, Van Rooyen MW, Bothma JdP. 2008**. Growth rate of selected woody species in northern Maputaland, KwaZulu-Natal, South Africa. *South African Journal of Botany,* **74**: 85-92.
**Gignoux J, Lahoreau G, Julliard R, Barot S. 2009**. Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology,* **97**: 484-495.
**Govender N, Trollope WSW, Van Wilgen BW. 2006**. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology,* **43**: 748-758.
**Griffiths ME. 1959**. A revision of the African Species of *Terminalia*. *Journal of the Linnean Society of London Botany,* **25**: 364.

**Hara T, Kimura M, Kikuzawa K. 1991**. Growth patterns of tree height and stem diameter in populations of *Abies Veitchii, A. Mariesii* and *Betula Ermanii*. *Journal of Ecology,* **79**: 1085-1098.
**Hardesty LH. 1984**. The challenge of integrated brush management in Semi-arid tropics. *Rangelands,* **6**: 249-253.
**Hardesty LH. 1987**. Coppicing: Using a forester's tool on rangelands. *Rangelands,* **9**: 129-132.
**Hardesty LH, Box TW. 1988**. Defoliation impacts on coppicing browse species in north-east Brazil. *Journal of Range Management,* **41**: 1.
**Heichel GH, Turner NC. 1983**. C02 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia,* **57**: 14-19.
**Henderson DE, Jose S. 2010**. Biomass production potential of three short rotation woody crop species under varying nitrogen and water availability. *Agroforestry Systems,* **80**: 259-273.
**Hetherington AM, Woodward IF. 2003**. The role of stomata in sensing and driving environmental change. *Nature,* **424**: 901-908.
**Higgins SI, Bond WJ, Trollope WSW. 2000**. Fire, resprouting and variability: A recipe for grass-tree coexistence in Savanna. *Journal of Ecology,* **88**: 213-229.
**Higgins SI, Delgado-Cartay MD, February EC, Combrink HJ. 2011**. Is there a temporal niche separation in the leaf phenology of savanna trees and grasses? *Journal of Biogeography,* **38**: 2165-2175.
**Hoffmann WA, Schroeder W, Jackson RB. 2002**. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysics Research Letters,* **29**: 2052-2056.
**Holdo RM. 2005**. Stem mortality following fire in Kalahari sand vegetation: Effects of frost, prior damage, and tree neighbourhoods. *Plant Ecology,* **180**: 77-86.
**Holdo RM. 2007**. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications,* **17**: 558–568.
**Holdo RM, Holt RD, Fryxell JM. 2009**. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications,* **19**: 95-109.
**Houehounha R, Avohou H, Gaoue O, Assogbadjo A, Sinsin B. 2010**. Weed removal improves coppice growth of *Daniellia oliveri* and its use as fuelwood in traditional fallows in Benin. *Agroforestry Systems,* **78**: 115-125.
**Howe GA, Jander G. 2008**. Plant immunity to insect herbivores. *Annual Review in Plant Biology,* **59**: 41-66.
**Hrabar H, Hattas D, Du Toit JT. 2009**. Differential effects of defoliation by mopane caterpillars and pruning by African elephants on the regrowth of C*olophospermum mopane* foliage. *Journal of Tropical Ecology,* **25**: 301-309.
**Hytonen J, Kaunisto S. 1999**. Effect of fertilization on the biomass production of coppiced mixed birch and willow stands on a cut-away peatland. *Biomass and Bioenergy,* **17**: 455-469.
**Ibrahima A, Mapongmetsem PM, Bouitang D, Hassana B. 2007**. Regeneration of some fuelwood tree species of humid savanna of Adamawa, Cameroon: effects of season and cutting height. *Ghana Journal of Science,* **47**: 45-57.
**Iwasa Y, Kubo T. 1997**. Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology,* **11**: 41-65.

**Jaoudé RA, Lagomarsino A, De Angelis P. 2011**. Impacts of nitrogen fertilisation and coppicing on total and heterotrophic soil CO2 efflux in a short rotation poplar plantation. *Plant Soil* **339**: 219-230.

**Jenerette GD, Scott RS, Huete AR. 2010**. Functional differences between summer and winter season rain assessed with MODIS-derived phenology in a semi-arid region. *Journal of Vegetation Science,* **21**: 16-30.

**Johansson T. 1992**. Sprouting of 2- to 5-year-old birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth) in relation to stump height and felling time. *Forest Ecology and Management,* **53**: 263-281.

**Jolly WM, Neman R, Running SW. 2005**. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change and Biology,* **11**: 619-632.

**Jolly WM, Running SW. 2004**. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari. *Global Change Biology,* **10**: 303-308.

**Jones BE, Lile DF, Tate KW. 2009**. Effect of simulated browsing on Aspen regeneration: Implications for restoration. *Rangeland Ecology and Management,* **62**: 557-563.

**Kabeya D, Sakai A, Matsui K, Sakai S. 2003**. Resprouting ability of *Quercus crispula* seedlings depends on the vegetation cover of their microhabitats. *Journal of Plant Research,* **116**: 207-216.

**Kabeya D, Sakai S. 2005**. The relative importance of carbohydrate and nitrogen for the resprouting ability of *Quercus crispula* seedlings. *Annals of Botany,* **96**: 479-488.

**Kaitaniemi P, Neuvonen S, Nyyssonen T. 1999**. Effects of cumulative defoliations on growth, reproduction, and insect resistance in mountain birch. *Ecology,* **80**: 524-532.

**Karlsson SP. 1985**. Effects of water and mineral nutrient supply on a deciduous and an evergreen dwarf shrub:*Vaccinium uliginosum* L. and *V. vitis-idaea* L. *Holarctic Ecology,* **8**: 1-8.

**Kaschula S, Twine W, Scholes M. 2005a**. Coppice harvesting of fuelwood species on a South African common: Utilizing scientific and indigenous knowledge in Community Based Natural Resource Management. *Human Ecology,* **33**: 387-418.

**Kaschula SA, Twine WC, Scholes MC. 2005b**. The effect of catena position and stump characteristics on the coppice response of three savannah fuelwood species. *Environmental Conservation,* **32**: 76-84.

**Katjiua M, Ward D. 2006a**. Resistance and tolerance of *Terminalia sericea* trees to simulated herbivore damage under different soil nutrient and moisture conditions. *Journal of Chemical Ecology,* **32**: 1431-1443.

**Katjiua MLJ, Ward D. 2006b**. Cattle diet selection during the hot-dry season in a semi-arid region of Namibia. *African Journal of Range & Forage Science,* **23**: 59-67.

**Kennedy AD. 1998**. Coppicing of *Tarconanthus camphorates* (Compositae) as a source of sustainable fuelwood production: an example from the Laikipia Plateau, Kenya. *African Journal of Ecology,* **36**.

**Kennedy AD, Potgieter ALR. 2003**. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology,* **167**: 179-192.

**Khan ML, Tripathi RS. 1986**. Tree regeneration in a disturbed sub-tropical wet hill forest of north-east India: Effect of stump diameter and height on sprouting of four tree species. *Forest Ecology and Management,* **17**: 199-209.
**Kohyani TP, Bossuyt B, Bonte D, Hoffmann M. 2008**. Grazing as a management tool in dune grasslands: Evidence of soil and scale dependence of the effect of large herbivores on plant diversity. *Biological Conservation,* **141**: 1687-1694.
**Kosola KR, Dickmann DI, Paul EA, Parry D. 2001**. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia,* **129**: 65-74.
**Kozlowski TT. 1992**. Carbohydrate sources and sinks in woody plants. *Botanical Reviews,* **58**: 107–223.
**Kozlowski TT. 2002**. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. *Forest Ecology and Management,* **158**: 195-221.
**Kraaij T, Ward D. 2006**. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology,* **186**: 235-246.
**Krauss KW, Allen JA. 2003**. Factors influencing the regeneration of the mangrove *Bruguiera gymnorrhiza* (L.) Lamk. on a tropical Pacific island. *Forest Ecology and Management,* **176**: 49-60.
**Kudo G. 1996**. Herbivory pattern and induced responses to simulated herbivory in *Quercus mongolica* var. *grosseserrata*. *Ecological Research,* **11**: 283-289.
**Kurokawa H, Kitahashi Y, Koike T, Lai J, Nakashizuka T. 2004**. Allocation to defense or growth in *Dipterocarp* forest seedlings in Borneo. *Oecologia,* **140**: 261-270.
**Kutsch WL, Hanan N, Scholes RJ, McHugh I, Kubheka W, Eckhardt H, Williams C. 2008**. Response of carbon fluxes to water relations in a savanna ecosystem in South Africa. *Biogeosciences Discuss,* **5**: 2197-2235.
**Lamont BB, Enright NJ, He T. 2011**. Fitness and evolution of resprouters in relation to fire. *Plant Ecology,* **212**: 1945-1957.
**Landhausser SM, Lieffers VJ. 2002**. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology,* **90**: 658-665.
**Latt CR, Nair PKR, Kang BT. 2000**. Interactions among cutting frequency, reserve carbohydrates, and post-cutting biomass production in *Gliricidia sepium* and *Leucaena leucocephala*. *Agroforestry Systems,* **50**: 27-46.
**Laureysens I, Deraedt W, Indeherberge T, Ceulemans R. 2003**. Population dynamics in a 6-year old coppice culture of poplar. I. Clonal differences in stool mortality, shoot dynamics and shoot diameter distribution in relation to biomass production. *Biomass and Bioenergy,* **24**.
**Laureysens I, Deraedt W, Indeherberge T, Ceulemans R. 2005**. Population dynamics in a 6-year old coppice culture of poplar I. Clonal differences in stool mortality, shoot dynamics and shoot diameter distribution in relation to biomass production. *Biomass and Bioenergy,* **24**.
**Lavigne MB, Little CHA, Major JE. 2001**. Increasing the sink:source balance enhances photosynthetic rate of 1-year-old balsam fir foliage by increasing allocation of mineral nutrients. *Tree Physiology,* **21**: 417-426.
**Lawes MJ, Clarke PJ. 2011**. Ecology of plant resprouting: populations to community responses in fire-prone ecosystems. *Plant Ecology,* **212**: 1937-1943.

**Lawes MJ, Obiri JAF. 2003**. Using the spatial grain of regeneration to select harvestable tree species in subtropical forest. *Forest Ecology and Management,* **184**: 105-114.
**Lehtila K, Syrjanen K. 1995**. Compensatory responses of two *Melampyrum* species after damage. *Functional Ecology,* **9**: 511-517.
**Lévesque M, McLaren KP, McDonald MA. 2011**. Recovery and dynamics of a primary tropical dry forest in Jamaica, 10 years after human disturbance. *Forest Ecology and Management,* **262**: 817-826.
**Li J, Loneragan WA, Duggin JA, Grant CD. 2004**. Issues affecting the measurement of disturbance response patterns in herbaceous vegetation: A test of the intermediate disturbance hypothesis. *Plant Ecology,* **172**: 11-26.
**Li MH, Hoch G, Körner C. 2002**. Source/sink removal affects mobile carbohydrates in *Pinus cembra* at the Swiss treeline. *Trees,* **16**: 331-337.
**Liedloff AC, Cook GD. 2007**. Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the Flames simulation model. *Ecological modelling,* **201**: 269–282.
**Liu Z, Dickmann DI. 1996**. Effects of water and nitrogen interaction on net photosynthesis, stomatal conductance, and water-use efficiency in two hybrid poplar clones. *Physilogia Plantarium,* **97**: 507-512.
**Lloret F, Lopez-Soria L. 1993**. Resprouting of *Erica multiflora* after experimental fire treatments. *Journal of Vegetation Science,* **4**: 367-374.
**Lovelock CE, Feller IC, McKee KL, Engelbrecht BMJ, Ball MC. 2004**. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology,* **18**: 25-33.
**Lovett GM, Tobiessen P. 1993**. Carbon and nitrogen assimilation in red oaks (*Quercus rubra* L.) subject to defoliation and nitrogen stress. *Tree Physiology,* **12**: 259-269.
**Luoga EJ, Witkowski ETF, Balkwill K. 2004**. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management,* **189**: 23-35.
**Luostarinen K, Kauppi A. 2005**. Effects of coppicing on the root and stump carbohydrate dynamics in birches. *New Forests,* **29**: 289-303.
**Marchant R. 2010**. Understanding complexity in savannas: climate, biodiversity and people. *Current Opinion in Environmental Sustainability,* **2**: 101-108.
**Maron JL. 1998**. Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology,* **79**: 1281-1293.
**Mason CF, MacDonald SM. 2002**. Responses of ground flora to coppice management in an English woodland – a study using permanent quadrats. *Biodiversity and Conservation,* **11**: 1773-1789.
**Mauricio R. 2000**. Natural selection and the joint evolution of tolerance and resistance as plant defenses. *Evolutionary Ecology,* **14**: 491-507.
**Mbatha KR, Ward D. 2010**. The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. *Journal of Arid Environments,* **74**: 1294-1301.
**McGraw JB, Gottschalk KK, Vavrek MC, Chester AL. 1990**. Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings. *Tree Physiology,* **7**: 247-254.
**McLaren KP, McDonald MA. 2003**. Coppice regrowth in a disturbed tropical dry limestone forest in Jamaica. *Forest Ecology and Management,* **180**: 99-111.

**McMichael BL, Quisenberry JE. 1993**. The impact of the soil environment on the growth of root systems. *Environmental and Experimental Botany,* **33**: 53-61.
**McPherson K, Williams K. 1998**. The role of carbohydrate reserves in the growth, resilience, and persistence of cabbage palm seedlings (*Sabal palmetto*). *Oecologia,* **117**: 460-468.
**Menzel A. 2002**. Phenology: its importance to the global change community. *Climate Change,* **54**: 379-385.
**Midgley JJ, Lawes MJ, Chamaillé-Jammes S. 2010**. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany,* **58**: 1-11.
**Millard P, Proe MF. 1992**. Storage and internal cycling of nitrogen in relation to seasonal growth of Sitka spruce. *Tree Physiology,* **10**: 33-43.
**Miller PM. 1999**. Coppice shoot and foliar crown growth after disturbance of a tropical deciduous forest in Mexico. *Forest Ecology and Management,* **116**: 163-173.
**Miyanishi K, Ellman M. 1986**. The role of root nutrient reserves in regrowth of two savanna shrubs. *Canadian Journal of Botany,* **64**: 1244-1248.
**Moncrieff GR, Kruger LM, Midgley JL. 2008**. Stem mortality of Acacia nigrescens induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. *Journal of Tropical Ecology,* **24**: 655-662.
**Mooney HA, Gulmon SL. 1982**. Constraints on leaf structure and function in reference to herbivory. *BioScience,* **32**: 198-201.
**Morrison KD, Reekie EG. 1995**. Pattern of defoliation and its effect on photosynthetic capacity in *Oenothera biennis*. *Journal of Ecology,* **83**: 759-767.
**Mundim FM, Bruna EM, Vieira-Neto EHM, Vasconcelos HL. 2012**. Attack frequency and the tolerance to herbivory of Neotropical savanna trees. *Oecologia,* **168**: 405-414.
**Murphy BP, Russell-Smith J, Priors LD. 2010**. Frequent fires reduce tree growth in northern Australian savannas: implications for tree demography and carbon sequestration. *Global Change Biology,* **16**: 331-343.
**Murphy J, Riley JP. 1962**. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta,* **27**: 31-36.
**Mwavu EN, Witkowski ETF. 2008**. Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda. *Forest Ecology and Management*, **255**: 982-992.
**Neke KS. 2004**. *The regeneration ecology of savanna woodlands in relation to human utilisation,* PhD, University of the Witwatersrand, Johannesburg.
**Neke KS, Owen-Smith N, Witkowski ETF. 2006**. Comparative resprouting response of Savanna woody plant species following harvesting: the value of persistence. *Forest Ecology and Management,* **232**: 114-123.
**Norman JC. 1989**. Phenology of some tropical woody landscape species in Kumasi, Ghana. I. Observations on flowering. *Landscape and Urban Planning,* **17**: 205-213.
**Noumi Z, Touzard B, Michalet R, Chaieb M. 2010**. The effects of browsing on the structure of *Acacia tortilis* (Forssk.) Hayne ssp. *raddiana* (Savi) Brenan along a gradient of water availability in arid zones of Tunisia. *Journal of Arid Environments,* **74**: 625-631.
**Nowak RS, Caldwell MM. 1984**. A test of compensatory photosynthesis in the filed: implications for herbivory tolerance. *Oecologia,* **61**: 311-318.

**Nygård R, Sawadogo L, Elfving B. 2004**. Wood-fuel yields in short-rotation coppice growth in the north Sudan savanna in Burkina Faso. *Forest Ecology and Management,* **189**: 77-85.

**Nzunda EF, Griffiths ME, Lawes MJ. 2008**. Sprouting by remobilization of above-ground resources ensures persistence after disturbance of coastal dune forest trees. *Functional Ecology,* **22**: 577-582.

**O'Connor TG, Crow VRT. 1999**. Rate and pattern of bush encroachment in Eastern Cape savanna and grassland. *African Journal of Range and Forage Science,* **16**: 26-31.

**Onoda Y, Hikosaka AK, Hirose T. 2004**. Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. *Functional Ecology* **18**: 419-425.

**Osman HE, AboHassan AA. 2010**. Effect of NPK fertilization on growth and dry matter accumulation in Mangrove [*Avicennia marina* (Forssk) vierh] grown in Western Saudi Arabia. *Environmental & Arid Land Agricultural Science,* **21**: 57-70.

**Owen-Smith N, Cooper SM. 1987**. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology,* **68**: 319-331.

**Pahlsson AB. 1992**. Influence of nitrogen fertilization on minerals, carbohydrates, amino acids and phenolic compounds in beech (*Fugus sylvatica* L.) leaves. *Tree Physiology,* **10**: 93-100.

**Palmer SCF, Mitchell RJ, Truscott AM, Welch D. 2004**. Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. *Forest Ecology and Management,* **192**: 251-265.

**Palmer SCF, Truscott AM. 2003**. Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management,* **182**: 31-47.

**Parry MAJ, Keys AJ, Madgwick PJ, Carmo-Silva AE, Andralojc PJ. 2008**. Rubisco regulation: a role for inhibitors. *Journal of Experimental Botany,* **59**: 1569-1580.

**Paula S, Ojeda F. 2006**. Resistance of three co-occurring resprouter *Erica* species to highly frequent disturbance. *Plant Ecology,* **183**: 329-336.

**Paula S, Ojeda F. 2011**. Response to recurrent disturbance in two co-occurring resprouter heath species: the ecological consequences of withstanding herbivores. *Plant Ecology,* **212**: 2035-2045.

**Pepin D, Renaud PC, Boscardin Y, Goulard M, Mallet C, Anglard F, Ballon P. 2006**. Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings-An enclosure-based experiment. *Forest Ecology and Management,* **222**: 302-313.

**Perevolotsky A, Haimov Y. 1992**. The effect of thinning and goat browsing on the structure and development of Mediterranean woodland in Israel. *Forest Ecology and Management,* **49**: 61-74.

**Pinkard EA, Battaglia M, Mohammed CL. 2007**. Defoliation and nitrogen effects on photosynthesis and growth of *Eucalyptus globulus. Tree Physiology,* **27**: 1053-1063.

**Pinto CA, Henriques MO, Figueiredo JP, David JS, Abreu FG, Pereira JS, Correia I, David TS. 2011**. Phenology and growth dynamics in Mediterranean evergreen oaks: Effects of environmental conditions and water relations. *Forest Ecology and Management,* **262**: 500-508.

**Polley HW, Mayeux HS, Johnson HB, Tischler CR. 1997**. Viewpoint: Atmospheric CO2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management,* **50**: 278-284.
**Poorter H, Evans JR. 1998**. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia,* **116**: 26-37.
**Pote J, Shackleton C, Cocks M, Lubke R. 2006**. Fuelwood harvesting and selection in Valley Thicket, South Africa. *Journal of Arid Environments,* **67**: 270-287.
**Rao SJ, Iason GR, Hulbert IAR, Daniels MJ, Racey PA. 2003**. Tree browsing by mountain hares (*Lepus timidus*) in young Scots pine (*Pinus sylvestris*) and birch (*Betula pendula*) woodland. *Forest Ecology and Management,* **176**: 459-471.
**Reich PB. 1995**. Phenology of tropical forests: patterns, causes, and consequences. *Canadian Journal of Botany,* **73**: 164-174.
**Reich PB, Borchert R. 1982**. Phenology and ecophysiology of the Tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology*, **63**: 294-299.
**Reich PB, Borchert R. 1984**. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **72**: 61-74.
**Reich PB, Oleksyn J, Wright IJ. 2009**. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. *Oecologia,* **160**: 207-212.
**Reich PB, Waiters MB, Krause SC, Vanderklein DW, Raffa KF, Tabone T. 1993**. Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. *Trees,* **7**: 67-77.
**Reichardt PB, Chapin III FS, Bryant JP, Mattes BR, Clausen TP. 1991**. Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: Potential importance of metabolite turnover. *Oecologia,* **88**: 401-406.
**Rendón-Carmona H, Martínez-Yrízar A, Balvanera P, Pérez-Salicrup D. 2009**. Selective cutting of woody species in a Mexican tropical dry forest: Incompatibility between use and conservation. *Forest Ecology and Management,* **257**: 567-579.
**Rich PM, Breshears DD, White AB. 2008**. Phenology of mixed woody-herbaceous ecosystems following extreme events: Net and differential responses. *Ecology,* **89**: 342-352.
**Richards JH. 1993**. Physiology of plants recovering from defoliation. In: Association NZG ed. *International Grassland Congress.* Hamilton, New Zealand.
**Rijks MH, Malta E, Zagt RJ. 1998**. Regeneration through sprout formation in *Chlorocardium rodiei* (Lauraceae) in Guyana. *Journal of Tropical Ecology,* **14**: 463-475.
**Rodgers HL, Brakke MP, J. EJ. 1995**. Shoot damage effects on starch reserves of *Cedrela odorata*. *Biotropica,* **27**: 71-77.
**Rooke T, Bergstrom R. 2007**. Growth, chemical responses and herbivory after simulated leaf browsing in *Combretum apiculatum*. *Plant Ecology,* **189**: 201-212.
**Rooke T, Bergström R, Skarpe C, Danell K. 2004**. Morphological responses of woody species to simulated twig-browsing in Botswana. *Journal of Tropical Ecology,* **20**: 281-289.
**Roques KG, O'Connor TG, Watkinson AR. 2001**. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology,* **38**: 268-280.

**Rossatto DR, Hoffmann WA, Franco AC. 2009**. Differences in growth patterns between co-occurring forest and savanna trees affect the forest–savanna boundary. *Functional Ecology*, **23**: 689-698.

**Sakai A, Sakai S. 1998**. A test for the Resource Remobilization Hypothesis: Tree sprouting using carbohydrates from above-ground parts. *Annals of Botany*, **82**: 213-216.

**Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N. 2005**. Determinants of woody cover in African savannas. *Nature*, **438**: 846-849.

**Sankaran M, Jayashree R, Niall PH. 2004**. Tree - grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**: 480-490.

**Sankaran M, Ratnam J, Hanan N. 2008**. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, **17**: 236-245.

**Sayer SMA, Goelz JCG, Chambers JL, Tang Z, Dean TJ, Haywood JD, Leduc DJ. 2004**. Long-term trends in loblolly pine productivity and stand characteristics in response to thinning and fertilization in the West Gulf region. *Forest Ecology and Management*, **192**: 71-96.

**Scholes RJ. 1987**. *Response of three semi-arid savannas on contrasting soils to the removal of the woody component*, PhD, University of the Witwatersrand, Johhanesburg.

**Scholes RJ. 2004.** Woodlands of South Africa. In: Lawes MJ, Eeley HC, Shackleton CM, Geach BGS eds. *Indigenous Forests and Woodlands in South Africa: Policy, People and Practice.* Pietermaritzburg, University of Kwazulu Natal Press.

**Scholes RJ. 2009**. Syndromes of dryland degradation in southern Africa. *African Journal of Range and Forage Science*, **26**: 113-125.

**Scholes RJ, Archer SR. 1997**. Tree-grass interactions in savannas. *Annual Review Ecological Systems*, **28**: 517–44.

**Scholes RJ, Dowty PR, Caylor K, Parsons DAB, Frost PGH, Shugart HH. 2002**. Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science* **13**: 419-428

**Scholes MC, Scholes RJ, Otter LB, Woghiren AJ, 2003.** Biogeochemistry: the cycling of elements. In: Du Toit JT, Rogers KH, Biggs HC. (Eds.), The Kruger Experience. Island Press, Washington, U.S.A. pp. 130–148.

**Scholes RJ, Walker BH. 1993**. An African savanna; synthesis of the Nylsvley Study. UK, Cambridge.

**Schutz AEN, Bond WJ, Cramer MD. 2009**. Juggling carbon: allocation patterns of a dominant tree in a fire-prone savanna. *Oecologia*, **160**: 235-246.

**Scogings P, Macanda M. 2005**. *Acacia karroo* responses to early dormant season defoliation and debarking by goats in a semi-arid subtropical savanna. *Plant Ecology*, **179**: 193-206.

**Scogings PF, Mopipi K. 2008**. Effects of water, grass and N on responses of *Acacia karroo* seedlings to early wet season simulated browsing: Leaf N, fibre and tannin concentrations. *Journal of Arid Environments*, **72**: 1666-1674.

**Scott DA, Burger JA, Kaczmarek DJ, Kane MB. 2004**. Growth and nutrition response of young sweetgum plantations to repeated nitrogen fertilization on two site types. *Biomass and Bioenergy,* **27**: 313-325.

**Seghieri J, Carreau J, Boulain N, De Rosnay P, Arjounin M, Timouk F. 2012**. Is water availability really the main environmental factor controlling the phenology of woody vegetation in the central Sahel? *Plant Ecology,* **213**: 861-870.

**Seghieri J, Floret C, Pontanier R. 1995**. Plant phenology in relation to water availability: Herbaceous and woody species in the savannas of Northern Cameroon. *Journal of Tropical Ecology,* **11**: 237-254.

**Seghieri J, Vescovo A, Padel K, Soubie R, Arjounin M, Boulain N, de Rosnay P, Galle S, Gosset M, Mouctar AH, Peugeot C, Timouk F. 2009**. Relationships between climate, soil moisture and phenology of the woody cover in two sites located along the West African latitudinal gradient. *Journal of Hydrology,* **375**: 78-89.

**Sekhwela MBM, Yates DJ. 2007**. A phenological study of dominant *Acacia* tree species in areas with different rainfall regimes in the Kalahari of Botswana. *Journal of Arid Environments,* **70**: 1-17.

**Sennerby-Forsse L, Zsuffa L. 1995**. Bud structure and resprouting in coppiced stools of *Salix viminalis* L., *S. eriocephala* Michx., and *S. amygdaloides* Anders. *Trees - Structure and Function,* **9**: 224-234.

**Senock RS, Sisson WB, Donart GB. 1991**. Compensatory photosynthesis of *Sporobolus flexuosus* (Thurb.) Rydb. following simulated herbivory in the Northern Chihuahuan desert. *Botanical Gazette,* **152**: 275-281.

**Seydack AHW, Vermeulen WJ. 2004.** Timber harvesting from Southern Cape Forests; The quest for sustainable levels of resource use. In: Lawes MJ, Eeley HAC, Shackleton CM, Geach BGS eds. *Indigenous Forests and Woodlands in South Africa: Policy, People and Practice.* Pietermaritzburg, University of Kwazulu Natal Press.

**Seymour C. 2008**. Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology,* **197**: 131-138.

**Shackelton CM, Grundy IM, Williams A. 2004.** Use of South Africa's Woodlands for Energy and Construction. In: Lawes MJ, Eeley HC, Shackleton CM, Geach BGS eds. *Indigenous Forests and Woodlands in South Africa: Policy, People and Practice.* Pietermaritzburg, University of Kwazulu Natal Press.

**Shackleton CM. 1993**. Fuelwood harvesting and sustainable utilisation in a communal grazing land and protected area of the Eastern Transvaal lowveld *Biological Conservation,* **63**: 247-254.

**Shackleton CM. 1997**. *The prediction of woody plant productivity in the Savanna biome, South Africa.*, PhD, University of the Witwatersrand, Johannesburg.

**Shackleton CM. 1999**. Rainfall and topo-edaphic influences on woody community phenology in South African savannas. *Global Ecology and Biogeography,* **8**: 125-136.

**Shackleton CM. 2001**. Managing regrowth of an indigenous savanna tree species (*Terminalia sericea*) for fuelwood: the influence of stump dimensions and post-harvest coppice pruning. *Biomass and Bioenergy,* **20**: 261–270.

**Shackleton CM, Buiten E, Annecke W, Banks D, Bester J, Everson T, Fabricius C, Ham C, Kees M, Modise M, Phago M, Prasad G, Smit W, Twine W, Underwood M, von Maltitz G, Wenzel P. 2004**. Fuelwood and poverty

alleviation in South Africa: Opportunities, constraints and intervention options. Pretoria, Department of Water Affairs and Forestry.

**Shackleton CM, Clarke JM. 2007**. Research and management of Miombo woodlands for products in support of local livelihoods. Johannesburg, World Bank.

**Shackleton CM, Shackleton SE. 2000**. Direct use values of secondary resources harvested from communal savannas in the Bushbuckridge Lowveld, South Africa. *Journal of Tropical Forests Products,* **6**: 28-47.

**Shackleton CM, Shackleton SE, Buiten E, Bird N. 2007**. The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa. *Forest Policy and Economics,* **9**: 558-577.

**Sheffield MCP, Gagnon JL, Jack SB, McConville DJ. 2003**. Phenological patterns of mature longleaf pine (*Pinus palustris* Miller) under two different soil moisture regimes. *Forest Ecology and Management,* **179**: 157-167.

**Shen Y, Yang G, Huang J. 2011**. Comparison of tree sprouting in three regeneration stages of an evergreen broadleaved forest in a karst landscape, SW China. *Acta Ecologica Sinica,* **31**: 126-132.

**Simoes MP, Madeira M, Gazarini L. 2008**. The role of phenology, growth and nutrient retention during leaf fall in the competitive potential of two species of mediterranean shrubs in the context of global climate changes. *Flora,* **203**: 578-589.

**Singh G. 2004**. Influence of soil moisture and nutrient gradient on growth and biomass production of *Calligonum polygonoides* in Indian desert affected by surface vegetation. *Journal of Arid Environments,* **56**: 541-558.

**Skarpe C, Bergstrom R, Braten AL, Danell K. 2000**. Browsing in a heterogeneous savanna. *Ecography,* **23**: 632-640.

**Skov KR, Kolb TE, Wallin KF. 2004**. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *Forest Science,* **50**: 81-91.

**Staver CA, Bond WJ, Stock WD, Van Rensburg SJ, Waldram MS. 2009**. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications,* **19**: 1909-1919.

**Sunderlin WD, Angelsen A, Belcher B, Burgers P, Nasi R, Santoso L, Wunder S. 2005**. Livelihoods, forests, and conservation in developing countries: An Overview. *World Development,* **33**: 1383-1402.

**Tainton N. 1999**. *Veld Management in South Africa,* Pietermaritzburg, University of Natal Press.

**Tang J, Zielinski R, Aldea M, DeLucia E. 2009**. Spatial association of photosynthesis and chemical defense in *Arabidopsis thaliana* following herbivory by *Trichoplusia ni*. *Physiologia Plantarum,* **137**: 115-124.

**Tang Z, Chambers JL, Guddanti S, Yu S, Barnett JP. 1999**. Seasonal shoot and needle growth of loblolly pine responds to thinning, fertilization, and crown position. *Forest Ecology and Management,* **120**: 117-130.

**Teich I, Cingolani AM, Renison D, Hensen I, Giorgis MA. 2005**. Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? *Forest Ecology and Management,* **219**: 229-241.

**Thakadu OT. 2005**. Success factors in community based natural resources management in northern Botswana: Lessons from practice. *Natural Resources Forum,* **29**: 199-212.

**Tschaplinski TJ, Blake TJ. 1989**. Photosynthetic reinvigoration of leaves following shoot decapitation and accelerated growth of coppice shoots. *Physiologia Plantarum,* **75**: 157-165.
**Tschaplinski TJ, Blake TJ. 1995**. Growth and carbohydrate status of coppice shoots of hybrid poplar following shoot pruning. *Tree Physiology,* **15**: 333-338.
**Turnbull TL, Adams MA, Warren CR. 2007**. Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* seedlings is not caused by increased leaf nitrogen. *Tree Physiology,* **27**: 1481-1492.
**Twine WC, Moshe D, Netshiluvhi T, Siphugu V. 2003**. Consumption and direct-use values of savanna bio-resources used by rural households in Mametja, a semi-arid area of Limpopo province, South Africa. *South African Journal of Science,* **99**: 467-473.
**Valderrhbano J, Mufioz F, Delgado I. 1996**. Browsing ability and utilization by sheep and goats of *Atriplex halimus* L. shrubs. *Small Ruminant Research,* **19**: 131-136.
**Van der Heyden F, Stock WD. 1996**. Regrowth of a semiarid shrub following simulated browsing: the role of reserve carbon. *Functional Ecology,* **10**: 647-653.
**van der Meijden E, Wijn M, Verkaar HJ. 1988**. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos,* **51**: 355-363.
**Van Langevelde F, Van De Vijver CADM, Kumar L, Van De Koppel J, De Ridder N, Van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M. 2003**. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology,* **84**: 337–350.
**van Wyk B, van Wyk P. 1997**. *Field Guide to trees of Southern Africa,* Cape Town, Struik Publishers.
**Vesk PA. 2006**. Plant size and resprouting ability: Trading tolerance and avoidance of damage? *Journal of Ecology,* **94**: 1027-1034.
**Vesk PA, Warton DI, Westoby M. 2004**. Sprouting by semi-arid plants: Testing a dichotomy and predictive traits. *Oikos,* **107**: 72-89.
**Vitasse Y, Francois C, Delpierre N, Dufrêne E, Kremer A, Chuinee I, Delzon S. 2011**. Assessing the effects of climate change on the phenology of European temperate trees. *Agricultural and Forest Meteorology,* **151**: 969-980.
**Wang J, Ives NE, Lechowicz MJ. 1992**. The relation of foliar phenology to xylem embolism in trees. *Functional Ecology,* **6**: 469-475.
**Ward D. 2005**. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science,* **22**: 101-105.
**Wassie A, Sterck FJ, Teketay D, Bongers F. 2009**. Effects of livestock exclusion on tree regeneration in church forests of Ethiopia. *Forest Ecology and Management,* **257**: 765-772.
**Wendler R, Carvalho PO, Pereira JS, Millard P. 1995**. Role of nitrogen remobilization from old leaves for new leaf growth of *Eucalyptus globulus* seedlings. *Tree Physiology,* **15**: 679-683.
**Wendler R, Millard P. 1996**. Impacts of water and nitrogen supplies on the physiology, leaf demography and nitrogen dynamics of *Betula pendula*. *Tree Physiology,* **16**: 153-159.
**Wessels KJ, Mathieu R, Erasmus BFN, Asner GP, Smit IPJ, va Aardt JAN, Main R, Fisher J, Marais W, Kennedy-Bowdoin T, Knapp DE, Ermerson R, Jacobson J. 2011**. Impact of communal land use and conversation on

woody vegetaion structure in the Lowveld savannas of South Africa. *Forest Ecology and Management,* **261**: 19-29.

**Wiegand K, Saltz D, Ward D. 2006**. A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics,* **7**: 229-242.

**Wielgolaski FE. 2001**. Phenological modifications in plants by various edaphic factors. *International Journal of Biometeorology,* **45**: 196-202.

**Wildly DT, Pate JS. 2002**. Quantifying above- and below-ground growth responses of Western Australian Oil Mallee, *Eucalyptus kochii* subs. *plenissima,* to contrasting decapitation regimes. *Annals of Botany,* **90**: 185-197.

**Wildy DT, Pate JS. 2002**. Quantifying above- and below-ground growth responses of Western Australian Oil Mallee, *Eucalyptus kochii* subs. *plenissima,* to contrasting decapitation regimes. *Annals of Botany,* **90**: 185-197.

**Wilkinson GR, Neilsen WA. 1995**. Implications of early browsing damage on the long term productivity of eucalypt forests. *Forest Ecology and Management,* **74**: 117-I 24.

**Williams RJ, Myers BA, Eamus D, Duff AG. 1999**. Reproductive phenology of woody species in a North Australian Tropical savanna. *Biotropica,* **31**: 626-636.

**Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D. 1997**. Leaf phenology of woody species in a north Australian tropical savanna. *Ecology,* **78**: 2542-2552.

**Wilson B. 2002**. *Population dynamics and the regeneration ecology of the African savanna tree Burkea africana,* MSc, University of the Witwatersrand, Johannesburg.

**Wilson TB, Witkowski ETF. 1998**. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments,* **38**: 541-550.

**Witkowski ETF, Mitchell DT, Stock WD. 1990**. Response of a Cape fynbos ecosystem to nutrient additions: shoot growth and nutrient contents of a proteoid (*Leucospermum parile*) and ericoid (*Phylica cephalantha*) evergreen shrub. *Acta Ecologica,* **11**: 311-326.

**Zida D, Sawadogo L, Tigabu M, Tiveau D, Oden PC. 2007**. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. *Forest Ecology and Management,* **243**.