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The influence of post-harvest treatments on the coppice response of two woody savanna species

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477 429



A Dissertation submitted to the Faculty of Science,
University of the Witwatersrand,
in partial fulfilment of the requirements
for the degree of Master of Science,
Johannesburg, South Africa
2017

DECLARATION

I, Christopher James Rankin (Student number: 477 429) am a student registered for MSc (Dissertation) in the year 2015.

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- I have followed the required conventions in referencing the thoughts and ideas of others.
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ACKNOWLEDGEMENTS

To my supervisor Associate Professor Wayne Twine: I would like to thank you for all the support, guidance and motivation through the study as well as providing funding for the research. Aside from the project I would like to thank you for teaching me how to manage myself in situations which I was unfamiliar with and providing me with valuable life lessons. To Associate Professor Sally Archibald: I would like to thank you for the input in the project from the proposal stage till the end of the project. Your willingness to help when I had no idea who to contact regarding stored reserves analyses brought calmness to a stressful time in the project. To Professor Edward Witkowski: I would like to thank you too for the input in the project from the proposal to the final stages of the project. Your knowledge around statistical analyses and presenting the data is highly valued. I really appreciate you opening your lab doors and providing me a desk to work from. To Doctor Melissa Whitecross, Nic Venter and Megan McKay: I would like to thank you both for participating in the heavy debates regarding data analyses and management. To the University of the Witwatersrand: I would like to thank the university for allowing me the opportunity to conduct the study and proving me funding, post-graduate merit award (PGMA), for two years. To the Wits Rural Facility: I would like to thank all the staff at Wits Rural Facility for allowing me to conduct the study on the premises but also for welcoming into the family. From management, Cameron Watt, to the administration staff everyone was so welcoming and made spending time away from home more tolerable. To my field assistants, Frank Nyathi and Thabo Sibuya: I would like to thank both of you for all the hours spent in the field, from cutting of trees to having long chats about life. I would like to thank you both for exposing me to different lifestyles and cultures.

A special thanks to my friends Blair Cowie and Robin Cook for providing support through the project. For the endless feedback and commitment to help me with whatever I needed is truly appreciated. To the rest of my friends, which the list is too long to mention, I would like to thank you all for the motivation, encouragement and belief in me. A special mention must go to Mike Donze for visiting me in the field and keeping me sane when times were tough. To my two brothers, William and Alistair Rankin, I would like to thank you for the continued support and motivation. Lastly, and most importantly, I would like to thank my parents, William and Maureen Rankin. The continued belief and support in me completing the project is appreciated. I will forever be grateful for the sacrifices you have both made for me, not only for this project.

ABSTRACT

Fuelwood is still heavily relied upon by rural communities as a source of energy. The current levels of wood harvesting have been deemed unsustainable, with models predicting the local exhaustion of wood resources in most cases. However, wood depletion has generally not happened to the level of severity predicted by the models. This may partially due to under-accounting for coppice regeneration. Many savanna species that are harvested for fuelwood demonstrate strong coppicing ability, which allows for regrowth after a disturbance. This ability to regrow or coppice is a key functional trait which allows species to persist and survive in frequently disturbed environments. There is surprisingly limited knowledge about coppice dynamics in savanna trees and how managerial actions might influence the coppice response and production of savanna species. To address this problem, this study investigated the influence of four post-harvest treatments on various aspects of the coppice response of *Terminalia sericea* and *Dichrostachys cinerea* – two important savanna fuelwood species – in a field experiment. A total of 108 felled trees per species were exposed to one of four treatments, which were applied monthly for 12 months. The treatments were (1) Control – no coppice shoots were removed for 12 months, (2) Harvest – all coppice shots were removed monthly, (3) Single prune – the coppice shoot with the widest diameter was left on the stump, and (4) Usable – coppice shoots that reached a diameter of 2 cm were removed. The effect that these treatments had on the average diameter, length and cumulative number of coppice shoots produced per stump was compared. The measurements of diameter and length were used in developing allometric equations for the prediction of coppice shoot biomass. The predicted biomass produced through the study was compared across treatments to gain an understanding of how productivity could be influenced by management of coppice shoots. The mean shoot diameter, length, as well as cumulative number of coppice shoots produced per stump was higher in the single prune treatment for both species while the harvest treatment resulted in high numbers of coppice shoots but with low average diameter and length. Applying the growth rates of coppice shoots found in this study it can be assumed that unmanaged coppice shoots will take approximately 5.5 years to reach a preferred harvestable diameter of 4 cm, while single prune coppice shoots would take 3.3 years to reach the preferred harvestable diameter. Diameter had more of an influence on the

predicted coppice biomass production of *T*. *sericea* while *D*. *cinerea* biomass prediction was more influenced by shoot length. However, only diameter was used to compare the prediction of coppice biomass with previously developed equations as these equations did not consider length for predicting biomass of different components of trees. From the derived models, the calculated biomass at the end of the study period as well as the calculated biomass produced through the year was greatest for the control treatment. The predicted dry shoot stem biomass at the harvestable diameter of 4 cm was 114.60 g for *T*. *sericea* and 95.88 g for *D*. *cinerea*. From the findings of this study it is clear that post-harvest management can be utilised to manipulate coppice response and biomass production.

Keywords: Fuelwood; Coppice shoot; Post-harvest treatment; Diameter; Length; Biomass

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Chapter 1

GENERAL INTRODUCTION

1.1 Rationale

Fuelwood is still heavily relied upon by rural communities in South Africa as the major source of energy (Shackleton 1993, 2001; Kaschula *et al*. 2005b; Neke *et al*. 2006; Matsika *et al*. 2012; Pouliot and Treue 2013). This reliance places a great deal of harvesting pressure on the wood resource supply, with the demand apparently exceeding the local supply in most cases (Shackleton 1993, 2001; Neke *et al*. 2006). Most "energy gap" models for rural areas predict that current harvesting levels are unsustainable and will result in severe to total deforestation (Banks *et al*. 1996; Wessels *et al*. 2013). However, in reality these areas are more typically transformed from heterogeneous savanna woodlands into coppice shrub-lands (Shackleton *et al*. 1994; Fisher *et al*. 2011). This suggests that the ability of savanna tree species to coppice (resprout) has been ignored or under-valued in previous fuelwood supply-and-demand models (Shackleton 2001).

There is a lack of understanding and data on coppicing in savanna tree species (Shackleton 2000, 2001; Moyo *et al*. 2015b). Furthermore, the knowledge required to manage these coppicing trees in a sustainable manner for harvesting by rural communities in African communal systems is deficient. Most of the knowledge regarding harvesting management practice and plant properties influencing coppice regrowth is borrowed from silvicultural studies conducted in the northern hemisphere (Kaschula *et al*. 2005b). This information could possibly be adapted and utilised by rural land managers and aid in the implementation of sustainable harvesting techniques such as rotational harvesting of coppice or post-harvesting treatments of the coppice (Shackleton 2000; Kaschula *et al*. 2005b; Neke *et al*. 2006). Successful coppice management should not only be concerned with the number of shoots produced, but also optimising both shoot diameter and length (Kaschula *et al*. 2005b). Management of shoots can be manipulated to maximise or suppress growth rates of the coppice shoots (Shackleton 2000). However, the effects of differing harvesting regimes and pruning treatments on coppice dynamics and biomass need to be further investigated, as not all management options have been studied. There is also limited data on coppice biomass production, which is important for understanding the

contribution of coppice to the fuelwood resource. Finally, there is a paucity of allometric data on the relationship between coppice shoot diameter and coppice biomass. These are essential for the modelling of coppice production. This study addresses these knowledge gaps by investigating the influence of four different post-harvest treatments on the coppice response of *Terminalia sericea* Burch. Ex. DC and *Dichrostachys cinerea* (L.) Wight and Arn., two common savanna species that are widely used for fuelwood.

1.2 Literature Review

1.2.1 *The savanna and people*

The savanna biome covers a large area of the tropics, including the sub-tropics, and is inhabited by a fifth of the world's human population (Scholes 1997; Neke 2004). Savannas cover approximately one half of the African continent and is the largest biome in southern Africa (Scholes and Walker 1993; Neke 2004), covering approximately 34% of South Africa (Shackleton 2001). Savannas are typically characterised by the co-existence of tree and grass species (Scholes and Archer 1997). The determinants of the savanna biome are moisture availability, soil nutrients, herbivory and fire (Scholes and Walker 1993; Scholes and Archer 1997; Shackleton 1997). The interactions between these four determinants can either be synergistic or antagonistic, resulting in positive feedbacks such as high levels of productivity or negative feedbacks such as loss of biodiversity (Scholes and Archer 1997).

The savanna biome is home to approximately 70% of rural households in South Africa (Shackleton 2001), providing a variety of resources that contribute to the livelihoods of these households (Neke *et al*. 2006; Egoh *et al*. 2012). The rural communities depend on the surrounding savanna biome for resources, including fuelwood, medicinal plants, wild fruits and timber (Shackleton *et al*. 2007; Twine *et al*. 2003). These resources are used for both subsistence and commercial use (Shackleton and Shackleton 2004). Having the ability to collect or harvest resources from the surrounding savanna vegetation also provides a "safety-net" for households (Paumgarten 2005).

1.2.2 *Fuelwood as a resource*

Across sub-Saharan Africa, over 80% of households regularly rely on fuelwood (Wessels *et al*. 2013), most commonly for cooking and for heating space and water (Kennedy 1998; Okello *et al*. 2001; Matsika *et al*. 2012). Fuelwood is an important source of energy for rural South African households (Shackleton 1993; Okello *et al*. 2001; Shackleton 2001 Kaschula *et al*. 2005b; Neke *et al*. 2006), as well as for some urban households, but not to the same extent (Shackleton *et al*. 2007). Rural households cannot take full advantage of an electrification programme supplied by the government due to the cost of electricity and cooking appliances (Kennedy 1989; Madubansi and Shackleton 2007; Matsika *et al*. 2012). By contrast, fuelwood is a free or low-cost source of energy. Thus, rural households will continue to utilise fuelwood for the foreseeable future (Kennedy 1989; Williams and Shackleton 2002; Matsika *et al*. 2012). Shackleton and Shackleton (2004) found that on average, a fuelwood-using household would consume over 5 000 kg of fuelwood in a year. However, households in the Bushbuckridge region of South Africa, which are connected to electricity, were found to use between 2 768 kg and 3 029 kg of fuelwood per year (Matsika *et al*. 2013).

Traditional authorities govern the use of unallocated communal land by communities in rural South Africa, including the harvesting of natural resources (Kirkland *et al*. 2007). These authorities, each headed by a chief, enforce laws that limit or prohibit the harvesting of live wood and valuable fruiting species (Shackleton 1993; Matsika *et al*. 2012). A variety of measures such as permits, fines or other forms of punishments, and employing local tree "police" to monitor and apprehend illegal harvesting, have been utilised by traditional authorities to enforce these wood harvesting laws and taboos (Kirkland *et al*. 2007). However, in practice, these often contravened as there is usually a lack of adequate dead wood in communal lands (Shackleton 1993). Since the introduction of democracy and freedom in post-apartheid South Africa, some local authorities have lost the cooperation of community members (Twine *et al*. 2003; Kirkland *et al*. 2007). The addition of formal governing bodies to the traditional authorities has created confusion among the communities as to which mandate is to be followed (Kirkland *et al*. 2007). This has also caused shifts in political views, in some circumstances resulting in the modification of budgets, reducing the tree "police" from 20 to 3 personal in a community (Kirkland *et al*.

2007). These types of conflicts between formal governing bodies and local authorities have left the local authorities seemingly ineffective in regulating the use of natural resources (Kirkland *et al*. 2007).

Fuelwood harvesting of livewood is considered to be unsustainable if the harvesting results in changes of the woodland structure, that reduce the availability and quality of fuelwood such that it hampers economic and social wellbeing of the users (Matsika *et al*. 2012). As rural populations and the concentration of villages increase so does the pressure on the surrounding savanna with the unsustainable harvesting of trees (Shackleton 1993; Neke *et al*. 2006). If not controlled, the continuous unsustainable harvesting will lead to localised shortages of fuelwood for villages (Shackleton 2001).

1.2.3 *Harvesting models*

There has been much concern about the unsustainable harvesting of fuelwood in rural communities (Bembridge and Tarlton 1990; Shackleton1993, 2001; Moyo *et al*. 2015b). Previously developed models have predicted severe deforestation or complete depletion of the wood resource within decades if current harvesting persists in most cases (Banks *et al*. 1996; Wessels *et al*. 2013). However, these predictions have generally not come to fruition, but rather the vegetation has been heavily impacted with a change in vegetation structure, decrease in the wood resource availability, with complete depletion rarely occurring (Matsika *et al*. 2012). One of the major impacts that fuelwood harvesting has on a savanna is the conversion of a vertically heterogeneous landscape into a landscape characterised by short shrubs with coppice production (Shackleton *et al*. 1994; Fisher *et al*. 2011). Coppice is defined as the production of vegetative shoots from the remaining stump or base of the stem following a disturbance (Van Wyk and Van Wyk 1997; Kaschula *et al*. 2005a, b). The fact that the wood supply has not been totally depleted but rather a transformation in vegetation structure has occurred suggests that the models have not accounted for, or under-appreciated, the value of savanna trees being able to coppice under intensive harvesting (Shackleton 2001). Banks *et al*. (1996) assumed an annual recruitment and coppice contribution of 20 kg ha^{-1} yr^{-1}, in the absence of data. However this is well below the coppice regrowth estimate for *T. sericea* of 89 kg ha^{-1} yr^{-1} by Twine 2011.

The model created by Banks *et al*. (1996) to determine the rate of change in a wood standing crop is expressed as:

$$\frac{dS}{dt} = f(S) + g(A) - h(P,z) - c(\frac{dP}{dt})$$

where *f(S)* is the increase in standing crop as a result of woodland productivity. Annual recruitment and coppice regrowth were accounted for by *g(A)*. The 20 kg ha^{-1} yr^{-1} assumption of coppice production was based on the expectation that annual recruitment and coppice regrowth would be proportional to the woodland area (Banks *et al*. 1996). Fuelwood removal rate is represented by *h(P,z)* and this is to account for wood which was harvested and bought by community members (Banks *et al*. 1996). A population size is unlikely to be stable and therefore the population growth and the increase in the need for timber was considered by the last term of the equation (Banks *et al*. 1996). Banks *et al*. (1996) placed much emphasis on projected wood demand under different human population growth scenarios. With a growing human population the demand for fuelwood would increase and the harvesting of fuelwood would intensify (Banks *et al*. 1996).

Wessels *et al*. (2013) developed a similar equation which was expressed as

$$\Delta S/\Delta T = f(S) + g(A) - h(w,P,z)$$

However, the population growth and need for timber were assumed to be zero, while the inclusion of percentage of households which rely solely on fuelwood was included (*w*). The total contribution to the increase of standing crop from recruitment and coppice regrowth, *g*(*A*), was calculated to be 4.19 t yr^{-1} for the study area of 1 568 ha.

Parameters in these models were kept constant from year to year which in reality is unlikely as changes in the parameters will occur (Banks *et al*. 1996; Wessels *et al*. 2013). The changes to the parameters are difficult to quantify and predict as they rely on the reactions of individuals to complex social and environmental factors (Banks *et al*. 1996). Wessels *et al*. (2013) predicted that the fuelwood resource would deplete within 13 years of the study around the selected village. This prediction included a 2% reduction in the number of households using fuelwood.

1.2.4 *Coppicing abilities and strategies of trees*

Within the savanna biome, trees are exposed to numerous disturbances that affect their development, production and survival. Surviving meristems and stored reserves allow for a plant to respond to a disturbance by means of resprouting or coppicing (Bond and Midgley 2001). The ability of savanna trees to coppice after a disturbance is an important trait for their persistence and survival (Shackleton 2000; Bond and Midgley 2001; Kaschula *et al*. 2005b; Neke *et al*. 2006; Handavu *et al*. 2011; Moyo 2013; Moyo *et al*. 2015b). The ability to coppice and persist is dependent upon the severity of disturbance or damage, the availability of water and nutrients, and the mobilization of resources within the plant (Moyo *et al*. 2015b). The ability to coppice suggests that the species is allocating resources to persistence rather than to reproduction (Bellingham and Sparrow 2000; Clarke *et al*. 2010). The coppice response varies both between and within species, and may be dependent upon the frequency and severity of disturbance (Bellingham and Sparrow 2000). In systems with few disturbances, species benefit from a monopodial growth form by growing tall and gaining an advantage in the competition for light (Bellingham and Sparrow 2000). However, in systems where disturbances are frequent and severe, adapting a multi-stemmed basal coppicing strategy is more beneficial (Bellingham and Sparrow 2000). This strategy allows for a greater area to be covered at ground level (Bellingham and Sparrow 2000).

Coppicing trees have access to stored nutrients (e.g. carbon and nitrogen) as well as to water by means of the well-developed root system of the adult tree (Forrester *et al*. 2003). Both stored nutrients and water support the growth of coppice after the removal of the above-ground woody biomass (Forrester *et al*. 2003; Moyo *et al*. 2015b). Thus, the initial growth of the coppice is quicker than that of seedlings or saplings of a comparable size, as the coppice shoots have the potential to intercept solar radiation as a function of a greater leaf area index (Harrington and Fownes 1995; Okello *et al*. 2001; Moyo *et al*. 2015b). The higher leaf area index may be a result of the coppice shoots having access to stored reserves, but also from photosynthates produced by the other coppice shoots from the same rootstock (Holdo 2006). However, coppice shoots experience the effects of competition sooner than saplings and therefore the growth rate of shoots is reduced until apical dominance can be established (Harrington and Fownes 1995). Having the ability to coppice, along with the initial fast growth rates of the coppice shoots, allows an opportunity

for the maximization of fuelwood production through managerial actions such as the rotational harvesting of the coppice shoots (Shackleton 2001; Luoga *et al*. 2004; Neke *et al*. 2006). Studies in East Africa suggest that annual fuelwood production from the rotational harvesting of *Acacia drepanolobium* coppice can exceed 1 000 kg dry mass per hectare (Kennedy 1998; Okello *et al*. 2001). This amount is far greater than the 20 kg ha^{-1} yr^{-1} in South Africa that was estimated by a previous supply-and-demand fuelwood model (Banks *et al*. 1996).

Most of the savanna trees that are harvested for fuelwood demonstrate a strong coppicing potential (Shackleton 2000; Luoga *et al*. 2004; Neke *et al*. 2006). However, different species utilise different resource allocation strategies and therefore have different sprouting abilities (Mwavu and Witkowski 2008). For example, a species may coppice with multiple small shoots (e.g. *Dichrostachys cinerea*) and this can be considered a "quantity-driven" strategy (Kaschula *et al*. 2005b). This strategy could be compared with the "Stay and Resist" life strategy proposed by Gignoux *et al*. (1997) (Neke *et al*. 2006). This life strategy is characterised by having multiple stems which enables the species to survive in a frequently disturbed area (Kaschula *et al*. 2005b; Neke *et al*. 2006). On the other extreme, a species may produce few large coppice shoots (e.g. *Combretum zeyheri* and *Combretum collinum*) and this strategy could be considered a "quality-driven" strategy (Kaschula *et al*. 2005b). This type of strategy could be compared to the "gulliver" life strategy hypothesised by Higgins *et al*. (2000) and Bond and Midgley (2001). This strategy is characterised by a species investing resources towards increasing the height of a single (or few shoots) to escape the zone of highest potential damage (Neke *et al*. 2006). There are species which demonstrate a combination or can switch between these strategies by coppicing multiple relatively large shoots (e.g. *Terminalia sericea*), suggesting a fast growth rate of the shoots (Moyo 2013).

Species-specific responses are also mediated by least three additional factors that influence coppicing, namely (1) the size (diameter) of the stem being harvested, (2) the height at which the stem is cut, and (3) the pruning of the coppice shoots (Shackleton 2000, 2001; Neke *et al*. 2006). The influence these factors are explored individually below.

Stem size

It has been demonstrated that coppice production characteristics are influenced by the size (diameter) of the cut stem (Shackleton 2000, 2001; Kaschula *et al*. 2005b; Neke *et al*. 2006). The two coppice production characteristics most influenced by stem size are the number of coppice shoots produced and the cumulative diameter of shoots produced per stem, which both share a positive relationship with stem size in most cases (Shackleton 2001; Kaschula *et al*. 2005b). However, there have been studies that suggest the total number of shoots produced decrease with increasing stem size (MacDonald and Powell 1983; Khan and Tripathi 1986; Shackleton 2000). Shackleton (2000) found that *D. cinerea* had a negative relationship between cut stem size and the number of shoots produced, while Shackleton (2001) found the relationship to be positive for *T. sericea*. A positive relationship between stump size classes and shoot length has been found for both *D. cinerea* and *T. sericea* (Shackleton 2001; Twine 2011). Larger stumps of *T. sericea* took longer to coppice after a cutting event, but after a few months of growth the larger size classes of stumps had a greater cumulative shoot length than the smaller stumps (Shackleton 2001). Neke *et al*. (2006) noted that the resprout vigour (the composite shoot diameter relative to the composite stump diameter) decreases with increasing the cut stem size. This means that the cumulative diameter of the coppice shoots relative to the total stump diameter decreases with an increasing stump size, even though the number of shoots might increase with stump size.

Cutting height

The number of coppice shoots produced has been noted to be influenced by cutting height (Kaschula *et al*. 2005b; Handavu *et al*. 2011). In most cases, an increase in cutting height results in an increase in the number of shoots produced (Bowersox *et al*. 1990; Shackleton 2000, 2001; Mwavu and Witkowski 2008). However, other studies have shown that cutting height can have no significant influence on the number of shoots produced (Neke *et al*. 2006). Shackleton (2001) suggests that the influence of cutting height becomes apparent only after the second year after harvesting, and the study conducted by Neke *et al*. (2006) did not span a two year period. Shackleton (2001) found that cutting height had no influence on both the mean and cumulative shoot length. Different species will respond differently with coppicing ability to different cutting heights (Shackleton 2000). The

probability of coppice shoots sprouting from the top of the cut stem increases with cutting height (Neke *et al*. 2006). In terms of the stems survival, stems have a higher chance of survival with increased cutting height (Shackleton 2000, 2001).

Pruning

The action of pruning has been identified as an important managerial tool in situations when there is high demand but low supply of fuelwood (Shackleton 2001). A study conducted on *T. sericea* compared the effects of two different pruning treatments with a control treatment of no pruning (Shackleton 2001). The longest shoot was left in the 'single prune' treatment whilst the two longest shoots were left in the 'double prune' treatment (Shackleton 2001). New shoots were removed monthly while the pruning treatments took place after three months of the initial harvest (Shackleton 2001). Pruning treatments needed to be repeated until the end of the second season after initial harvesting, as this is when apical dominance was established in this study (Shackleton 2001). The pruning treatments had an influence on mean shoot length, with the 'single prune' and 'double prune' treatments having 54% and 40% greater mean shoot lengths, respectively, in comparison to that of the control treatment (Shackleton 2001). However, the control treatment or unpruned treatment had the highest cumulative shoot length per stump, although this could be a result of the unpruned treatment also having the highest number of shoots per stump (Shackleton 2001). The increase in number of shoots per stump increases the possibility of shoot dieback, leaving a few dominant shoots to grow (Neke *et al*. 2006). Overall productivity (cumulative shoot length) was considered to be highest for the unpruned treatment, even though the coppice shoots were thinner and shorter (Shackleton 2001). Shackleton (2001) noted that pruning has an impact on the growth of the coppice shoots of *T. sericea*.

Other factors

Other factors that have been noted to influence the coppicing ability of trees include environmental conditions such as the availability of water and nutrients (Moyo 2013), and the harvesting frequency (Neke *et al*. 2006; Moyo *et al*. 2015b). Neke *et al*. (2006) found that *D. cinerea* trees had higher coppice growth when situated in clayey bottomlands rather than in sandy uplands along a catena in a dystrophic savanna. Supplementing cut *T. sericea*

trees with water and nutrients had a positive effect on the coppice shoot growth but not on the number of shoots produced (Moyo 2013). Moyo *et al*. (2015b) found that trees cut more often (8 times) within a two year period had more coppice shoots per stump area than those trees cut only once or twice within the same period. However, the shoots that were produced in the more frequently cut trees were thinner and shorter than the shoots produced in the trees cut less frequently (Moyo *et al*. 2015b). Water and nutrients may not always be readily available and therefore the three factors explored prior are more easily selected for and managed by harvesters and rural community authorities.

1.2.5 *Harvest rotation time*

A major concern over the managing of coppice production is the harvest rotation time, which is the time it will take for the coppice shoots to reach the favoured harvesting size (Shackleton 2000). The harvest rotation time is dependent on the desired size of the shoot and the growth rate of the shoot. A study in Bushbuckridge, South Africa, found that the preferred size class of stems cut for fuelwood was 5-6 cm, but that stems ranging from 2-10 cm in diameter would also be utilised for fuelwood (Shackleton 1993). Shackleton (2001) measured stems in wood bundles and found that the mean diameter was 5.4 cm and the mean length was 171 cm for all species except for *T. sericea*, where the mean diameter was 6.1 cm and 194 cm was the mean length. Neke *et al*. (2006) found that the majority of stems cut in an intensively harvested area had a diameter of 4-10 cm. This was the same diameter found in a lightly impacted village, while in a heavily impacted village challenged with fuelwood shortages, the diameter of cut stems decreased to 1-4 cm (Matsika *et al*. 2012). Using the preferred size class of stems cut and the growth rate of the coppice, harvest rotation times can be calculated while considering factors such as stem size, cutting height, species, pruning and environmental conditions (Shackleton 2001). However, coppice growth rates are not well understood as data are severely lacking.

Shackleton (2001) provides some insight on growth rates of *T. sericea*. Under unmanaged conditions, *T. sericea* will reach the desired length of 194 cm within 5-6 years (Shackleton 2001; Twine 2011). Shackleton (2001) found that unmanaged shoots had a quicker extension rate from stems cut at 20 cm rather than 50 cm, regardless of stem diameter.

However, shoots from stems with a diameter larger than 9 cm had a greater extension rate than shoots from stems with a diameter of less than 6 cm (Shackleton 2001). Shoots from the larger stems (> 9 cm) were predicted to reach the desired length of 194 cm in 2-5 years while shoots from the smaller stems (< 6 cm) would take 3-9 years, depending on cutting height and pruning treatment (Shackleton 2001). Predicting rotation time on shoot diameter would be more appropriate than length as harvesters are more likely to select fuelwood based on shoot diameter than length (Twine 2011). The preferred diameter of harvested *T. sericea* was found to be 6.1 cm (Shackleton 2001; Twine 2011). Shackleton (2001) found that unmanaged shoots would take 6-13 years to reach the desired 6 cm diameter. However, this could be reduced to 4-5 years under a single prune treatment which would leave only one shoot on the stem (Shackleton 2001). This reduction was across all stem sizes and cutting heights (Shackleton 2001). The findings by Shackleton (2001) compare favourably with a study done by Abbot and Lowore (1999) conducted in Malawi, with the latter estimating that it would take 5 years for coppice shoots to reach the preferred diameter of 6 cm of *Combretum apiculatum* Sond. and *C. molle* R. Br. ex Don., two favoured fuelwood species. A coppice rotation time of 8-10 years was calculated by Kennedy (1998) for *Tarconanthus camphoratus* L., a hard-wooded shrub.

1.2.6 *Management of coppice*

The sustainable utilization of fuelwood is met when the total wood biomass removed is equal to or less than the total annual wood growth (Shackleton 1997, Chirwa *et al*. 2008). Concerns have been raised over maintaining the biodiversity and composition of the savanna biome whilst meeting the demands for resources (Shackleton *et al*. 2004). Three management practices, adopted from silvicultural systems, have been suggested as possible solutions to these concerns: (1) Coppice with standards; (2) Selection system; and (3) Clear felling (Chirwa *et al*. 2008).

Coppice with standards

The coppice with standards system allows for a few trees to be preserved over the harvested area. These preserved trees can reach maturity allowing for fruiting and seed production which may contribute to new recruitment (Chirwa *et al*. 2008). These mature

trees are generally understood to be high-valued species (Chirwa *et al*. 2008). The regeneration from the cut trees is managed to produce resources needed such as fuelwood and poles (Shackleton and Clarke 2007). In Malawi, small-scale farmers have been advised to use this system as a means of obtaining fuelwood whilst still retaining the high value species which meet other requirements (fruit and shade) of the people (Lowore and Abbott 1995; Chirwa *et al*. 2008). An additional benefit of this system is the protection of the area from soil erosion and sun scorch by the remaining trees (Chirwa *et al*. 2008; Moyo 2013).

Selection system

The trees that are cut in this system are selected for by certain morphological criteria, often stump diameter (Chirwa *et al*. 2008). According to Hosier (1993), there are two concepts which need to be understood for selective harvesting: species mix and tree growth, with the latter including regrowth. The difference in management of plantations and natural woodlands/forests is often due to the species mix concept (Hosier 1993). In the more natural environments, there is a variety of species and tree ages whilst in plantations there is often a single species (monoculture) and all trees are of similar age. This difference allows for plantations to optimize harvesting, by being able to harvest all trees in a single occurrence. This is difficult to do in the more natural environments as not all the trees may have reached the selected harvesting size (Hosier 1993). Therefore, each individual tree in the natural environments must be judged on its own maturity and suitability for the intended product (Hosier 1993; Chidumayo *et al*. 1996; Chirwa *et al*. 2008). The tree growth concept is one which allows for trees which have not reached a suitable size for harvesting to be left alone and grow until the favoured size is reached (Hosier 1993). Once harvested, some trees have the ability to regrow or coppice. This regrowth or coppice may reach favourable harvesting size in the future depending on management and environmental conditions, such as shading by canopy trees (Hosier 1993; Chirwa *et al*. 2008). A criticism of the selective harvesting system is that the selectivity by harvesters can be altered by socio-economic factors, such as an increase in poverty among harvesters which can lead towards lowered selectively and over exploitation of the harvested species (Hosier 1993; Chirwa *et al*. 2008).

Clear felling

In this system of management a large area is cleared (Chirwa *et al*. 2008). This system is often used in the charcoal industry (Chirwa *et al*. 2008). The clear felling referred to previously must not be confused with clearance of space for agriculture. Clear felling allows for the trees to regenerate and is considered to produce the highest rate of regrowth of the three systems (Chirwa *et al*. 2008). Clearance for agriculture often occurs after several years of selective harvesting once the preferred timber and fuelwood species have been depleted (Hosier 1993). Clear felling allows for the potential management of regrowth according to the product requirement (Chirwa *et al*. 2008).

1.1.3 Aim

The aim of was study is to investigate the influence of four different post-harvest treatments on the coppice response of two fuelwood savanna tree species, *Terminalia sericea* and *Dichrostachys cinerea*.

1.1.4 Objectives and Key Questions

1. Determine the effects of different post-harvest regimes (control, total reharvest, pruning, and disturbing apical dominance) on the coppice production of two savanna tree species.

- How does post-harvest treatment influence the diameter growth rate of coppice shoots?
- How does post-harvest treatment influence the length growth rate of coppice shoots?
- How does post-harvest treatment influence the number of coppice shoots produced?

2. Determine the allometric relationship between shoot diameter and coppice biomass for the savanna species.

- Which measurable variable (diameter or length) or a combination of the two is the best predictor of shoot biomass?

3. Determine the effects of different post-harvest regimes on coppice biomass yield of the savanna species.

- What is the influence of post-harvest treatment on the coppice biomass dynamics of the savanna species?

1.3. General Methods

1.3.1 Study site

The study was conducted at the Wits Rural Facility (WRF) (24° 34'00.06" S; 31° 05'54.67" E) (Figure 1.1) located within the Maruleng local municipality in the Limpopo Province, South Africa (Moyo *et al*. 2015b). The research facility is a protected area owned by the University of the Witwatersrand and covers an area of 350 ha in the central lowveld savanna region in the northeast of the country (Shackleton 2001; Moyo *et al*. 2015b). Three replicate sites which had an abundance of the study species were selected within WRF (Figure 1.1).

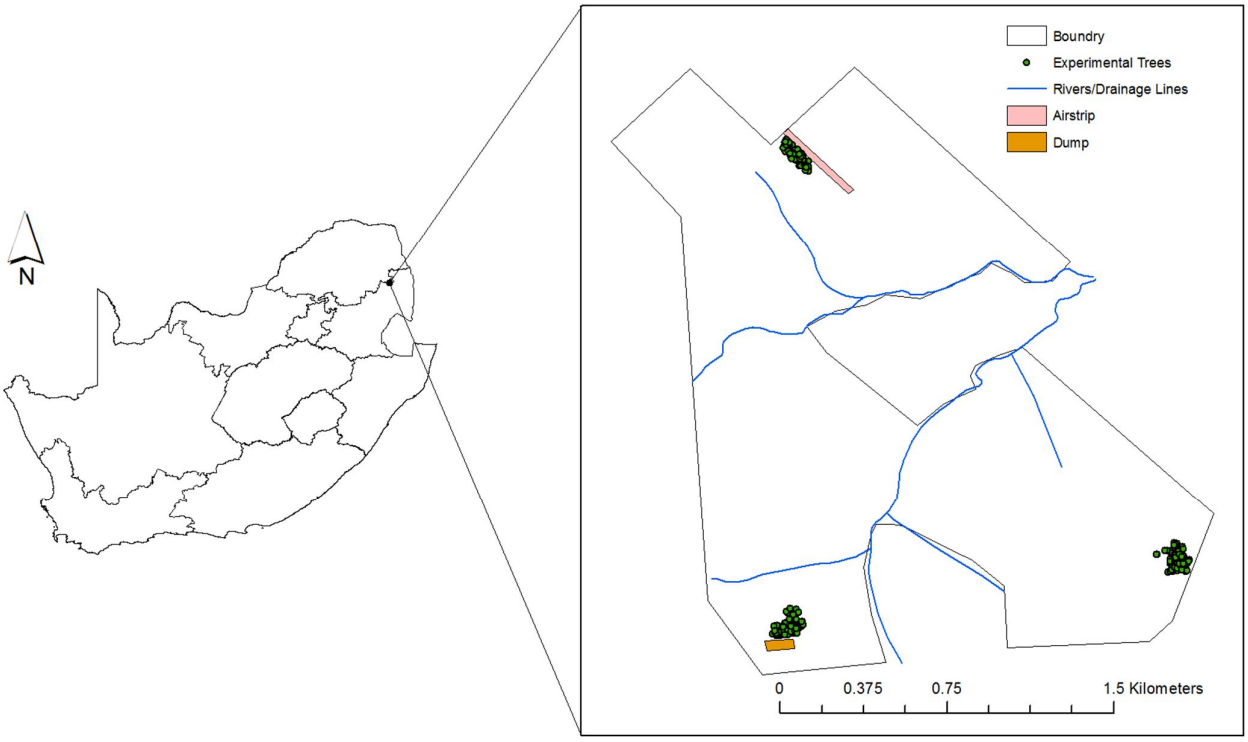

Figure 1.1: Location of study plots on the WRF on the border of the Limpopo and Mpumalanga Provinces of South Africa.

The region receives a mean annual rainfall of 665 ± 123 mm, with the majority concentrated in the summer season (October to April) in the form of conventional thunderstorms (Shackleton 1997; Shackleton 2001; Kaschula *et al*. 2005a). However, before and during the study period the rainfall was considerably lower (2014/2015 = 603 mm and 2015/2016 =

312 mm) The mean annual temperature for the region is 22 °C (Shackleton 1993; Neke *et al*. 2006), with possible drought events occurring every 4 years (Moyo *et al*. 2015b) and frost presence rare (Shackleton 2001). The geology is typified by granite gneiss of the Bandelierkop Complex (Neke 2004; Kaschula *et al*. 2005b). A catena phenomenon has been created by the slight undulating landscape (Kaschula *et al*. 2005a). The soils at the top of the crests are nutrient poor, with shallow sandy soils being the most common while at the bottom of the catena deep duplex soils are common (Shackleton 2001; Kaschula *et al*. 2005a; Neke *et al*. 2006). The vegetation is characteristic of the Mixed Lowveld Bushveld type, dominated by the Combretaceae and Mimosaceae families (Shackleton 1993, 2001; Neke *et al*. 2006; Moyo *et al*. 2015b).

1.2.2 Study species

The species chosen for this study were *Terminalia sericea* and *Dichrostachys cinerea* as both of these species are common in the broad leaf savannas of the lowveld and are commonly harvested and utilised by surrounding rural communities for fuelwood (Neke *et al*. 2006; Matsika *et al*. 2012). These two particular species were chosen as each of them have been known to represent a different coppice strategy. *Terminalia sericea* was considered as more of a "quality-driven" species, while *D. cinerea* was considered a "quantity-driven" species (Kaschula *et al*. 2005b).

Terminalia sericea ("silver cluster leaf") is found in dystrophic savannas and its distribution spans from central Africa to southern Africa (Coates-Palgrave 2002; Moyo *et al*. 2015b). *T. sericea* is a semi-deciduous single stemmed tree when uncut and can grow up to a height of 8 m. However, it can be considered a multi-stem shrub of 4-6 m tall when cut (Coates-Palgrave 2002; Moyo *et al*. 2015b). The species is known to be drought tolerant and can adapt well to saline soils (Griffiths 1959; Moyo 2013). *T. sericea* is commonly found in dense stands occurring on sandy soils (Van Wyk and Van Wyk 1997). When cut or burnt, *T. sericea* can form dense thickets which may prevent grass growth (Moyo 2013).

Dichrostachys cinerea ("sickle bush") is widely distributed through all parts of Africa (Coates-Palgrave 2002). *D. cinerea* is considered a shrub or small tree and can be 5-6 m tall (Van

Wyk and Van Wyk 1997; Coates-Palgrave 2002). The species occurs across a variety of soils and is often invasive in degraded or overgrazed areas (Van Wyk and Van Wyk 1997; Coates-Palgrave 2002). *D. cinerea* has been known to form impenetrable thickets, which may cause problems to cattle herders (Van Wyk and Van Wyk 1997; Coates-Palgrave 2002).

1.2.3 Study design and protocol

This study achieved the objectives by means of an experimental approach by examining the coppice response of felled *T. sericea* and *D. cinerea* trees under different post-harvest treatments in which tree stumps were exposed to different cutting regimes through the year. This study was conducted over a 12 month period, beginning in August 2015 and concluding in July 2016, allowing for one full growing season. However, it was the beginning of a long term project that extends beyond the scope of the study reported here. A total of 216 individual trees (108 individuals of each species) with a wide range of cumulative basal diameters (3.5 to 24.5 cm) were selected. A total of 36 individuals of each species were selected at each of three replicate study sites. Multiple study sites were used to account for environmental variability and influence on coppicing ability (Figure 1) (Moyo *et al*. 2015b). Four treatments were evenly distributed among the individuals, resulting in 9 individuals per treatment per site, and 27 per treatment in total. Treatments were allocated using the randomize feature in Microsoft Excel. Three coppicing harvest treatments and a control treatment were applied. The three monthly coppice treatments were: (1) Harvest - a complete harvest of all coppice shoot growth; this treatment was used to emulate extreme and intense harvesting and goat browsing, (2) Single prune - the pruning of shoots to leave the largest coppice shoot with the largest diameter; this treatment was used as a possible management tool with the thought of being able to optimize coppice shoot growth, and (3) Usable - the harvesting of any shoots which reached a basal diameter of 2 cm; this was to investigate the effect of interrupting the development of apical dominance and is the minimum diameter used by harvesters (Shackleton 2001). The control treatment did not have any coppice shoots removed the duration of the study. Individual coppice shoots in the control and usable treatments were not tracked monthly making comparisons of largest coppice shoots difficult. Few shoots (five *D. cinerea* and no *T. sericea* shoots) in the usable treatment reached the harvestable threshold of 2 cm in 12 months, so this treatment was

very similar to the control treatment in most respects in this initial phase of the broader project. To minimise for the effects of browsing on coppice production by games, such as impala, chicken-mesh exclusion cages (50 mm diameter) were placed around each individual cut stump.

Before felling, the stem basal diameter was measured using callipers; every stem was measured if the selected tree was a multi-stemmed individual. Trees with an individual stem basal diameter of greater than 10 cm were not included in the study as trees of this size are seldom utilized for fuelwood (Shackleton 1993). The height of a selected tree was measured using a Nikon clinometer. The mean crown diameter was calculated by averaging the length of the widest canopy axis and the length of the perpendicular axis. The lengths were measured using a tape measure. The mean crown diameter gives an indication of the possible light interception capability of an individual tree. Tree characteristics such as basal diameter have been shown to have an influence on coppice production in previous studies (Shackleton 2001; Luoga *et al*. 2004), but mean canopy diameter and shading of a stump have not been investigated previously. The nearest tree species and distance to a selected tree within four quadrants around the study tree were recorded. The selected experimental tree was the origin with the quadrants being from north to east, east to south, south to west and west to north. Knowing the species composition and distances to nearest neighbouring trees around an experimental tree gives an understanding of possible competition being experienced by the experimental tree. All selected trees were cut at a standardized height of 25 cm above ground in July 2015 so as to minimise the effects of stump height on the coppicing ability of the species (Moyo *et al*. 2015).

1.2.4 Measurements

Measurements were taken on a monthly basis before treatments were applied to the selected experimental trees. The number of shoots per stump was counted. The basal diameter of each coppice shoot was measured using callipers. A tape measure was used to measure the length of each coppice shoot; the length was measured from the base of the shoot to the longest point of the shoot stem, and buds and leaves were not included in the length measurement. Coppice shoots which were removed during the study were weighed

using hanging scales. Nine stumps of each treatment, including the control, were fully harvested in July 2016, the end of the first year of the experiment, so as to gather data on the standing coppice biomass in each treatment. The weighing of fresh shoots was completed in four phases. The first was to obtain total shoot wet biomass, including leaves and side branches of the shoot. The second phase was weighing the coppice shoot without leaves, this was to gain the woody biomass produced. The coppice shoot was then striped of side branches and the main shoot stem was then weighed, to give the shoot stem wet mass. A random sub-sample of the harvested shoot stems were then oven dried at 75°C for 24 hours and weighed on a weighing scale, to obtain the dry mass of each shoot. The mass categories are referred to as (1) Total wet mass; (2) Wood wet mass; (3) Shoot stem wet mass and (4) Shoot stem dry mass.

1.2.5 Thesis structure

Descriptions of any additional methods needed to address an objective are dealt within the relevant data chapter (chapters 2-4). To avoid unnecessary repetition through the thesis the methods section regarding study site and species, as well as the general design and protocol of the study can be found in the introductory chapter. The following chapters, 2 to 4, each address a specific objective.

- Chapter 2 addresses the objective regarding the coppice response to different post-harvest treatments.
- Chapter 3 develops allometric equations for the prediction of coppice shoot biomass by measured variables, diameter and length.
- Chapter 4 uses the allometric equations to predict how coppice biomass production is influenced by post-harvest treatments.

Chapter 5 is a discussion and synthesis chapter which combines the findings from the data chapters and provides a conclusion to the study.

Chapter 2

THE EFFECTS OF TREE CHARACTERISTICS AND POST-HARVEST TREATMENTS ON THE COPPICE RESPONSES OF TWO SAVANNA FUELWOOD SPECIES

2.1 Introduction

The ability of savanna trees to persist through coppicing has been given much attention in recent years (Shackleton 2001; Luoga *et al*. 2004; Kaschula *et al*. 2005b; Moyo *et al*. 2015b). Coppice is defined as any vegetative regrowth from the remaining stump or root system of an individual tree following a disturbance (Van Wyk and Van Wyk 1997). Coppice shoots grow quicker than seedlings as the coppice shoots are sprouting from a stump or root system which has already accumulated stored reserves (Forrester *et al*. 2003). The effect of stump characteristics on the coppice response of numerous woody species has been well documented (Shackleton 2000, 2001; Kaschula *et al*. 2005b; Handavu *et al*. 2011). Other influences on coppice production including catena positioning, repeat cuttings and pruning of coppice shoots as well as land use types have also been investigated (Shackleton 2001; Luoga *et al*. 2004; Kaschula *et al*. 2005b; Moyo *et al*. 2015b). The key to understanding coppice production dynamics of a species is to understand how the tree characteristics and post-harvest treatments will influence the coppice shoot size and the number of shoots produced.

The management of coppice regrowth through rotational harvesting has been previously proposed as a long term solution to the increasing demand of fuelwood in rural communities (Gandar 1997; Kennedy 1998; Shackleton 2001). Rotational harvesting times are dependent on the growth rate of the species as well as the desired size of fuelwood (Twine 2011). Numerous factors are known to influence coppice production of species, including cutting height but the factors which will be explored and tested here are (1) the stem size of the tree being harvested, (2) the frequency of an individual tree being exposed to a cutting event (repeat harvesting), and (3) the pruning of the coppice shoots (Shackleton 2001).

The number of coppice shoots per stump, length of coppice shoots and the cumulative diameter of coppice shoots have been found to be positively correlated with *stem size* for

numerous savanna tree species (Shackleton 2000; Kaschula *et al*. 2005b; Neke *et al*. 2006). One species, *Dichrostachys cinerea*, has been found to have a negative relationship between stem size and number of shoots (Shackleton 2000). This negative relationship has been attributed to an increase in bark thickness found in larger stems which may thwart the emergence of new buds (Khan and Triphati 1986). Several sub-tropical forest species have been found to have a negative relationship between stem size and the number of coppice shoots produced per stump (Khan and Triphati 1986; Chidumayo *et al*. 1996).

There has been a positive relationship found between the *number of cutting events* and shoot production per unit area (Moyo *et al*. 2015b). Trees exposed to eight cutting events produced significantly more coppice shoots per unit area for five months after the ending of the experiment (Moyo *et al*. 2015b). While a negative relationship was found between the number of cutting events and the diameter and length of coppice shoots produced (Moyo *et al*. 2015b). Both, diameter and length were found to be significantly lower in the frequently cut treatment for five months after the last cutting event (Moyo *et al*. 2015b).

The trimming or *pruning* of coppice shoots to leave one or two coppice shoots promotes quicker tree regrowth (Hosier 1993). The pruning of coppice shoots is a more intensive management action than the selection of tree size and cutting height (Shackleton 2001). There exists a negative relationship between pruning and number of shoots per stump (Shackleton 2001). Both the single (leaving one shoot) and double (leaving two shoots) prune treatments had greater mean shoot lengths than the no-prune (control) treatment after four growing seasons, 54% and 40% respectively (Shackleton 2001). Aerts *et al*. (2008) found a 46% increase in shoot length of a single prune treatment of a coppicing tree in Ethiopia after one year of growth. The higher shoot length in pruned treatments has been accredited to a decrease in shoot density and therefore reduced intershoot competition (Shackleton 2000).

Previous studies have found the averaged desired diameter of utilised fuelwood poles is approximately 6 cm, but in heavily harvested sites harvesters will collect poles of smaller size classes of 2-4 cm (Shackleton 1993; Shackleton 2001; Neke *et al*. 2006). In addition to the management of coppicing shoots through pruning processes the application of fertilizer,

either chemical or organic, has been proposed as a management scheme to enhance coppice growth (Hosier 1993; Moyo *et al*. 2015b). However, rural communities do not utilise the practice of fertilizing very often as this method is costly and impractical (Hosier 1993) and the management of coppice growth through pruning is a more practical scheme. Little is known about how savanna tree coppice will respond to different management schemes. Therefore, the objective of this chapter was to investigate the influence of different post-harvest treatments, after controlling for the influence of tree characteristics, on coppice response of two popular fuelwood savanna tree species, *Terminalia sericea* and *Dichrostachys cinerea*, which are known to exhibit different coppicing strategies.

2.2 Methods

2.2.1 *Study site and species*

See Chapter 1.

2.2.2 *Design and protocol*

See Chapter 1.

2.2.3 *Data analysis*

A One-Way ANOVA was conducted to test for differences in average diameter, length and number of coppice shoots produced between the four post-harvest treatments after one year of growth. If any significant difference was found, a pairwise post-hoc analysis was conducted. Spearman rank correlation tests were done on average canopy diameter and cumulative basal area to ensure no co-variance would occur in the model. A generalised linear mixed model was used to assess the influence of post-harvest treatments on average shoot diameter and length, the number of coppice shoots produced per stump relative to the control treatment, after controlling for cumulative stump basal area of the stump, the number of stumps of the tree, the mean shading of the stump (Table 2.1). Site was treated as a random effect in the model. The basal diameter of stumps was converted to basal area to provide an understanding of coppice shoot production per unit area. Measurements taken of the control, single prune and usable treatments after 12 months (in July 2016) were

used for the mean diameter and length of coppice shoots in these treatments. All shoots of the harvest treatment were included in the calculations for this treatment. The number of shoots was considered to be the final count in July 2016 for the control treatment, the final count in July 2016 adding whatever shoots had been cut through the year for the usable treatment, the sum of all shoots cut for the harvest treatment and the sum of all shoots cut plus one for the single prune treatment. The single prune treatment had a single shoot left on the stump through the months and therefore that shoot needed to be accounted for in the total count of shoots produced. A likelihood ratio test was conducted to assess the influence of the random effect variable on the response variables. This was done by removing the random effect variable, running a linear model with the fixed effect variables and then conducting an ANOVA between the model including the random effect and the model excluding the random effect. Welch two sample T-tests were conducted to test for differences between species within each treatment. All analyses were performed in R statistics software (R studio version 3.2.5).

Table 2.1: Mean, standard deviation, standard error, minimum and maximum of selected independent variables for tree species *Terminalia sericea* and *Dichrostachys cinerea* utilised in the general linear mixed model.

Species	Independent Variable	Mean	Standard Deviation	Standard Error	Minimum	Maximum
T. sericea	Shading (%)	40.63	28.81	2.73	3.12	96.20
	Canopy Diameter (m)	4.34	1.17	1.76	1.90	7.90
	Basal area (cm^2)	36.93	18.03	0.12	12.57	98.52
	Basal Diameter (cm)	6.68	1.58	0.15	4.00	11.20
D. cinerea	Shading (%)	28.63	24.94	2.53	2.08	99.84
	Canopy Diameter (m)	2.57	0.76	1.82	1.40	5.50
	Basal area (cm^2)	29.01	17.92	0.08	9.62	134.75
	Basal Diameter (cm)	6.94	3.38	0.34	3.50	24.50

2.3 Results

2.3.1 *Co-variance in independent variables*

Average canopy diameter (m) was found to have a weak but significant positive correlation with cumulative basal diameter (cm^2) for all sprouting trees (Figure 2.1). The correlation

between average canopy diameter (m) and cumulative basal area (cm^2) was stronger for *T. sericea* than *D. cinerea* (Figure 2.1).

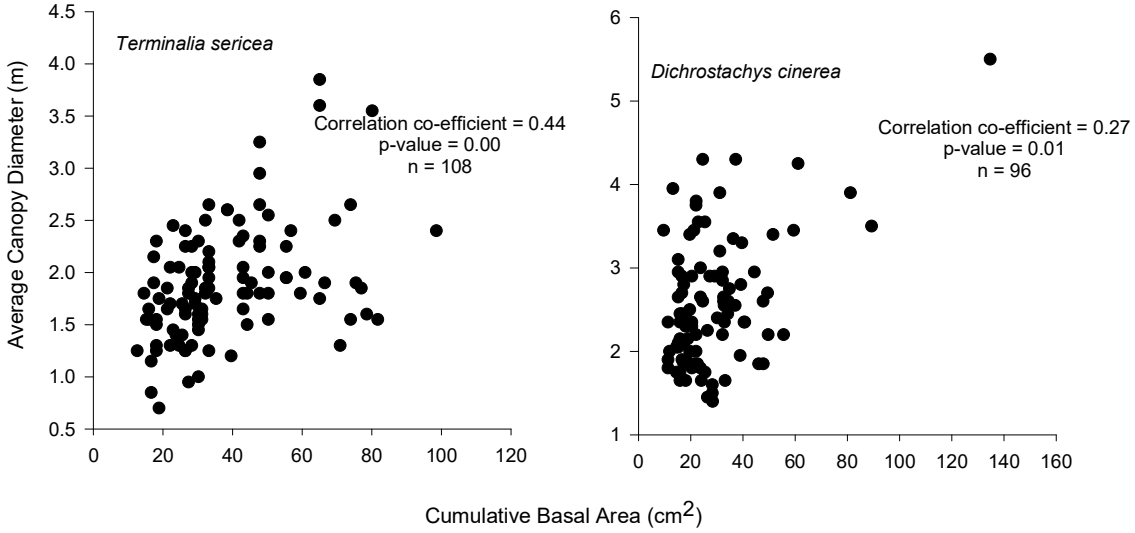

Figure 2.1: Correlation of cumulative basal area (cm^2) and average canopy diameter (m) for all trees as well as individual species.

2.3.2 *Terminalia sericea* coppice production

All cut *T. sericea* individuals sprouted and produced coppice shoots through the study period. By the end of the study period (July 2016) the harvest treatment trees had stopped sprouting coppice shoots but all other individual trees had survived. A total of 806 *T. sericea* coppice shoots were produced through the study period with diameters ranging from 0.1 to 2.4 cm. As average canopy diameter and cumulative basal area were correlated, one variable needed to be excluded from the generalised mixed model. Average canopy diameter was selected to be excluded as measuring of cumulative basal area was more accurate.

Diameter

The average coppice shoot diameter was significantly different between treatments (F_3 = 65.16; $p < 0.001$) (Figure 2.2). The month-old coppice shoots produced by the harvest treatment had the lowest average diameter ($\bar{x}$ = 0.40 ± 0.01 cm), which was nearly half the diameter of the coppice shoots produced by the control ($\bar{x}$ = 0.73 ± 0.03 cm) and usable treatments ($\bar{x}$ = 0.74 ± 0.04 cm) which had been growing for the 12 month study period

(Figure 2.2). The single prune treatment produced the coppice shoots with the highest average diameter ($\bar{x}$ = 1.230 ± 0.063 cm) after 12 months of growth, which was over double the width of the monthly coppice shoots produced by the harvest treatment and almost double the thickness of coppice shoots produced by the control and usable treatments (Figure 2.2). There was no significant difference in the average coppice shoot diameter between the control and usable treatments (Figure 2.2; Appendix I).

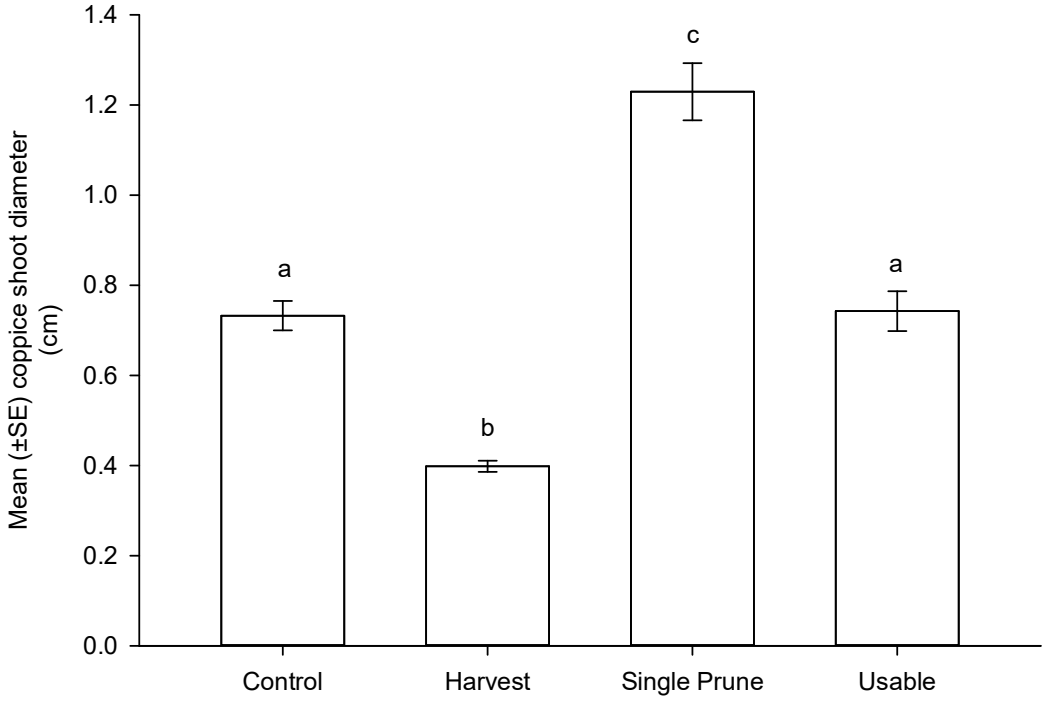

Figure 2.2: Mean (± SE) coppice shoot diameter (cm) of *Terminalia sericea* for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The number of stumps had to be excluded from the generalised mixed model for *T. sericea* as all experimental trees of this species were single stemmed. There was a significantly positive relationship between the cumulative basal area of a tree before felling and the mean coppice shoot diameter (Table 2.2a). The remaining tree-specific variables tested (the mean shading of the stump, distance to closest neighbouring tree and average distance to surrounding trees) did not have a significant influence on the average diameter of coppice shoots (Table 2.2a). Two of the three post-harvest treatments had a significant influence on the average diameter of coppice shoots when compared to the control treatment, after

controlling for tree-level factors (Table 2.2a, Appendix I). The random effect of site did not have an influence on the average diameter of coppice shoots (Likelihood ratio test p = 0.89; Table 2.2b).

Table 2.2: Generalised mixed model of (a) fixed effects and (b) random effect on the average diameter of coppice shoots of *Terminalia sericea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	2.223	1.330	< 0.001
Cumulative Basal Area	0.208	0.056	< 0.001
Mean Shading	0.035	0.145	0.809
Distance to closest Neighbour	-0.350	0.652	0.884
Average Distance to Neighbours	-0.158	0.535	0.768
Harvest Treatment	-1.168	0.807	< 0.001
Single Prune Treatment	1.808	0.785	< 0.001
Usable Treatment	0.439	0.810	0.883

b)

Random Effect	Coefficient	Std Deviation
Site	0.000	0.000
Residuals	0.597	0.773

Length

The average coppice shoot length differed significantly between post-harvest treatments (F_3 = 64.95; p < 0.001) (Figure 2.3). The single prune ($\bar{x}$ = 81.03 ± 5.05 cm), control ($\bar{x}$ = 51.51 ± 2.89 cm) and usable treatments ($\bar{x}$ = 50.08 ± 1.77 cm) produced significantly longer coppice shoots than that of the harvest treatment ($\bar{x}$ = 15.46 ± 0.75 cm) (Figure 2.3). The single prune treatment produced significantly longer coppice shoots than the control and usable treatments (Figure 2.3). There was no significant difference in average coppice shoot length between the control and usable treatments (Figure 2.3; Appendix I).

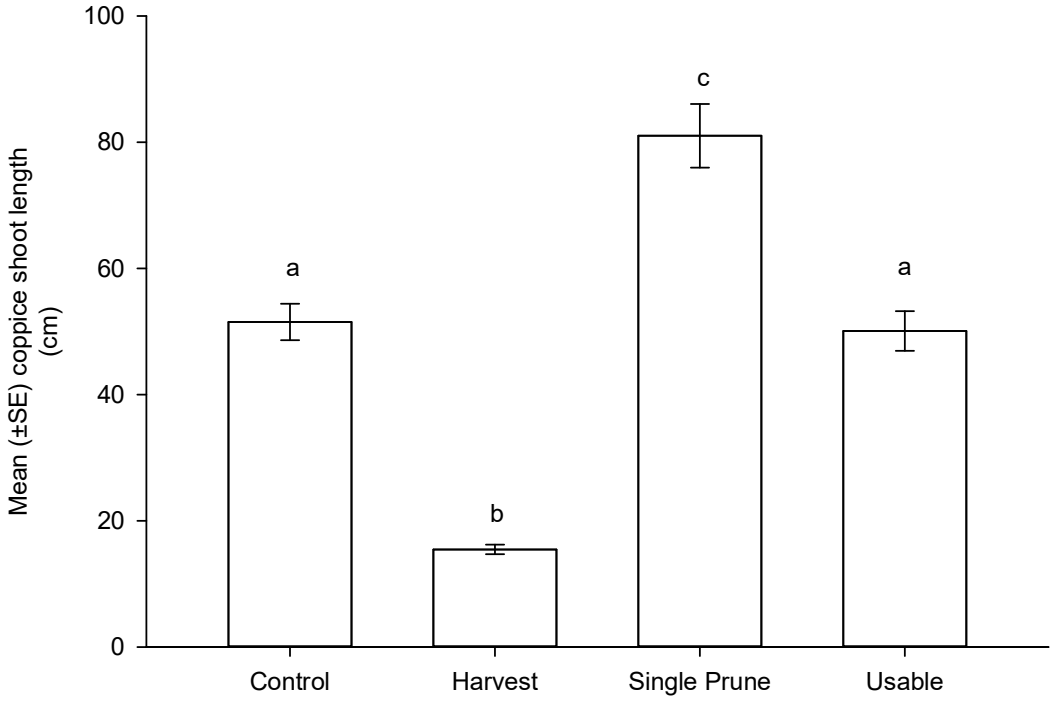

Figure 2.3: Mean (± SE) coppice shoot length (cm) of *Terminalia sericea* for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The tree-specific variables tested (cumulative basal area, the mean shading of the stump, distance to closest neighbouring tree and average distance to surrounding trees) did not have a significant influence on the average length of coppice shoots (Table 2.3a). The post-harvest treatments had a significant influence on the average length of coppice shoots when compared to the control treatment, after controlling for tree characteristics (Table 2.3a). The harvest treatment produced significantly shorter coppice shoots on average (Table 2.3a). The random effect of site did not have a significant influence on the average coppice shoot length (Table 2.3b; Likelihood ratio test $p = 0.49$).

Table 2.3: Generalised mixed model of (a) fixed effects and (b) random effect on the average length of coppice shoots of *Terminalia sericea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	42.980	8.081	< 0.001
Cumulative Basal Area	0.152	0.093	0.105
Mean Shading	-0.002	0.065	0.976
Distance to closest Neighbour	-4.946	3.964	0.215
Average Distance to Neighbours	3.670	3.254	0.262
Harvest Treatment	-34.319	4.904	< 0.001
Single Prune Treatment	29.469	4.772	< 0.001
Usable Treatment	-0.480	4.923	0.923

b)

Random Effect	Coefficient	Std Deviation
Site	0.00	0.00
Residuals	298.4	17.28

Number of shoots

The average number of coppice shoots produced through the year was found to be significantly different between treatments (F_3 = 35.66; p < 0.001) (Figure 2.4). The harvest and single prune treatments produced significantly higher average cumulative numbers of coppice shoots through the study year compared to the control and usable treatments (Figure 2.4). There was no significant difference between the harvest and single prune treatments in the production of coppice shoots (Figure 2.4). No significant difference was found between the control and usable treatments in the production of coppice shoots per experimental tree (Figure 2.4). The treatments which were exposed to multiple cutting events (harvest ($\bar{x}$ = 18.7 ± 2.147) and single prune ($\bar{x}$ = 16.63 ± 1.03)) produced over three times the average number of coppice shoots per experimental stump over 12 months than the treatments that experienced less cutting events (control ($\bar{x}$ = 5.15 ± 0.39) and usable ($\bar{x}$ = 5.04 ± 0.39)) (Figure 2.4; Appendix I).

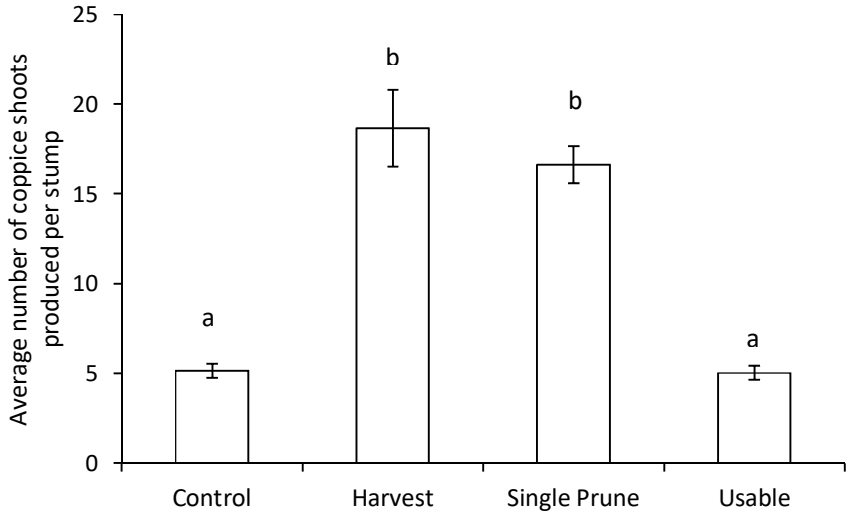

Figure 2.4: Average number of coppice shoots (± SE) produced per experimental tree of *Terminalia sericea* for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The post-harvest treatments were the only fixed effect variables to have an influence on the average number of coppice shoots produced per experimental tree (Table 2.4a). Site as a random effect variable did have a significant influence on the number of coppice shoots produced per experimental tree (Table 2.4b; Likelihood ratio test $p < 0.05$).

Table 2.4: Generalised mixed model of (a) fixed effects and (b) random effect on the number of coppice shoots produced per experimental tree of coppice shoots of *Terminalia sericea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	0.073	3.141	0.982
Cumulative Basal Area	-0.010	0.035	0.784
Mean Shading	0.038	0.024	0.125
Distance to closest Neighbour	-0.284	1.384	0.838
Average Distance to Neighbours	1.425	1.150	0.218
Harvest Treatment	14.507	1.707	< 0.001
Single Prune Treatment	12.250	1.661	< 0.001
Usable Treatment	1.285	1.714	0.455

b)

Random Effect	Coefficient	Std Deviation
Site	5.529	2.351
Residuals	36.112	6.009

2.3.3 *Dichrostachys cinerea* coppice production

Not all cut individuals of *D. cinerea* sprouted and 90% of stumps produced coppice shoots through the study period. The harvest treatment individual trees had stopped sprouting by the end of the study period (July 2016), but all other individual trees which had sprouted survived through the year. A total of 689 coppice shoots were produced through the study period with diameters ranging from 0.1 to 2.6 cm. As average canopy diameter and cumulative basal area were correlated, one variable needed to be excluded from the generalised mixed model. Average canopy diameter was selected to be excluded as measuring of cumulative basal area was more accurate.

Diameter

The average coppice shoot diameter was found to be significantly different between post-harvest treatments (F_3 = 28.54; $p < 0.001$) (Figure 2.4). The harvest treatment produced significantly thinner coppice shoots than the other three post-harvest treatments (Figure 2.4). The single prune treatment produced significantly thicker coppice shoots with an average diameter ($\bar{x}$ = 1.21 ± 0.10 cm) than that of coppice shoots produced by the control ($\bar{x}$ = 0.70 ± 0.04 cm) and usable ($\bar{x}$ = 0.84 ± 0.06 cm) treatments and over double that of coppice shoots produced by the harvest treatment ($\bar{x}$ = 0.43 ± 0.02 cm) (Figure 2.4). There was no significant difference found between control and usable treatments in the average diameter of coppice shoots (Figure 2.4; Appendix II).

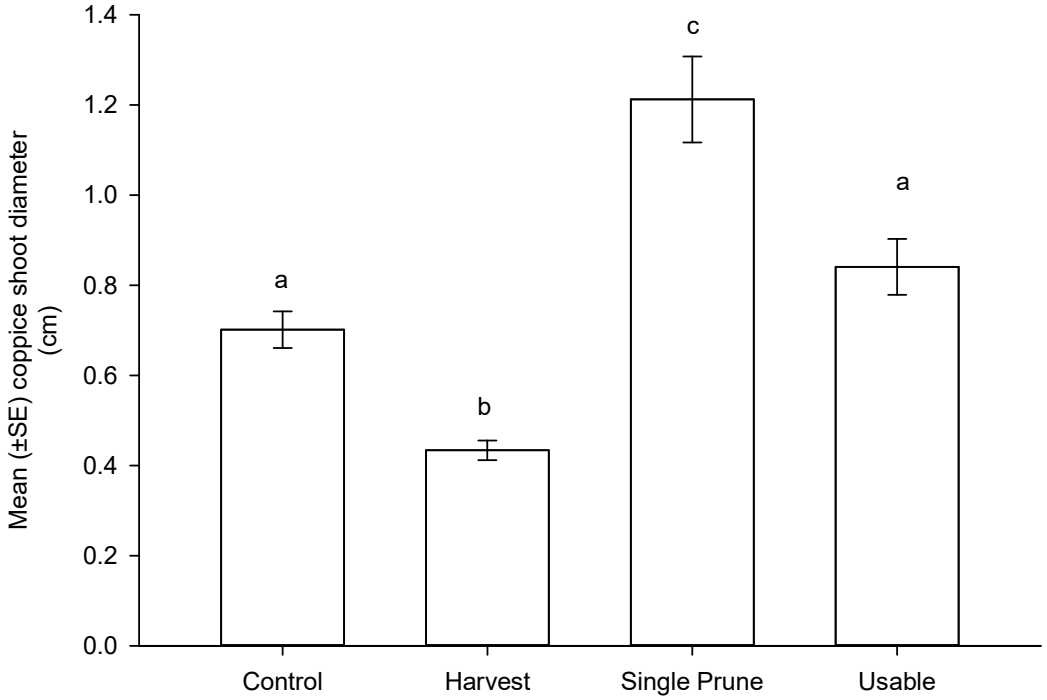

Figure 2.4: Mean (± SE) average diameter (cm) of *Dichrostachys cinerea* coppice shoots for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The post-harvest treatments had a significant influence on the average diameter of coppice shoots produced per experimental tree. After controlling for tree characteristics, the harvest treatment produced significantly thinner average coppice shoot diameters and the single prune treatment produced significantly thicker coppice shoots when compared to the control treatment (Table 2.5a). The other fixed effects did not have an influence on the average diameter of coppice shoots produced per experimental tree (Table 2.5a). The random effect of site did not have a significant effect on the average diameter of coppice shoots produced per experimental tree (Table 2.5b; Likelihood ratio test $p = 0.96$).

Table 2.5: Generalised mixed model of (a) fixed effects and (b) random effect on the average diameter of coppice shoots of *Dichrostachys cinerea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	0.898	0.137	< 0.001
Cumulative Basal Area	0.002	0.002	0.267
Number of Stumps	-0.038	0.040	0.354
Mean Shading	-0.001	0.001	0.715
Distance to closest Neighbour	-0.0385	0.062	0.533
Average Distance to Neighbours	-0.056	0.051	0.281
Harvest Treatment	-0.264	0.087	< 0.01
Single Prune Treatment	0.511	0.087	< 0.001
Usable Treatment	0.131	0.088	0.140

b)

Random Effect	Coefficient	Std Deviation
Site	0.006	0.075
Residuals	0.087	0.295

Length

The post-harvest treatments had a significant influence on the average coppice shoot length (F_3 = 28.66; p < 0.001) (Figure 2.6). The harvest treatment produced significantly shorter coppice shoots ($\bar{x}$ = 24.14 ± 1.86 cm) than the other three post-harvest treatments, which were almost half the length of the control ($\bar{x}$ = 49.01 ± 2.56 cm) and usable ($\bar{x}$ = 51.41 ± 2.350 cm) treatments (Figure 2.6). The single prune treatment produced significantly longer coppice shoots ($\bar{x}$ = 61.22 ± 4.52 cm) than the harvest and control treatments, no significant difference was found between the usable and single prune treatments (Figure 2.6). The coppice shoots produced through the study year by the single prune treatment were over two and a half times longer than the coppice shoots produced monthly by the harvest treatment. There was no significant difference in the average coppice shoot length between the control and usable treatments (Figure 2.6; Appendix II).

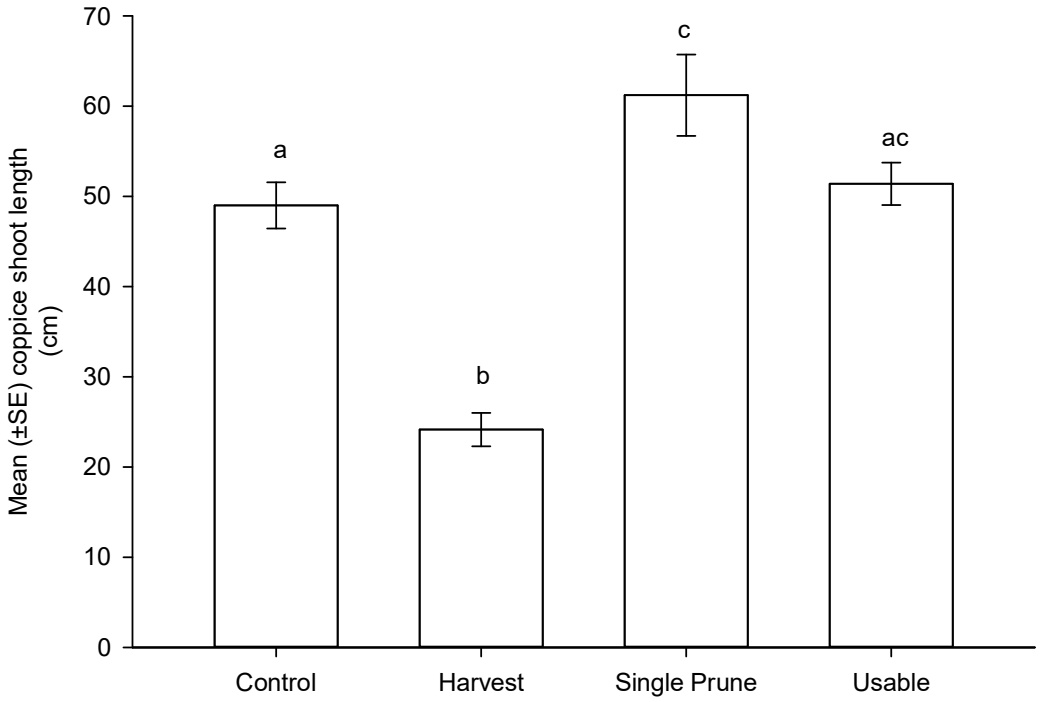

Figure 2.6: Mean (± SE) length (cm) of *Dichrostachys cinerea* coppice shoot length for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The post-harvest treatments had a significant influence on the average length of coppice shoots, after controlling for tree characteristics (Table 2.6a). The harvest treatment produced significantly shorter coppice shoots compared to the control treatment (Table 2.6a). Experimental tree characteristics did not have a significant influence on the length of coppice shoots (Table 2.6a). The random effect of site did not have a significant influence on the average length of coppice shoots produced by *D. cinerea* (Table 2.6b; Likelihood ratio test $p = 0.67$).

Table 2.6: Generalised mixed model of (a) fixed effects and (b) random effect on the average length of coppice shoots of *Dichrostachys cinerea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	57.343	6.419	< 0.001
Cumulative Basal Area	0.019	0.015	0.854
Number of Stumps	1.283	1.963	0.515
Mean Shading	-0.105	0.069	0.130
Distance to closest Neighbour	0.435	2.956	0.883
Average Distance to Neighbours	-3.239	2.446	0.189
Harvest Treatment	-25.833	4.235	< 0.001
Single Prune Treatment	12.798	4.216	< 0.01
Usable Treatment	1.901	4.283	0.658

b)

Random Effect	Coefficient	Std Deviation
Site	3.411	1.847
Residuals	206.784	14.380

Number of shoots

The average number of coppice shoots produced per stump differed significantly between treatments (F_3 = 12.55; p < 0.001) (Figure 2.7). There was no significant difference in the number of coppice shoots between the harvest ($\bar{x}$ = 15.44 ± 2.41) and single prune ($\bar{x}$ = 14.54 ± 1.66) treatments (Figure 2.7). The harvest and single prune treatments produced significantly more coppice shoots than the control ($\bar{x}$ = 6.26 ± 0.61) and usable ($\bar{x}$ = 4.88 ± 0.46) treatments after 12 months (Figure 2.7). The frequently harvested treatments (harvest and single prune) produced almost as much as four times as many coppice shoots on average per experimental stump when compared to the treatments which experienced less harvesting (control and usable) events. No significant difference was found between the control and usable treatments in the number of coppice shoots produced per experimental tree (Figure 2.7; Appendix II).

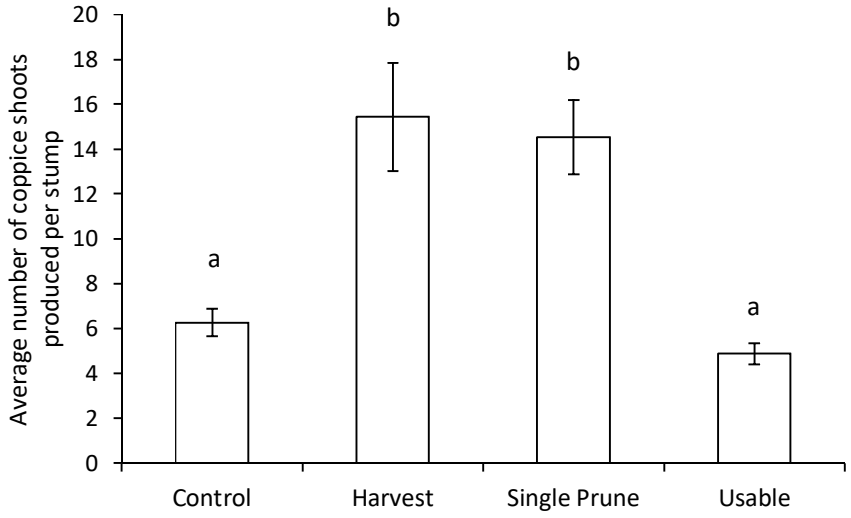

Figure 2.7: Average number of coppice shoots produced (± SE) per experimental tree of *Dichrostachys cinerea* for the four post-harvest treatments. Differing superscript letters indicate significance difference by manner of least square means ($p < 0.05$).

The post-harvest treatments had a significant influence on the average number of coppice shoots produced per experimental tree through the study period (Table 2.7a). Both the harvest and single prune treatments produced more coppice shoots per experimental tree than the control treatment after 12 months (Table 2.7a). Morphological stump characteristics did not have a significant influence on the number of coppice shoots produced (Table 2.7a). Site as a random effect variable did not have a significant influence on the average number of coppice shoots produced per experimental tree (Table 2.7b; Likelihood ratio test $p > 0.05$).

Table 2.7: Generalised mixed model of (a) fixed effects and (b) random effect on the number of coppice shoots produced per experimental tree of coppice shoots of *Dichrostachys cinerea*.

a)

Fixed Effect	Coefficient	Std Error	p-value
Intercept	1.915	3.244	0.555
Cumulative Basal Area	0.088	0.054	0.104
Number of Stumps	1.456	1.006	0.151
Mean Shading	-0.014	0.035	0.693
Distance to closest Neighbour	0.498	1.495	0.740
Average Distance to Neighbours	-0.304	1.237	0.806
Harvest Treatment	8.687	2.166	< 0.001
Single Prune Treatment	8.663	2.161	< 0.001
Usable Treatment	-0.758	2.194	0.730

b)

Random Effect	Coefficient	Std Deviation
Site	0.000	0
Residuals	54.36	7.373

2.3.4 *Comparing between species*

No significant differences were found between species in the diameter size and number of coppice shoots produced by any treatment ($p > 0.05$; Figure 2.8). The only significant difference between the species was found in the average coppice shoot length produced by the harvest ($t = 4.339$; $d.f = 32$; $p < 0.001$) and single prune ($t = -2.293$; $d.f = 49$; $p < 0.001$) treatments (Figure 2.8). *Dichrostachys cinerea* ($\bar{x} = 24.14 \pm 1.86$ cm) produced significantly longer coppice shoots in the harvest treatment than *T. sericea* ($\bar{x} = 15.46 \pm 0.75$ cm). However, in the single prune treatment *T. sericea* ($\bar{x} = 81.03 \pm 5.05$ cm) produced significantly longer coppice shoots than *D. cinerea* ($\bar{x} = 61.22 \pm 4.52$ cm).

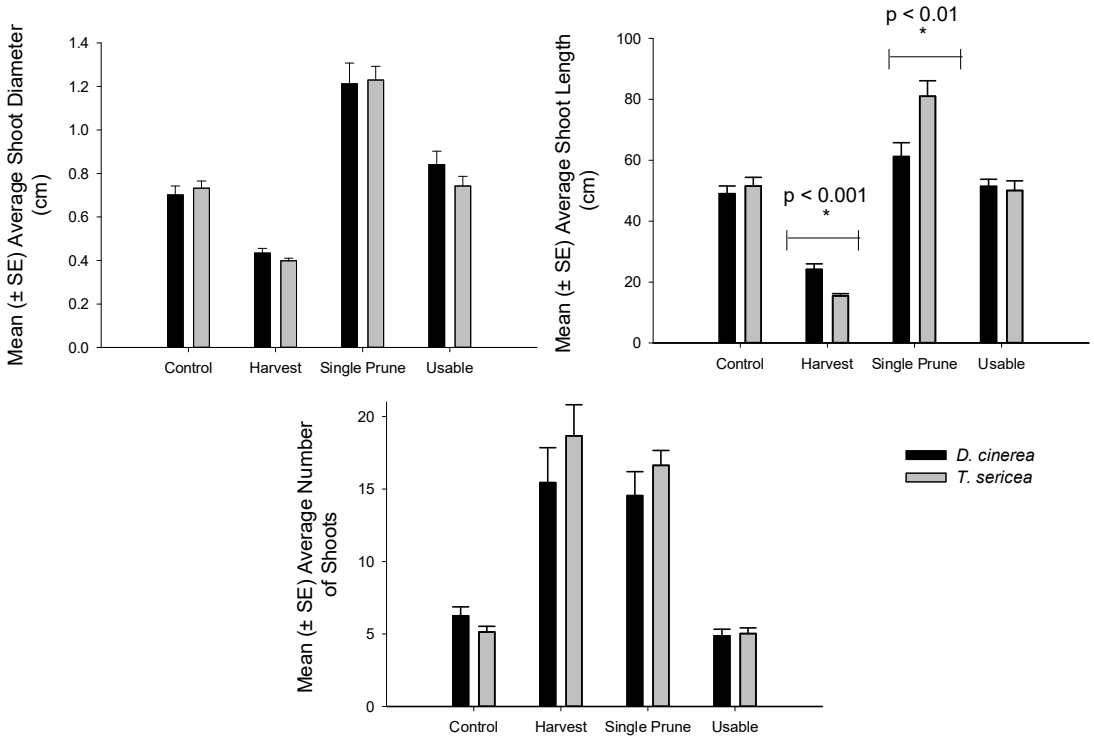

Figure 2.8: Comparison of mean (±SE) shoots diameter, length and number of shoots produced by T. sericea and D. cinerea.

2.4 Discussion

2.4.1 *Diameter*

The average diameter of coppice shoots produced by experimental trees was influenced by the applied post-harvest treatment. Shackleton (2001) found that pruning coppice shoots to leave either one or two coppice shoots resulted in higher mean diameters than a no prune treatment. The single prune treatment resulted in wider coppice shoots being produced than coppice shoots produced by the control and usable treatments after a year of growth for both species. The monthly removal of additional coppice shoots for the single prune treatment would decrease the intra-specific competition for resources such as light, water and nutrients (starch and carbohydrates) resulting in coppice shoots with higher diameters than the other post-harvest treatments (Latt *et al*. 2000; Forrester *et al*. 2003). The harvest treatment, which only allowed for a month of growth, produced the narrowest coppice shoots in both species, as expected. The significantly lower diameter of coppice shoots in the frequently harvested treatment can be attributed to the insufficient time

allowed for growth and establishment of new photosynthetic mass (Latt *et al*. 2000; Moyo *et al*. 2015b). Moyo *et al*. (2015b) found that the diameter of coppice shoots produced from *T. sericea* stumps which were exposed to three-month cycle cuts over a two year period (cut 8 times) was significantly lower than the diameter of coppice shoots produced by *T. sericea* stumps exposed to fewer cutting events (cut once or twice) over the same period. This is supported by the control and usable treatments producing significantly higher diameters than the harvest treatment.

Terminalia sericea expressed a significant positive relationship between cumulative basal diameter and the average diameter of coppice shoots. Cumulative basal diameter and mean canopy diameter had a significant positive correlation. This suggests that individual trees with a higher cumulative basal diameter would have a wider mean canopy. A wider mean canopy diameter is known to lead to greater solar interception, which in turn leads to greater accumulation of carbon for biomass production (Oker-Blom *et al*. 1989). A wider canopy diameter will then allow for experimental trees to accumulate more stored reserves which can then be utilised in producing larger coppice shoots after a disturbance. Cumulative basal area (size of the stump) has been found to have a significant positive influence on the diameter of *D*. *cinerea* coppice shoots as well as the total diameter of coppice shoots produced by *T. sericea* (Kaschula *et al*. 2005b; Neke *et al*. 2006). However, this was not found in this study. It is interesting that while there is an allometric relationship between stem basal area and crown size, this is obviously not a tight relationship, within this stem diameter range, otherwise shoot diameter would have also been related to basal area for *D*. *cinerea*.

2.4.2 *Length*

The length of *T*. *sericea* and *D*. *cinerea* coppice shoots was significantly altered by the post-harvest treatments. The single prune treatment resulted in the production of the longest coppice shoots on average which is what Shackleton (2001) generally found with *T. sericea*, when comparing a single prune treatment to a double prune (leaving two coppice shoots) treatment and a no prune (control) treatment. However, the double prune treatment applied by Shackleton (2001) to larger stumps (> 30 cm basal circumference) cut at 20 cm

above ground had a greater mean shoot length than the other treatments. The effect of competition would have hampered the growth of the coppice shoots in the control and usable treatments, resulting in intermediate lengths when compared to the single prune treatment, which minimised the effect of intra-specific shoot competition. The competition for light would restrict growth of coppice shoots until apical dominance of a shoot is established which has been reported to take up to two growing seasons (Shackleton 2001). Once apical dominance is established the coppice shoot will then most likely out-compete the other lesser coppice shoots for light.

Coppice shoot length has been found to have a positive relationship with cumulative basal area (stump size) for both *T. sericea* and *D. cinerea* in previous studies (Shackleton 2001; Kaschula *et al*. 2005b). These previous studies had a much greater range of stump sizes with a maximum total basal diameter of 30 cm (Shackleton 2001), while in the current study the maximum cumulative basal diameter was less than 25 cm. In the current study the no experimental tree characteristic had a significant influence on the coppice shoot length of *T. sericea* and *D. cinerea*. Stump diameter has been reported to have a significant positive relationship with coppice shoot length of *D. cinerea* (Kaschula *et al*. 2005b), but that was not found in this study.

2.4.3 *Number of shoots*

The number of shoots produced through the year per experimental tree was significantly influenced by which post-harvest treatment was applied for both species. The post-harvest treatments which involved multiple cutting events (the harvest and single prune treatments) produced significantly more coppice shoots per experimental tree through the study year than the control and usable post-harvest treatments, which only had a single cutting event, or very few for the usable treatment (*D. cinerea* was the only species to reach the desired size of 2 cm through the year). The multiple cutting events act as a disturbance, initiating the mobilisation of resource reserves resulting in the persistence of the tree through new coppice shoots (Bellingham and Sparrow 2000; Bond and Midgley 2001; Moyo *et al*. 2015b). The continual production of coppice shoots is a tolerance strategy in plants known as compensatory regrowth which is induced by damage to the plant (Strauss and

Agrawal 1999; Zhao and Chen 2012). The findings in this study are supported by a previous study which found that repeat cutting events of *T. sericea* significantly increased the number of coppice shoots produced by an individual tree after five months (Moyo *et al*. 2015).

Cumulative basal area has been found to have a significant positive influence on the number of coppice shoots produced per stump for both *T. sericea* and *D*. *cinerea* in other studies (Shackleton 2001; Kaschula *et al*. 2005b; Neke *et al*. 2006). However, in this study cumulative basal area did not have a significant influence on the number of coppice shoots produced per experimental tree by either species. Previous studies have found similar results, Bowersox *et al*. (1990) found no relation between stump size and number of shoots produced while Khan and Tripathi (1986) found that coppicing ability decreased with increasing stump size. The larger stumps would tend to have thicker bark which has been proposed to hinder bud emergence (Khan and Tripathi 1986). Thick bark is considered to be an adaptation to a system that experiences burning events, such as a savanna (Shackleton 2000).

The number of coppice shoots produced by *T. sericea* was influenced by site. It has been reported that positioning along a catena sequence can influence shoot characteristics such as diameter and length in *D. cinerea* (Kaschula *et al*. 2005b), however in this study the coppicing dynamics of *D. cinerea* were not significantly influenced by site. The difference in the number of coppice shoots produced by *T. sericea* at varying sites may be as a result of differing soil characteristics. Soil characteristics were not tested in this study and should then be considered in future coppicing studies. Soil nutrients including calcium, magnesium, potassium and phosphorus have been thought to be important in the coppicing ability of savanna shrubs (Miyansishi and Kellman 1986).

2.4.4 *Sprouting strategies*

There was no clear difference in the sprouting strategies of these two species. Both species produced similar dimensions and number of shoots between treatments. The sprouting strategy to best describe these two species after 12 months of growth would be the

"quantity-driven" strategy (Kaschula *et al*. 2005b). This strategy is characterised by having multiple smaller shoots rather than less large shoots (Kaschula *et al*. 2005b; Neke *et al*. 2006). *Terminalia sericea* has been known to demonstrate a combination of strategies, producing multiple and relatively large coppice shoots (Moyo 2013). This could be understandable as *T*. *sericea* did produce longer coppice shoots in general but significantly longer in the single prune treatment at the same time as producing a similar number of coppice shoots per stump when compared with *D*. *cinerea*. Interestingly *D*. *cinerea* produced significantly longer coppice shoots than *T*. *sericea* in the harvest treatment. This would suggest that *D*. *cinerea* mobilises resources quicker than *T*. *sericea* when frequently disturbed. The mobilisation of these resources in frequently disturbed situations would aid in the potential escape from the kill zone of coppice shoots (Wigley *et al*. 2009).

2.5 Conclusion

Coppicing production can be manipulated by the utilisation of post-harvest treatments. In order to maximise coppicing metrics (diameter, length and number of coppice shoots) of both species, applying the single prune from this study would be most beneficial. However, the majority of coppice shoots produced through the single prune treatment would be of similar size to the coppice shoots produced by the harvest treatment and will therefore not be very useful, except maybe for kindling. Post-harvest treatments are not the only managerial tool which can be utilised to maximise coppicing dynamics. Less intensive management actions, including the selection of tree properties can have an influence on the coppicing dynamics of savanna species. Other easily selective variables should be considered in selecting an experimental tree. Initial characteristics of an experimental tree should be considered, as cumulative basal diameter did have an influence in this study and has been found to have a significant influence on coppicing dynamics of numerous species in other studies.

Appendix I

Tukey HSD pairwise comparisons between the four post-harvest treatments for the coppicing dynamics (diameter, length and number of shoots) of *Terminalia sericea*. Significance is indicated at a 95% confidence interval.

	Diameter		Length		Number of Shoots	
Contrast	Difference	p-value	Difference	p-value	Difference	p-value
Harvest-Control	-0.334	< 0.001	-36.049	< 0.001	13.519	< 0.001
Single Prune-Control	0.497	< 0.001	29.529	< 0.001	11.482	< 0.001
Usable-Control	0.010	0.998	-1.428	0.99	-0.111	0.999
Single Prune-Harvest	0.831	< 0.001	65.578	< 0.001	-2.037	0.642
Usable-Harvest	0.344	< 0.001	34.622	< 0.001	-13.63	< 0.001
Usable-Single Prune	-0.487	< 0.001	-30.956	< 0.001	-11.593	< 0.001

Appendix II

Tukey HSD pairwise comparisons between the four post-harvest treatments for the coppicing dynamics (diameter, length and number of shoots) of *Dichrostachys cinerea*. Significance is indicated at a 95% confidence interval.

	Diameter		Length		Number of Shoots	
Contrast	Difference	p-value	Difference	p-value	Difference	p-value
Harvest-Control	-0.268	< 0.05	-24.869	<0.001	9.179	< 0.001
Single Prune-Control	0.511	< 0.001	12.211	< 0.05	8.281	< 0.01
Usable-Control	0.139	0.388	2.398	0.943	-1.386	0.924
Single Prune-Harvest	0.778	< 0.001	37.080	< 0.001	-0.898	0.976
Usable-Harvest	0.407	< 0.001	27.267	< 0.001	-10.565	< 0.001
Usable-Single Prune	-0.372	< 0.001	-9.813	0.100	-9.667	< 0.001

Chapter 3

SPECIES-SPECIFIC ALLOMETRIC EQUATIONS FOR DETERMINING BIOMASS OF COPPICE SHOOTS OF TWO SAVANNA SPECIES

3.1 Introduction

The ability for savanna trees to regenerate and coppice after a disturbance has often been neglected or undervalued in previous biomass models (Banks *et al*. 1996; Shackleton 2001; Wessels *et al*. 2013). The ability to estimate contributions of coppice shoots to an area's woody biomass is imperative to gaining a better understanding of the availability of fuelwood as well as the potential for carbon sequestration in rural communities (Shackleton and Scholes 2011). Biomass can be estimated using two methods; direct and indirect (Araújo *et al*. 1999). Each method has its own advantages and disadvantages (Araújo *et al*. 1999). The direct method is destructive as it requires the cutting and weighing of the plant material (Araújo *et al*. 1999). Along with being destructive, direct sampling may also be time consuming, laborious and costly (Gehring *et al*. 2004; Nickless *et al*. 2011). The choice of area selected for the direct method can be biased as, in most cases, the sampled area contains few large trees in which simple extrapolations may lead to over-estimations of the landscape's biomass (Araújo *et al*. 1999).

The indirect method, in contrast, is based on the utilisation of mathematical models or allometry (Araújo *et al*. 1999). Allometry is defined as, "the use of mathematical relationships to predict difficult-to-measure variables from easy-to-measure variables" (Netshiluvhi and Scholes 2001). Easy-to-measure variables include the diameter and length/height of a plant, whilst the mass is classified as a difficult-to-measure variable. The mass of the component in question of the plant is usually plotted against a measured dimension namely the respective diameter and/or height (Baskerville 1972). The use of allometric equations for the estimation of aboveground biomass (AGB) has been documented in forests, woodlands and savannas (Araújo *et al*. 1999; Netshiluvhi and Scholes 2001; Archibald and Bond 2003). Allometric estimations are often preferred over destructive sampling methods, as they allow a greater area to be investigated with less impact on the local vegetation (Gehring *et al*. 2004). However, this method has also been scrutinised with concerns around the assumption that internal woody structures are solid

and not hollow as well as the differing errors associated with the selection of model or equation (Araújo *et al*. 1999; Nickless *et al*. 2011). Model error may arise from two main causes; (1) the incomplete sampling of stems (diameter or length) within a selected area and (2) the error in the applied allometric equation itself (Nickless *et al*. 2011). Most allometric studies focus on the trunk of a tree as larger woody component equations are more accurate than equations concerning smaller components such as twigs (Navar 2009; Sawadogo *et al*. 2010). However, there have been few studies which developed allometric equations for smaller woody components. Netshiluvhi and Scholes (2001) developed allometric relations for determining bark thickness and twig dry mass, among others, from diameter measurements of a number of South African woodland trees.

Allometric work has been conducted on both forest (Scroth *et al*. 2002; Chave *et al*. 2005) and savanna tree species (Rutherford 1979; Netshiluvhi and Scholes 2001), but these studies did not account for any new growth or coppice shoots. Shackleton and Scholes (2011) derived allometric equations for a number of different components of dominant lowveld species, including *Terminalia sericea* and *Dichrostachys cinerea*. However, these equations once again did not account for coppice growth, which is usually different to growth rates of similar sized seedlings and saplings (Twine 2011). Coppice shoot growth rates are quicker than those of similar sized seedlings and saplings, as coppice shoots have the capacity to intercept solar radiation through the rapid increase in leaf area index (Harrington and Fownes 1995; Twine 2011). The circumference-based allometric equations derived for total dry wood accounted for a large percentage of the variance in the data for both *T. sericea* and *D. cinerea*, 98% and 96% respectively (Shackleton and Scholes 2011; Twine 2011). The allometric equations derived for twig mass by Shackleton and Scholes (2011) accounted for 82% of the variance in the data for *T. sericea* and 87% for *D. cinerea*. These two species are desired and heavily utilised fuelwood species as they produce denser wood which burns for longer than other lowveld species (Twine 2011).

Understanding the allometric relations of coppice shoots can assist with the development of more precise “energy gap” models that more accurately account for coppice woody biomass. This would provide a better understanding of the biomass available in an area which may have previously thought to be depleted of fuelwood resources. Therefore, the

objective of this chapter is to develop and assess which allometric equations are best suited for predicting biomass from easy-to-measure variables of two savanna species, *T. sericea* and *D. cinerea*.

3.2 Methods

3.2.1 *Study site and species*

See Chapter 1.

3.2.2 *Design and protocol*

See Chapter 1.

Shoots that had been cut and dried throughout the study from October 2015 until July 2016 were used for this study. Drying the shoots enabled the development of allometric equations between shoot dimensions and dry biomass for shoots of various ages and up to a year old.

3.2.3 *Data analysis*

A spearman rank correlation test was conducted on shoot length and shoot diameter. Allometric equations were derived to determine length from diameter, as preferred shoot diameter sizes are known (4 cm) and the length would needed to calculate mass for those sizes. The intercept in these equations was set through the origin as if there is no diameter there can be no length. The relationship between diameter, length and a combination of these dimensions with shoot biomass was compared. Regression analyses were conducted in R statistical software (R studio version 3.2.5). Simple linear regressions were used in analyses transformed measurements in which one shoot dimension, length or diameter, was the independent variable with a biomass category being the dependent variable. The biomass was separated into four different categories namely (1) Total wet mass, (2) Wood wet mass, (3) Shoot stem wet mass and (4) Shoot stem dry mass. Total wet biomass included the entire shoot and leaves; wood wet biomass was measured when the leaves of

the shoot were removed; shoot stem wet biomass excluded the side branches of the shoot and dry shoot stem mass was the mass of shoot's main stem after being oven dried.

The data were transformed using the natural logarithmic (ln) function, as to obtain a linear relationship. The root mean standard error (RMSE) was used as a fit index of the linear allometric equations. The RMSE is an estimator of the overall deviations between predicted (P) and measured (M) values and was calculated as:

$$\text{RMSE} = \sqrt{\frac{1}{N}\sum(P_i - M_i)^2}$$

where P_i is the corresponding predicted value for the measured values of M_i. Lower values of the RMSE indicate a better performance of the allometric equation. The adjusted R^2 values along with the RMSE and the corrected Akaike Information Criterion (AIC_c) values were considered when comparing and assessing the effectiveness of the linear allometric equations. The AIC_c calculation was conducted as by Burnham and Anderson (2004).

Back transformations

The allometric equations derived for each mass category for each species needed to be back transformed for the comparison of predicted estimations with the measured value masses. In order to back transform from the natural logarithmic function, which all allometric equations used, the exponential function must be applied. The resulting equation gave the predicted estimation of each shoot. The back transformation equation is as follows:

$$\text{Predicted Biomass} = e^{(\alpha * \ln(x) + c)}$$

where *e*, is the exponential function, α is the coefficient for the natural logarithmic transformation of the shoot measurement, either diameter or length (ln(x)). The equation intercept is c, which could be a positive, negative or a zero value.

The back transformed data of the most appropriate models were linearly regressed against the measured mass values as to gain an understanding of how well a model could predict the measured mass of individual shoots. The adjusted R^2 values alone were used in assessing the adequacy of the models.

3.3 Results

3.3.1 *Shoot diameter:length relationships*

A total of 172 *T. sericea* and 138 *D. cinerea* coppice shoots were cut, dried and used in the regression analyses. The diameter of *T. sericea* coppice shoots ranged from 0.1 cm to 1.8 cm while *D. cinerea* coppice shoots had a range from 0.2 cm to 2.6 cm. The *T. sericea* coppice shoots spanned a length from 2.8 cm to 132.4 cm while *D. cinerea* coppice shoots varied from 13 cm to 123 cm. The allometric equations derived to determine shoot length from shoot diameter are presented on figure 3.1. The higher coefficient for *T. sericea* indicates that a change in shoot diameter has more of an influence on shoot length of *T. sericea* than that of *D. cinerea* (Figure 3.1). The goodness of fit values for both, *T. sericea* (R^2 = 0.48) and *D. cinerea* (R^2 = 0.15) were not very satisfactory. Even though the goodness of fit values was not very satisfactory, shoot length expressed a significant positive correlation for both species ($p < 0.001$). *Terminalia sericea* expressed a stronger positive correlation (Co-efficient = 0.709) than *D. cinerea* (Co-efficient = 0.595).

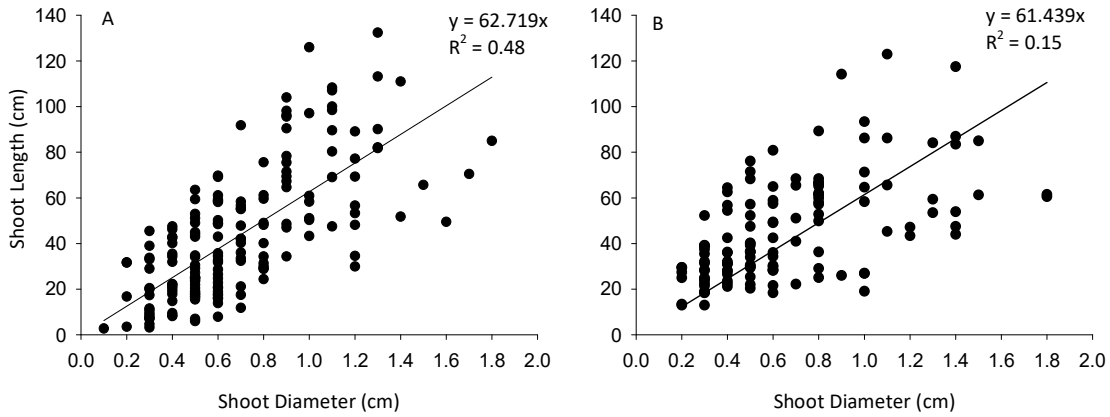

Figure 3.1: Allometric relationship between shoot diameter and shoot length for (A) *Terminalia sericea* and (B) *Dichrostachys cinerea*.

3.3.2 *Terminalia sericea* biomass relationships

Total shoot wet mass ranged from 0.25 g to 210 g. The exponential equations utilising diameter (Column A) and length (Column B) with the respective corresponding adjusted R^2 values are presented on figure 3.2. Length (R^2 = 0.28–0.79) was a better predictor for the raw mass data than as the adjusted R^2 values were consistently higher than those of

diameter (R^2 = 0.13–0.36) (Figure 3.2) in each mass category. However, an increase in diameter would lead to a greater increase in mass as the independent variable coefficient estimate was consistently higher than that of the length equations throughout the differing mass categories (Figure 3.2).

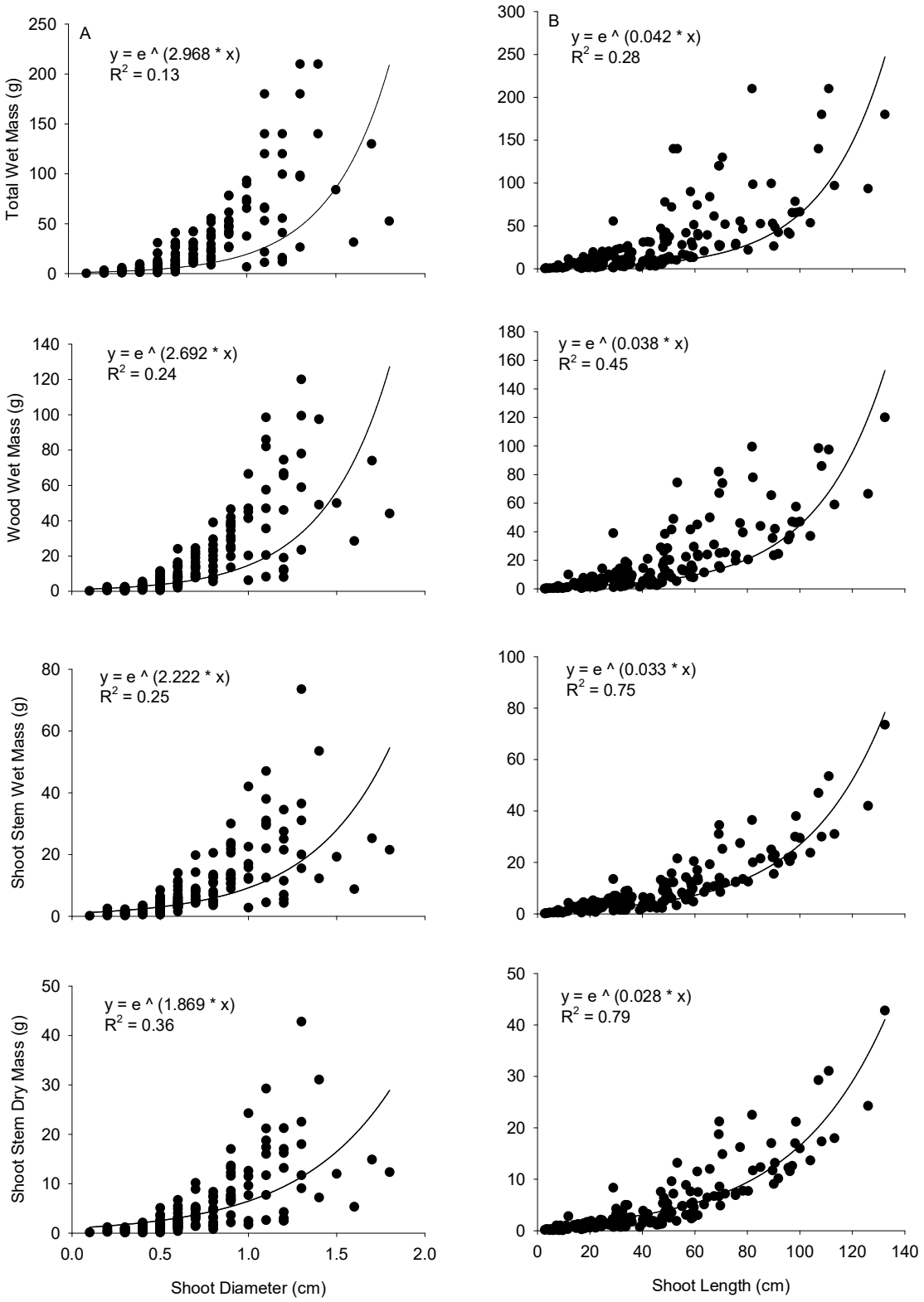

Figure 3.2: Exponential growth of between diameter (Column A), length (Column B) and differing mass categories of *Terminalia sericea*.

The natural logarithmic transformed mass data was linearly related to the natural logarithmic transformed values of both diameter (first column) and length (second column) (Figure 3.3). The equations, along with the corresponding adjusted R^2 and RMSE values, are presented on figure 3.3 for the transformed data. The simple linear regression equations, using either diameter or length as predictors, gave a moderate to strong accountability of the data (R^2 = 0.63-0.79) (Figure 3.3). Diameter gave a better accountability for the more complex mass categories (Total and Wood Mass) while the models utilising length as a predictor gave better accountability for the simpler mass categories (Shoot and Shoot Stem Dry Mass) (Figure 3.3).

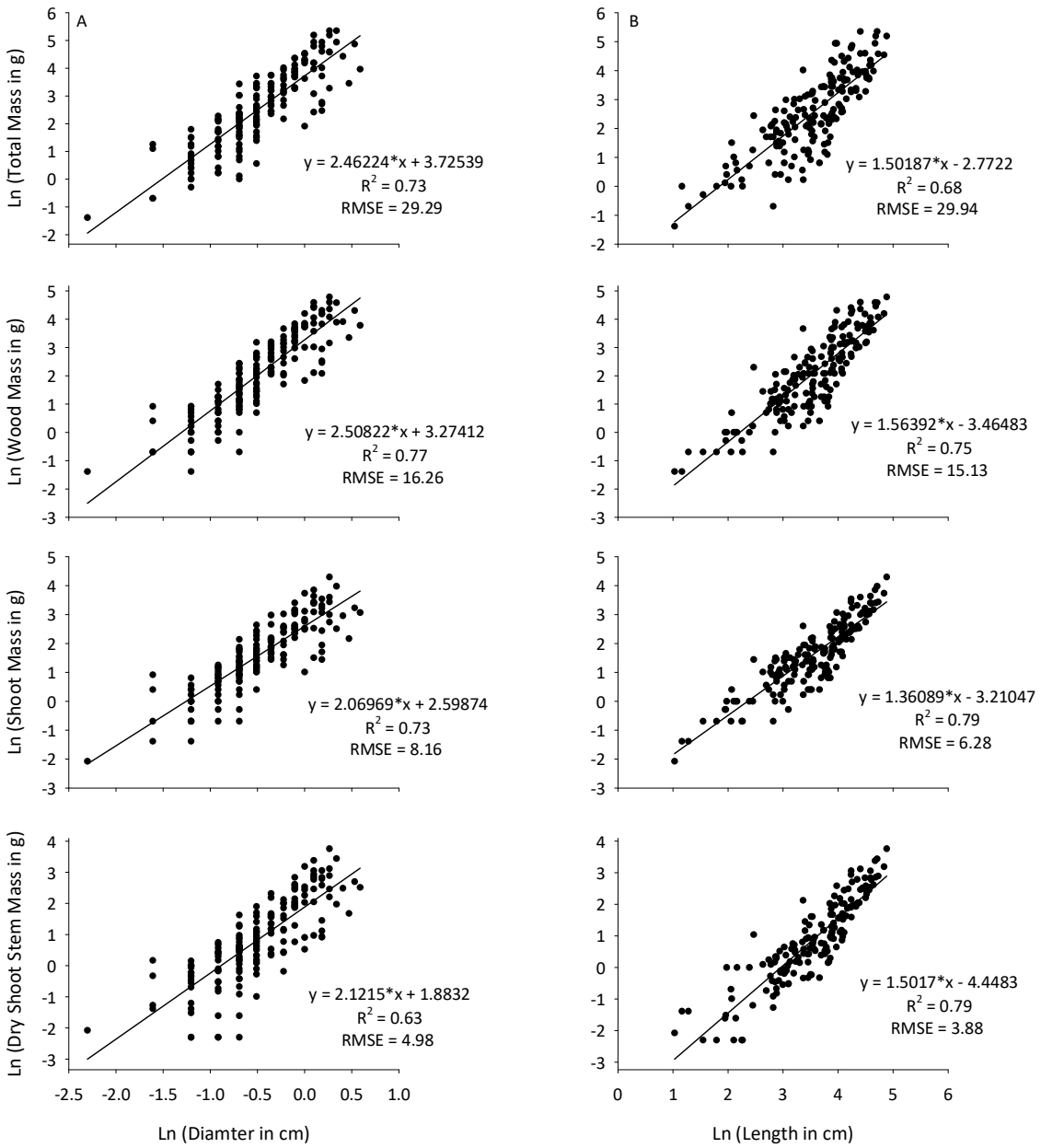

Figure 3.3: Ln-linear relationship between diameter (Colum A), length (Colum B) and the differing mass categories of *Terminalia sericea*.

The AIC_c model selection process supports the findings earlier that diameter is the more appropriate predictor for the more complex mass categories while length is the more appropriate predictor of the simpler mass categories (Table 3.1). The ΔAIC_c value is greater than 10 in every comparison and therefore there is little support for the model with the higher AIC_c value in the comparison.

Table 3.1: Corrected Akaike information criterion (AIC_c) values of regression relationships of *Terminalia sericea* mass categories and shoot measurements.

Mass Category	Diameter Model AIC_c	Length Model AIC_c	ΔAIC_c
Total Mass	382.6	415.1	32.5
Wood Mass	353.0	371.7	18.7
Shoot Mass	321.4	281.5	39.9
Dry Shoot Mass	409.6	313.3	96.3

Key: $\Delta AIC = AIC_{c(i)} - AIC_{c(min)}$

The back transformed data gave a moderate to good accountability of the measured mass values (R^2 = 0.48-0.77) (Table 3.2). The shoot and dry shoot stem mass models had the highest R^2 values, and could predict 77% of the measured mass values. The total mass model had the lowest R^2 and could only account for 48% of the variability in the measured mass values (Table 3.2).

Table 3.2: Regression relationship between the back transformed biomass predicted estimations and the measured biomass values of *Terminalia sericea* mass categories using the most appropriate previously derived allometric equations.

Model	Adjusted R^2
Total Mass ~ Diameter	0.48
Wood Mass ~ Diameter	0.53
Shoot Mass ~ Length	0.77
Dry Mass ~ Length	0.77

3.3.3 *Dichrostachys cinerea* biomass relationships

The total wet mass of coppice shoots varied from as little as 1.25 g to as much as 205.3 g. The exponential growth equations with corresponding adjusted R^2 values are represented on figure 3.4. Diameter was a better predictor for the more complex mass categories, total wet mass and wood wet mass, having higher adjusted R^2 values in these mass categories (R^2 = 0.313 – 0.361) than the equations based on length as the predictor variable (R^2 = 0.150 - 0.280). However, length was the better predictor in the mass categories concerning the coppice shoot stem only (R^2 = 0.613-0.637). Once again, an increase in diameter would lead to a greater change in mass than an increase in length as the independent variable coefficient was higher in the diameter dependent equations (Figure 3.4).

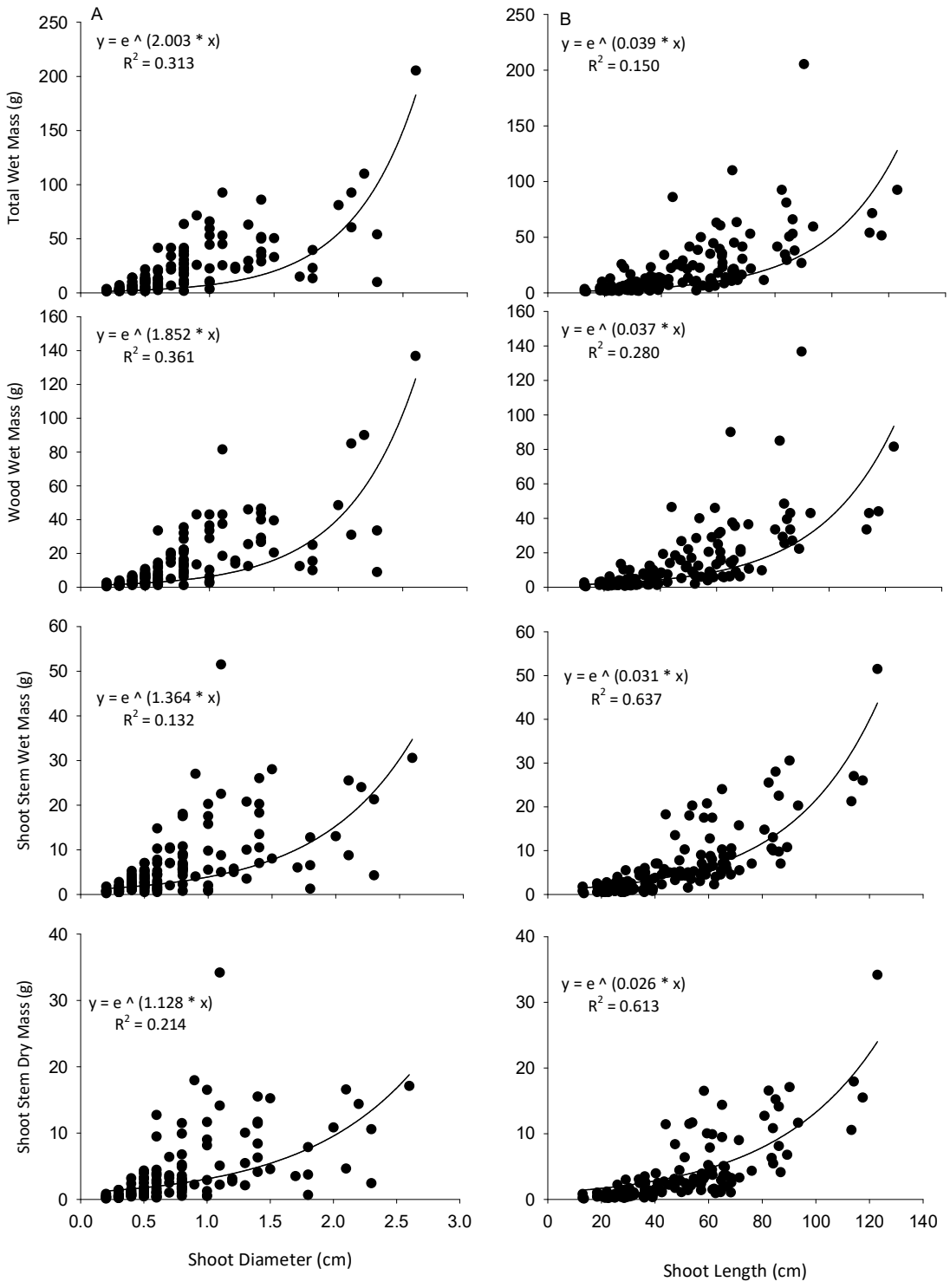

Figure 3.4: Exponential growth of between diameter (Column A), length (Column B) and differing mass categories of *Dichrostachys cinerea*.

The natural logarithmic transformed mass data was linearly related to the natural logarithmic transformed values of both diameter (first column) and length (second column)

(Figure 3.5). The equations for the transformed data of *D. cinerea*, along with the corresponding adjusted R^2 and RMSE values are presented on figure 3.5. The linear regression equations using either diameter or length as predictors gave weak to moderate accountability of the data (R^2 = 0.52-0.67). As with *T. sericea*, diameter gave a better accountability for the more complex mass categories (Total and Wood Mass) while the models utilising length as a predictor gave better accountability for the simpler mass categories (Shoot and Shoot Stem Dry Mass) (Figure 3.5). Length always had a higher coefficient than diameter (Figure 3.5). The high coefficient indicates that each mass category is more sensitive to a change in the coppice shoot length than a change in coppice shoot diameter.

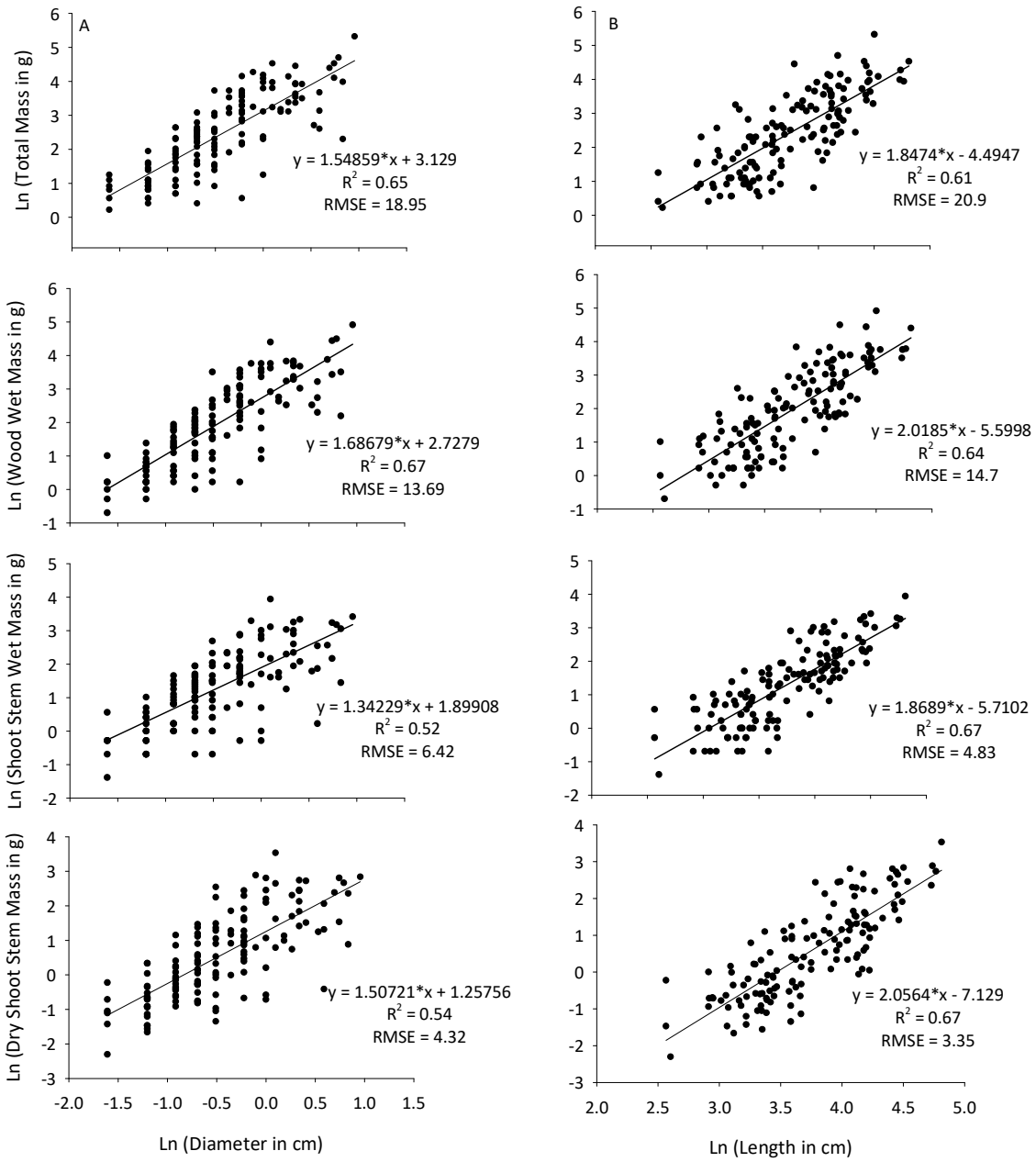

Figure 3.5: Ln-linear relationship between diameter (Colum A), length (Colum B) and the differing mass categories of *Dichrostachys cinerea*.

Table 3.3: Corrected Akaike information criterion (AIC_c) values of regression relationships of *Terminalia sericea* mass categories and shoot measurements.

Mass Category	Diameter Model AIC_c	Length Model AIC_c	ΔAIC_c
Total Mass	295.7	309.1	13.4
Wood Mass	302.7	316.2	13.5
Shoot Mass	327.7	275.8	51.9
Dry Shoot Mass	349.1	304.1	45.0

Key: $\Delta AIC = AIC_{c(i)} - AIC_{c(min)}$

The back transformed data gave a moderate to good accountability of the measured mass values (R^2 = 0.52-0.66) (Table 3.4). The shoot stem wet mass model had the highest R^2 value, and could predict 66% of the measured mass values using length as a predictor. The wood wet mass model using diameter as predictor had the lowest R^2 value and only accounted for 52% of the variability within the measured mass values (Table 3.4).

Table 3.4: Regression relationship between the back transformed biomass predicted estimations and the measured biomass values of *Terminalia sericea* mass categories using the most appropriate previously derived allometric equations.

Model	Adjusted R^2
Total Mass ~ Diameter	0.53
Wood Mass ~ Diameter	0.52
Shoot Mass ~ Length	0.66
Dry Mass ~ Length	0.63

3.3.4 *Derived equations versus literature equations*

For both species, *T. sericea* and *D. cinerea*, the equations derived by Shackleton and Scholes (2011) for twig dry mass predict lower values of coppice shoot dry mass than the equations derived from this study using diameter as a predictor variable. From the equations derived by Shackleton and Scholes (2011) coppice shoots with a diameter of 0.5 cm would have a dry weight of close to zero grams. From the equations derived in this study *D. cinerea* coppice shoots would weigh approximately 2 g and *T. sericea* coppice shoots would weigh approximately 5 g after being dried (Figure 3.6).

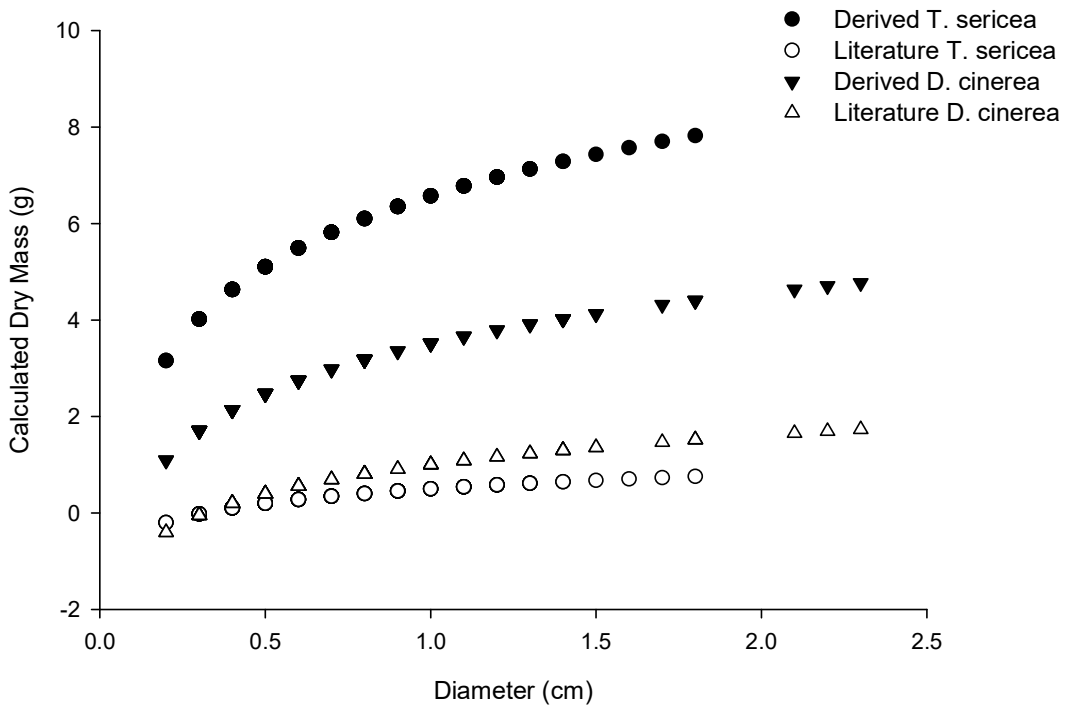

Figure 3.6: Calculated dry mass using equations derived by Shackleton and Scholes (2011) and equations derived from the current study.

3.4 Discussion

3.4.1 *Exponential versus linear models*

The mass model performance (R^2 value) was dependent on the model chosen, the predictor variable chosen, as well as the mass category being estimated. Litton and Kauffman (2008) derived satisfactory (R^2 = 0.78-0.95) exponential growth equations for the estimation of two woody plants in Hawaiian forests. However, there are concerns around the bias about predicting the biomass of an individual that exceeds the data range of which the exponential growth model was derived (Litton and Kauffman 2008). The simple linear models derived in the current study generally outperformed the exponential growth models. Packard *et al*. (2001) highlighted concerns over the use of log transformations in allometry studies, however other research has dismissed these concerns (Baskerville 1972; Kerkhoff and Enquist 2009; Mascaro *et al*. 2011). Log transformations allow for the normalisation of the response (*Y*) error along the range of the explanatory variable (X) (Baskerville 1972; Mascaro *et al*. 2011). Log transformations have been used in allometric

studies to (1) avoid overweighting large-magnitude observations; (2) normalise sample variance; and (3) reduce the influence of outliers (Kerkhoff and Enquist 2009). Therefore the fitting of linear models to log transformed data can be accepted and utilised in the predictions of coppice shoot biomass.

Allometric equation performances being different for differing mass components of a tree have been reported previously (Netshiluvhi and Scholes 2001; Shackleton and Scholes 2011). Shackleton and Scholes (2011) derived circumference-based allometric equations for five tree components, including total wood, stem, branch, leaves and twigs. The allometric equations of *T. sericea* and *D. cinerea* derived by Shackleton and Scholes (2011) performed well across the different components (R^2= 0.73-0.98). The branch component had the best performance for both species (R^2= 0.97 for *T. sericea* and 0.95 for *D. cinerea*) (Shackleton and Scholes 2011). Netshilvuhi and Scholes (2001) derived moderate and weak performing terminal scar diameter-based equations for the estimation of dry twig mass for both *T. sericea* (R^2= 0.64) and *D. cinerea* (R^2= 0.45), while Nickless *et al*. (2011) derived extremely satisfactory diameter-based allometric equations for the estimation of stem biomass for a number of species, including *T. sericea* (R^2= 0.99) and *D. cinerea* (R^2= 0.95). There have been few studies which incorporate both diameter and length as predictors for biomass. One such study found the predictability of liana biomass was enhanced from 73%, when using either diameter or length as single predictors, to 91% when using both diameter and length as predictor variables (Gehring *et al*. 2004). Colgan *et al*. (2014) used an interaction between diameter and height in order to estimate the stem dry mass of *T. sericea*. The interaction model produced a good performance (R^2= 0.71), however the interaction effect makes it difficult to assess which variable, diameter or height, is most influential on estimating stem dry biomass.

3.4.2 *Terminalia sericea* biomass relationships

The coefficients of the circumference-based equations derived for *T. sericea* by Shackleton and Scholes (2011) were similar to those found in this study with the exception of the twig component. Shackleton and Scholes' (2011) coefficient for converted diameter for the prediction of dry twig mass (1.594) was lower than the coefficient of diameter for the

prediction of shoot dry mass (2.122) found in this study. However, another study found a higher coefficient for the relationship between twig dry mass and the diameter of the terminal scar (Netshiluvhi and Scholes (2001). The study had a small sample size (n= 11) and the equation had a reasonable performance (R^2= 0.64) (Netshilvuhi and Scholes 2001). These results still leave some debate around whether the dry mass relationship with diameter of a coppice shoot is more sensitive to change in diameter than the dry mass relationship with diameter of a twig is to change in circumference. However, what is evident is that the mass component of a *T. sericea* tree can be predicted using diameter as the predictor variable.

3.4.3 *Dichrostachys cinerea* biomass relationships

The coefficients of the converted diameter equations derived by Shackleton and Scholes (2011) of *D. cinerea* are higher (2.014) than the coefficients of the diameter-based equations derived in this study (1.507). This indicates that the relationship between mass and diameter of twigs for *D. cinerea* is more sensitive to change in their circumferences than the relationship of coppice shoot mass and diameter is to changes in their diameter. This is supported by another study which found a very high coefficient for the relationship between twig dry mass and the terminal scar diameter but a very low model performance (R^2= 0.45) (Netshiluvhi and Scholes 2001). However, in the simple regression equations diameter did not have the highest coefficient but rather length in this study. In every simple regression allometric equation for *D. cinerea* length had the higher coefficient, indicating a greater effect by length than diameter on the mass categories of coppice shoots. In the multiple regression equations, length had a higher coefficient than diameter, supporting the concept that the mass of *D. cinerea* coppice shoots are more sensitive to a change in the length of coppice shoots.

Coppice shoots of *D. cinerea* are known to be shorter than other species at the same diameter (Twine 2011; Kaschula *et al*. 2005b), this was evident in this study as the intercepts of the *D. cinerea* equations were lower than those of the *T. sericea* allometric equations. However, *D. cinerea* coppice shoots have a high rate of extension relative to shoot diameter, which will result in long narrow shoots at higher shoot diameters (Twine 2011). The long

narrow shoots are characteristic of the height-growth pattern recognised in a previous study (Hara *et al*. 1991). The need to grow tall may be the rationale as to why length is the more influential predictor than diameter for *D. cinerea*.

3.4.4 *Diameter and length as predictors*

The need for a plant to grow tall could either be to increase the leaves to light exposure and increase shading of competitors (Henry and Aarssen 1999), or to escape fire and browsing zones (Bond and Midgley 2001). However, in order to grow tall a stem must be strong enough to resist buckling under its' own and any other mass (Niklas 1994). This is no different for coppice shoots. In order for a coppice shoot to outcompete neighbouring shoots, it must be able to grow quicker than the others and still maintain the mechanical strength to support its own weight (Henry and Aarseen 1999). An increase in mechanical strength is primarily a consequence of diameter growth (Tilman 1988). The need for mechanical strength in order to grow tall may be the reason why diameter generally has the highest effect on predicting shoot mass categories.

The inclusion of both diameter and length decreases the bias in the estimation of biomass (Chave *et al*. 2014), if the two variables are not correlated. If the variables are correlated then the error rate in the model can increase (Babyak 2004). The error rate in the model shares a positive relationship with the correlation between the two variables (Babyak 2004). The length (or height of a tree) is often considered difficult to accurately measure and is therefore frequently ignored in equations (Chave *et al*. 2005; Chave *et al*. 2014). However, the length of coppice shoots was easily and more accurately measured and therefore could be included in the allometric equations.

3.4.5 *Factors affecting allometric equations*

<u>Structure</u>

The structure of a species may influence the prediction ability of an allometric equation (Sawadogo *et al*. 2010). The more complex the structure the more difficult it becomes to accurately predict biomass (Sawadogo *et al*. 2010). Competition for light may account for some variation in allometric equations; individuals under high competition may produce

small branches while individuals experiencing little competition tend to grow wide canopies (Sawadogo *et al*. 2010). *Dichrostachys cinerea* is known to sprout vigorously with many coppice shoots (Kaschula *et al*. 2005b; Neke *et al*. 2006). This complex sprouting strategy may result in the allometric equations generally having a lower goodness of fit than that of *T. sericea* which has a simpler sprouting strategy. An increase in the number of coppice shoots produced would increase the intra-specific competition for light of shoots on a single stump.

Wood Density

Wood density should also be considered when deriving allometric equations (Komiyama *et al*. 2002; Navar 2009). These two species have been regarded to have heavy and thus dense wood (*T. sericea*: 720k g/cm^3 and *D. cinerea*: 800 kg/cm^3) within a savanna context (Van Wyk 1974; Twine 2011). *Dichrostachys cinerea* grows slower than *Terminalia sericea*, and with a more complex strategy the wood density would need to be greater and dispersed to the differing shoot components. *Terminalia sericea*, which has a simpler sprouting strategy, can allocate more resources to the stem of a coppice shoot. Sawadogo *et al*. (2010) suggests that allometric relations are stronger for trees which have a higher proportion of biomass in the stem. Within an individual tree there is likely to be varying wood specific gravity (weight per volume) between tree sections; wood specific gravity would be higher at the base of the stem than at the base of the living crown (Navar 2009; Sawadogo *et al*. 2010). However, when focusing on coppice shoots the sprouting position should be considered, as shoots which sprout from the ground may have higher wood specific gravity than those sprouting from the collar of a stump. This was not considered in this study.

Age

The coppice shoot diameter and length frequently harvested stumps was significantly lower than coppice shoots of less harvested stumps (Moyo *et al*. 2015b). Size is often a proxy for age and in this case the bigger coppice shoots were older as there was more time for the coppice shoots to establish and grow. The accuracy of predicting biomass decreases with when smaller components are measured (Navar 2009; Sawadogo *et al*. 2010). This would suggest that the accuracy for predicting the biomass of young shoots (one year) would be relatively low when compared to coppice shoots which may have had a few years to

establish. Considering most rotational systems would last for several years (Twine 2011) and this study only lasted one, the goodness of fit values of the allometric equations derived provide good insight as to the predictability of biomass produced by coppice shoots.

3.4.6 *The need for specific equations*

Allometric equations which are applicable to more than one species are more appropriate when trying to estimate the woody biomass of an entire area (Shackleton and Scholes 2001). Many previous studies have supported the use of allometric equations in the prediction of stand biomass across the world (Malimbwi *et al*. 1994; Netshiluvhi and Scholes 2001; Wang 2006; Nickless *et al*. 2011). These studies have covered a variety of vegetation types including savannas, woodlands and forests (Netshiluvhi and Scholes 2001; Williams *et al*. 2005; Wang 2006; Sawadogo *et al*. 2010; Nickless *et al*. 2011). However, there is a need for locally derived species specific equations, especially for the dominant species of an area, as previous studies have found a wide variation between common savanna species (Hofstad 2005; Shackleton and Scholes 2011; Colgan *et al*. 2014). The use of general allometric equations may lead to a bias in the estimation of a species and therefore species-specific equations can aid in more accurate estimations of biomass and linked factors such as carbon storage (Litton and Kauffman 2008; Navar 2009). This is evident from this and previous studies (Shackleton and Scholes 2011). Shackleton and Scholes (2011) found differing components of trees to have different allometric equations and coppice production was not considered in their study. The vast difference when comparing the calculated dry mass of coppice shoots when using the equations derived by Shackleton and Scholes (2011) for twig mass and the equations derived for coppice shoots in this study expresses the need for species-specific coppice allometric equations.

3.5 Conclusion

This study supports the idea of species-specific equations as allometric equations differed between the two species. The inclusion of older and bigger coppice shoots would be beneficial to the precision of the models, as one year of growth does not allow for the favoured size of 2cm in diameter to be reached. The understanding of allometric

relationships for coppice shoots may provide a better understanding and predictability of available fuelwood biomass in a region; even though the coppice shoots may not be used as a major source of fuelwood they could be used as tinder. This study provides a base for the inclusion of coppice shoots in future fuelwood supply models.

Chapter 4

THE INFLUENCE OF POST-HARVEST TREATMENTS ON THE COPPICE BIOMASS PRODUCTION OF TWO SAVANNA FUELWOOD SPECIES

4.1 Introduction

Numerous households in sub-Saharan Africa still rely on the use of fuelwood for cooking and for heating space and water (Kennedy 1998; Okello *et al*. 2001; Matsika *et al*. 2012; Wessels *et al*. 2013). Despite a government based electrification programme, which supplied rural households with 50 kWh per month (Shackleton *et al*. 2007), the cost of additional electricity is still unaffordable for many rural households (Kennedy 1988; Madubansi and Shackleton 2007; Matsika *et al*. 2012). This energy gap is often met by the use of fuelwood (Kennedy 1989; Madubansi and Shackleton 2007; Matsika *et al*. 2012; Shackleton *et al*. 2007). Rural households that have not been connected to the grid have been recorded to use more fuelwood in a year than households that are connected to the electricity grid (Shackleton and Shackleton 2004; Matsika *et al*. 2013). The need for fuelwood as a source of energy may place a great deal of pressure on the surrounding vegetation of rural communities (Shackleton 1993, 2001; Neke *et al*. 2006).

Deadwood is often preferred as a source of energy in comparison to livewood (Shackleton 1998). However, in many cases the demand for deadwood exceeds the supply and communities resort to harvesting livewood to meet their energy needs (Shackleton 1998; Neke *et al*. 2006). The harvesting practices utilised in many rural communities is perceived to be unsustainable (Twine 2011). Previous fuelwood models have predicted the local depletion of fuelwood resources from the surrounding environment if unsustainable practices are continued (Banks *et al*. 1996; Wessels *et al*. 2013). Although the complete depletion of fuelwood resources has not yet transpired, there has been a notable impact on vegetation resulting in a decrease of fuelwood availability (Matsika *et al*. 2012). This impact on the surrounding vegetation has led, in many cases, to the conversion of vegetation into shrub-land, characterised by vegetative shoots sprouting from the remaining stumps, known as coppice (Shackleton *et al*. 1994; Kaschula *et al*. 2005a, b; Fisher *et al*. 2011). The transformation of the landscape and the continual supply of fuelwood indicates that the previous fuelwood models failed to account for, or under-appreciated the regenerative

coppicing abilities of savanna trees after harvesting (Shackleton 2001; Williams and Shackleton 2002). A general fuelwood model assumed that 20 kg ha^{-1} yr^{-1} of biomass could be contributed by annual recruitment and coppice regrowth (Banks *et al*. 1996). However, calculations on species-specific data for *Terminalia sericea* by Twine 2011 indicated that coppice regrowth biomass could contribute as much as 89 kg ha^{-1} yr^{-1}.

This study focuses how biomass production differs between individual trees, but such data and understanding is necessary for the upscaling biomass production to landscape scale. There is a need to understand how coppice production will respond under differing circumstances and the potential amount of biomass that could be produced. Therefore the objective of this chapter was to assess how different post-harvest treatments will affect the different components of coppice biomass production of two savanna species.

4.2 Methods

4.2.1 *Study site and species*

See Chapter 1.

4.2.2 *Design and protocol*

See Chapter 1.

Mass components of coppice shoots were separated into four categories, namely

1. Total shoot wet mass
    - The shoot as it is harvested, including all leaves and side branches
2. Wood wet mass
    - The woody component of the coppice shoot, all leaves have been stripped but the side branches remain
3. Shoot stem wet mass
    - The main stem of the coppice shoot before drying, all leaves and side branches have been removed
4. Shoot stem dry mass

- The main stem of the coppice shoot after being dried for 24 hours at 75 °C

4.2.3 *Data analysis*

Back transformed allometric equations, derived using diameter or length as a predictor variable (Chapter 3), were used to predict the biomass of each shoot measured up to and including July 2016 for the control, largest and pruning treatments. For the harvest treatment each shoot which was harvested was predicted and considered in the biomass calculations. A Chi-squared test for homogeneity was conducted to test for differences between the proportions a mass category contributed to the sum of all mass categories of the four treatments. This was done to assess if the post-harvest treatments would have an influence on the allocation of biomass to differing shoot characteristics (e.g. leaves). Differences between the predicted standing biomass were compared using a Kruskal-Wallis Rank Sum test, as the data were highly skewed and could not be transformed to meet normality. The harvest treatment was not included in the analysis of standing biomass as by July 2016, the stumps of the harvest treatment had stopped coppicing. The difference in cumulative stump coppice biomass produced through the study year of each mass category of each treatment was compared using a Kruskal-Wallis Rank Sum test. Cumulative stump coppice biomass was considered the standing biomass of the control treatment, the sum of all coppice shoot biomass harvested through the year for the harvest treatment and, the standing biomass in July 2016 plus all additional cut coppice shoots through the year for the single prune and usable treatments. Kruskal-Wallis multiple comparison post-hoc tests in the "pgirmess" package of R statistical software (R studio version 3.2.5) were used to determine where any significant differences may be found for standing biomass and cumulative biomass. A Kruskal-Wallis Rank Sum test was conducted on the biomass production per unit area of the stump. Biomass production through the study year was divided by the cumulative basal area of an experimental tree to gain the mass production per unit area. If significant difference was found, then a post-hoc analysis was conducted. The cumulative biomass production through the study year of the three post-harvest cutting regimes was assessed as a percentage of the control treatment.

4.3 Results

4.3.1 *Mean mass per stump*

Even though the data were highly skewed and could not be transformed to achieve normality for parametric statistical testing, trends in mean biomass values calculated from the allometric equations are still evident in the data (Table 4.1). The calculated mean cumulative shoot stem dry mass was approximately half of the predictive cumulative mean shoot stem wet mass across all treatments for both species (Table 4.1). The harvest treatment produced approximately half of the predictive cumulative mass than the control treatment across all four mass categories of *T. sericea* (Table 4.1).

Table 4.1: Mean (± standard error) mass per stump of each treatment for each mass category of the cumulative biomass produced through the year of *Terminalia sericea* and *Dichrostachys cinerea*

		Mean (± SE) Mass (g)			
Species	Treatment	Total Shoot Wet Mass	Wood Wet Mass	Shoot stem wet mass	Shoot stem dry mass
T. sericea	Control	140.32 ± 13.31	90.40 ± 8.73	47.30 ± 4.23	24.12 ± 2.26
	Harvest	73.03 ± 6.62	43.98 ± 3.97	30.13 ± 2.69	13.37 ± 1.18
	Single Prune	105.48 ± 15.38	67.58 ± 10.30	33.47 ± 3.69	16.35 ±1.94
	Usable	126.47 ± 13.39	81.15 ± 8.80	42.97 ± 3.83	21.80 ± 2.05
D. cinerea	Control	109.13 ± 16.08	72.79 ± 11.14	35.00 ± 5.24	18.44 ± 2.87
	Harvest	71.58 ± 11.20	42.48 ± 6.69	22.17 ± 3.58	10.30 ± 1.67
	Single Prune	69.21 ± 8.34	44.58 ± 5.49	21.20 ± 2.65	10.75 ± 1.35
	Usable	107.55 ± 14.06	73.22 ± 10.16	32.40 ± 4.08	17.47 ± 2.36

4.3.2 *Terminalia sericea* biomass production

Each proportional composition of the three wet mass components did not differ significantly between treatments ($\chi^2 = 0.058$; $p = 1$) (Figure 4.1). Interestingly, the harvest treatment had the lowest proportion of shoot stem wet mass (0.190) and the highest proportion of branch wet mass (0.413), compared to the other three post-harvest treatments. The proportion of leaf wet mass was uniformly distributed through the post-harvest treatments (approximately 0.37) (Figure 4.1).

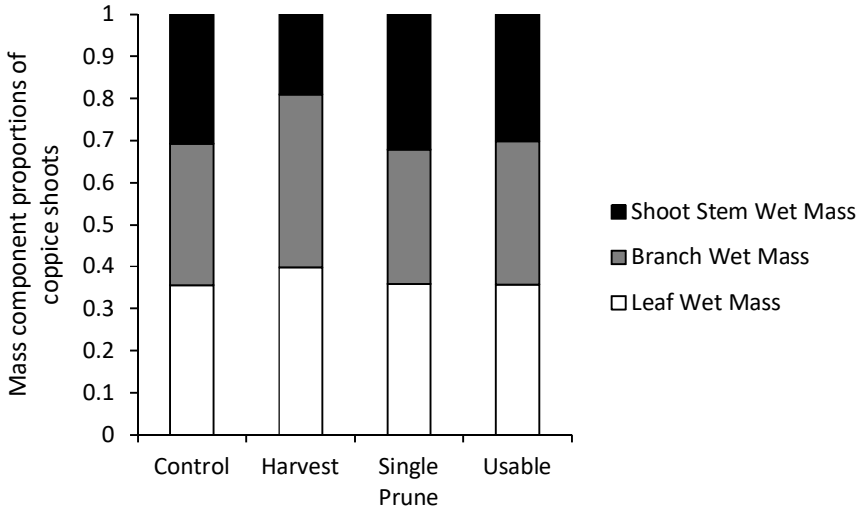

Figure 4.1: Proportions of mass components of *Terminalia sericea* coppice shoots to the contribution of total mass per treatment.

Calculated standing biomass differed significantly between treatments for each mass category ($p < 0.05$) (Figure 4.2 A-D). The single prune treatment resulted in a significantly lower calculated standing biomass compared to the control and usable treatments for each mass category (Figure 4.2 A-D). No significant difference was found between the control and usable treatments.

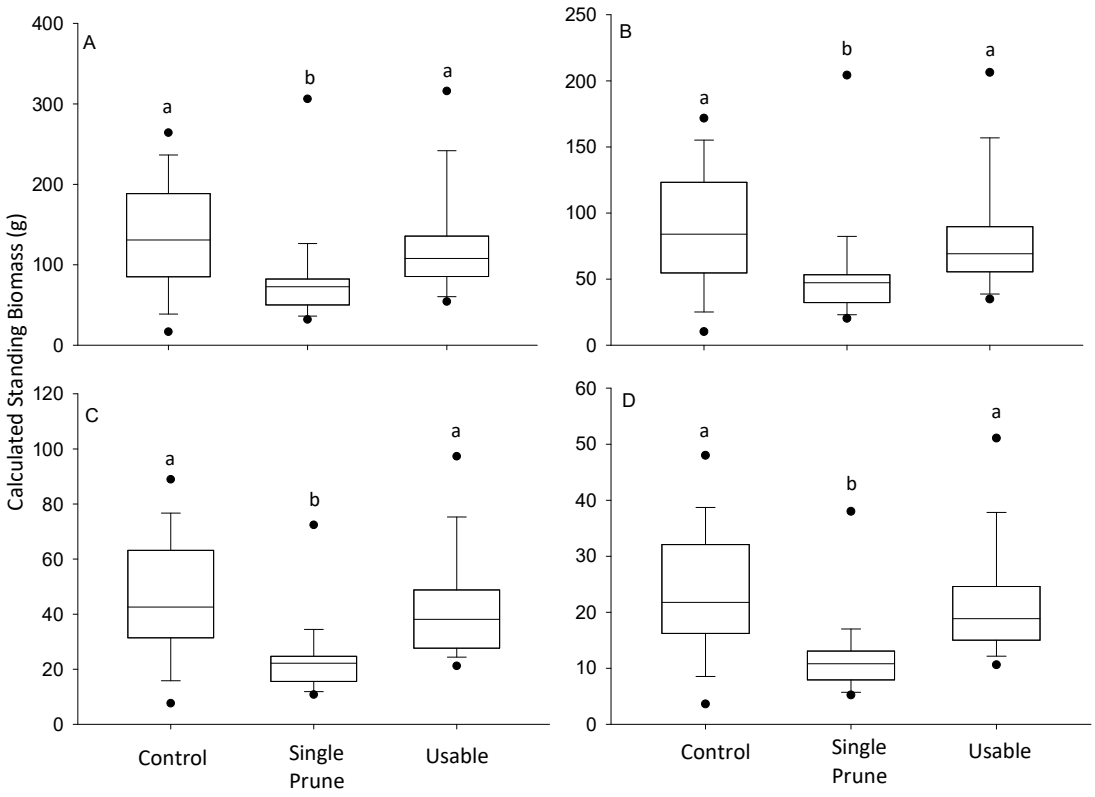

Figure 4.2: Calculated standing biomass (g) in July 2016 per *Terminalia sericea* experimental tree of four mass categories per treatment, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

The calculated cumulative biomass production through the study year differed significantly between treatments ($p < 0.05$) (Figure 4.3 A-D). The control treatment differed significantly from the harvest and single prune treatments in each mass category, while no significant difference was found between the control and the usable treatment in any of the mass categories (Figure 4.3 A-D). The harvest and single treatment did not differ significantly in any mass categories (Figure 4.3 A-D). The harvest and usable treatment differed significantly only in the shoot stem wet mass category (Figure 4.3C). The single prune treatment did not differ significantly from the usable treatment in any of the mass categories (Figure 4.3 A-D).

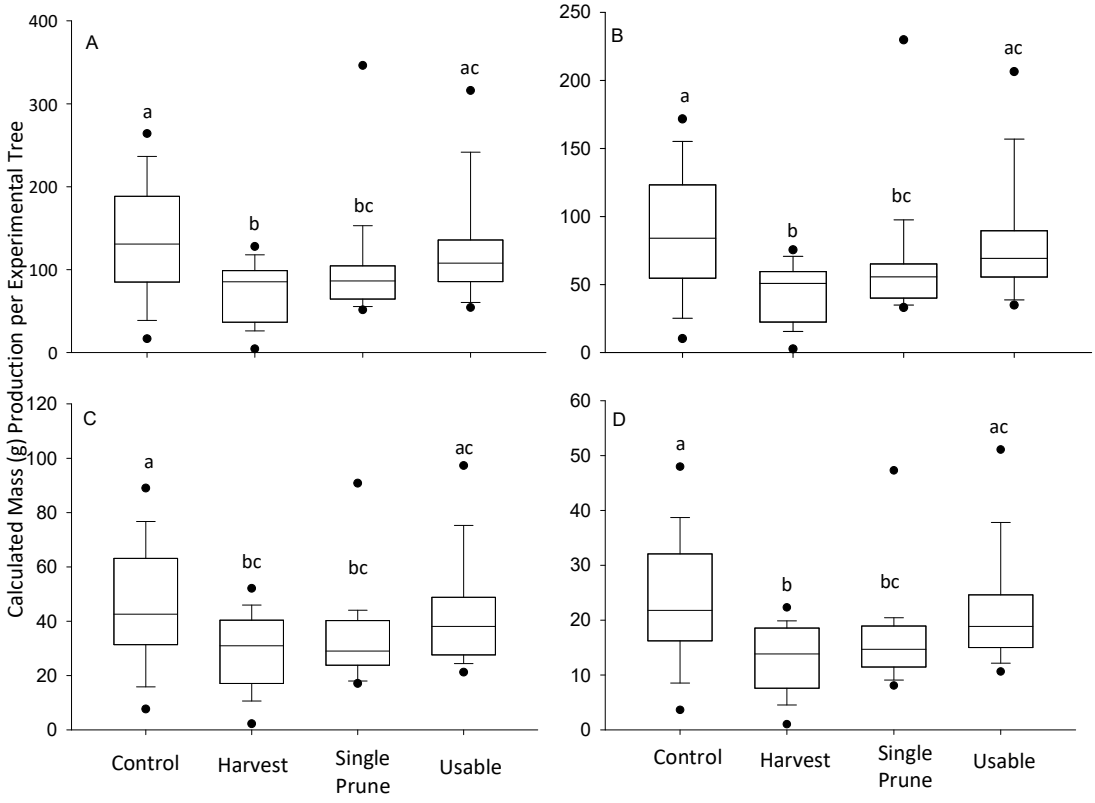

Figure 4.3: Calculated cumulative biomass (g) production per *Terminalia sericea* experimental tree through the study year of four mass categories, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

When compared to the control treatment, the harvest treatment had the lowest percentage of calculated cumulative biomass produced through the year. Depending on the mass category, the harvest treatment varied from approximately 48 - 64% of calculated cumulative biomass to the control treatment (Figure 4.4). The single prune treatment varied from approximately 67 - 74% of calculated cumulative biomass production relative to the control treatment (Figure 4.4). The usable treatment had the highest and fairly consistent percentage (approximately 87%) of calculated cumulative biomass produced in each mass category (Figure 4.4).

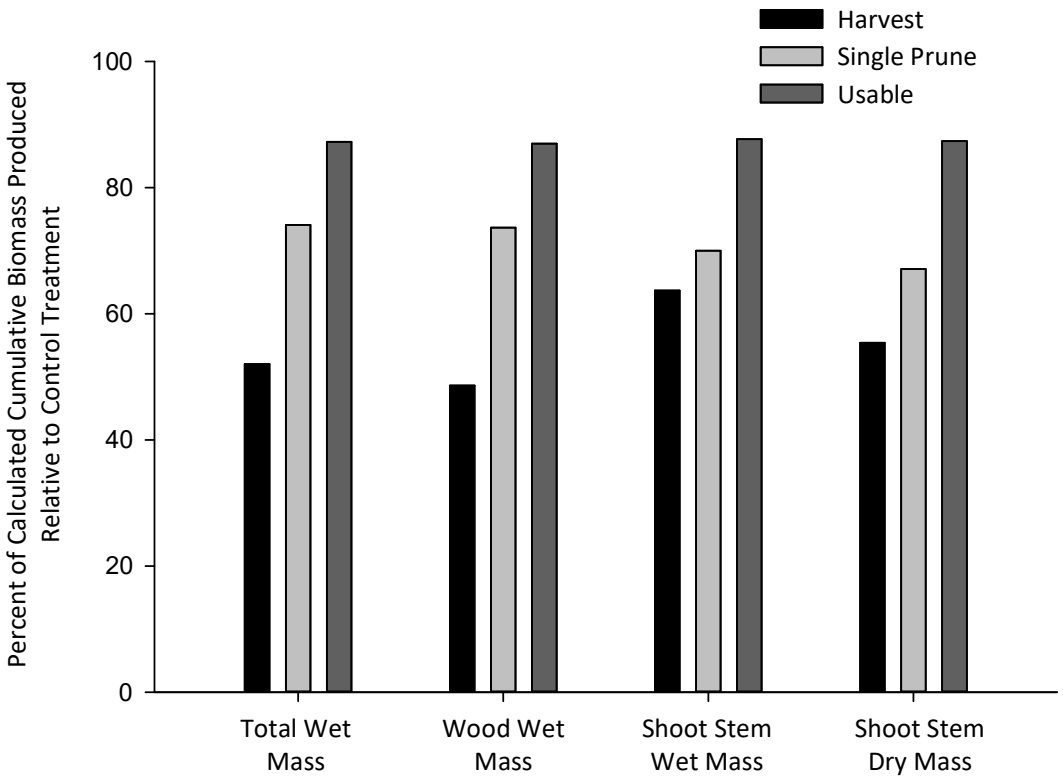

Figure 4.4: Calculated cumulative biomass produced by post-harvest treatments of *Terminalia sericea* as a percentage of the calculated cumulative biomass produced by the control treatment.

Calculated cumulative biomass produced per unit basal area differed significantly between the control and harvest treatments in two mass categories, total shoot wet mass and wood wet mass (Figure 4.5A and 4.5B). No significant difference was found between treatments in the shoot stem wet mass category ($H_{3;\ 103}$ = 6.217; p = 1) (Figure 4.5C). A significant difference was found in the calculation of cumulative biomass per unit basal area for the shoot stem dry mass category ($H_{3;\ 108}$ = 9.776; $p < 0.05$), however further post-hoc analyses found no significant difference between treatments (Figure 4.5D).

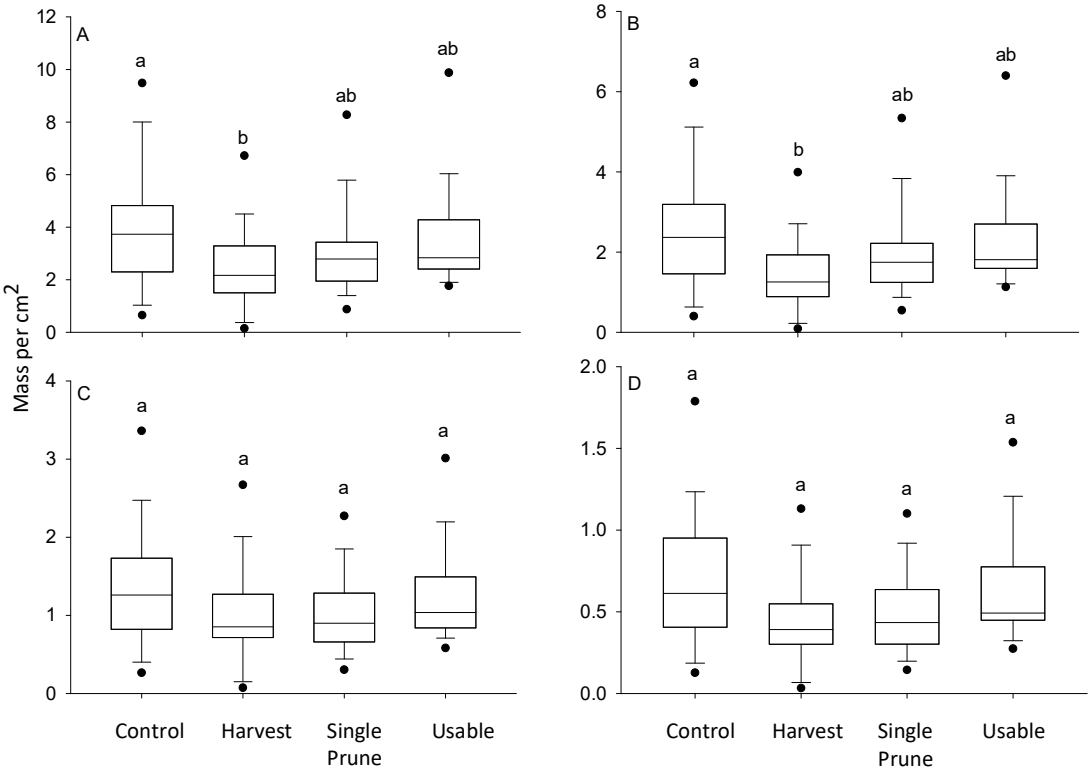

Figure 4.5: Calculation of cumulative biomass production per unit basal (g/cm^2) per *Terminalia sericea* experimental stump through the study year of four mass categories, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

4.3.3 *Dichrostachys cinerea* biomass production

Each proportional composition of the three wet mass components did not differ significantly between treatments ($\chi^2 = 0.027$; $p = 0.96$) (Figure 4.6). The harvest treatment had the highest proportion of leaf wet mass (0.407), whilst having the lowest proportion of branch wet mass (0.284). The proportion of shoot stem wet mass was fairly uniform through all the treatments (approximately 0.31) (Figure 4.6).

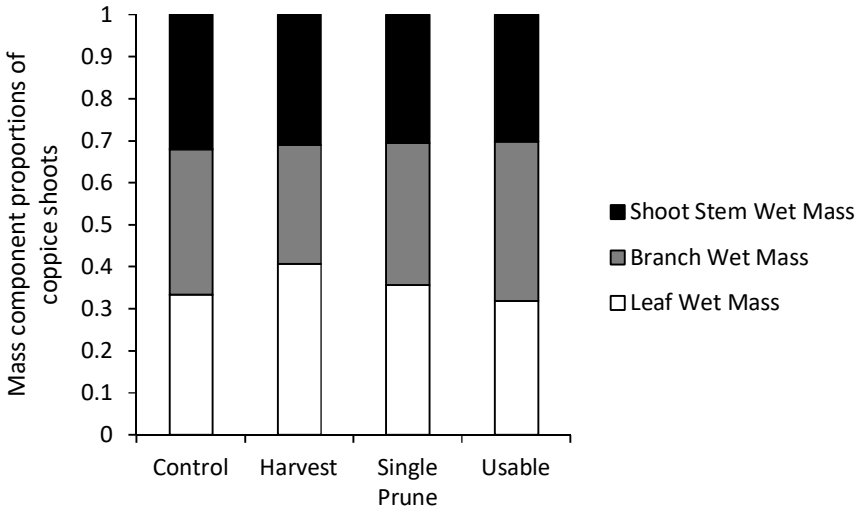

Figure 4.6: Proportions of mass components of *Dichrostachys cinerea* coppice shoots to the contribution of total mass per treatment.

Calculated standing biomass differed significantly between treatments for each mass category ($p < 0.05$) (Figure 4.7 A-D). The single prune treatment resulted in a significantly lower calculated standing biomass compared to the control and usable treatments for each mass category (Figure 4.7 A-D). No significant difference was found between the control and usable treatments.

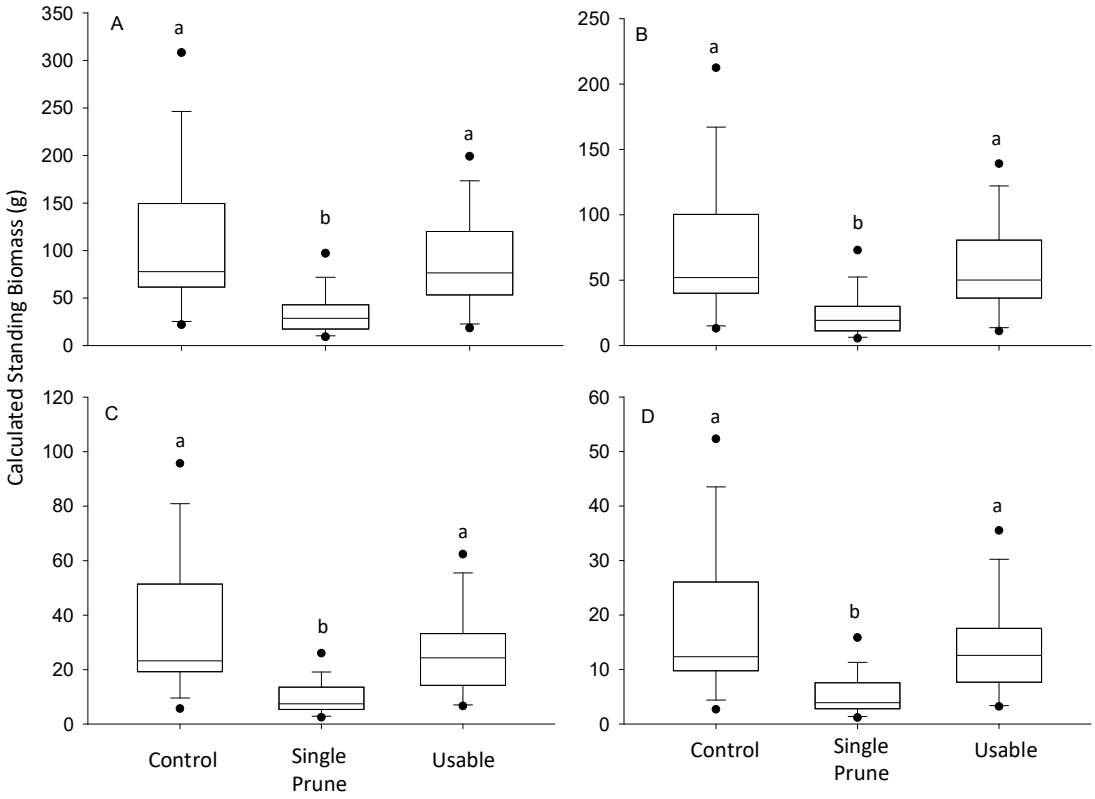

Figure 4.7: Calculated standing biomass (g) in July 2016 per *Dichrostachys cinerea* experimental tree of four mass categories per treatment, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

The calculation of cumulative biomass production through the study year per experimental tree differed significantly for each mass category ($p < 0.05$) (Figure 4.8 A-D). However, no significant differences were found between any of the treatments within any of the mass categories when further post-hoc analyses were conducted (Figure 4.8 A-D).

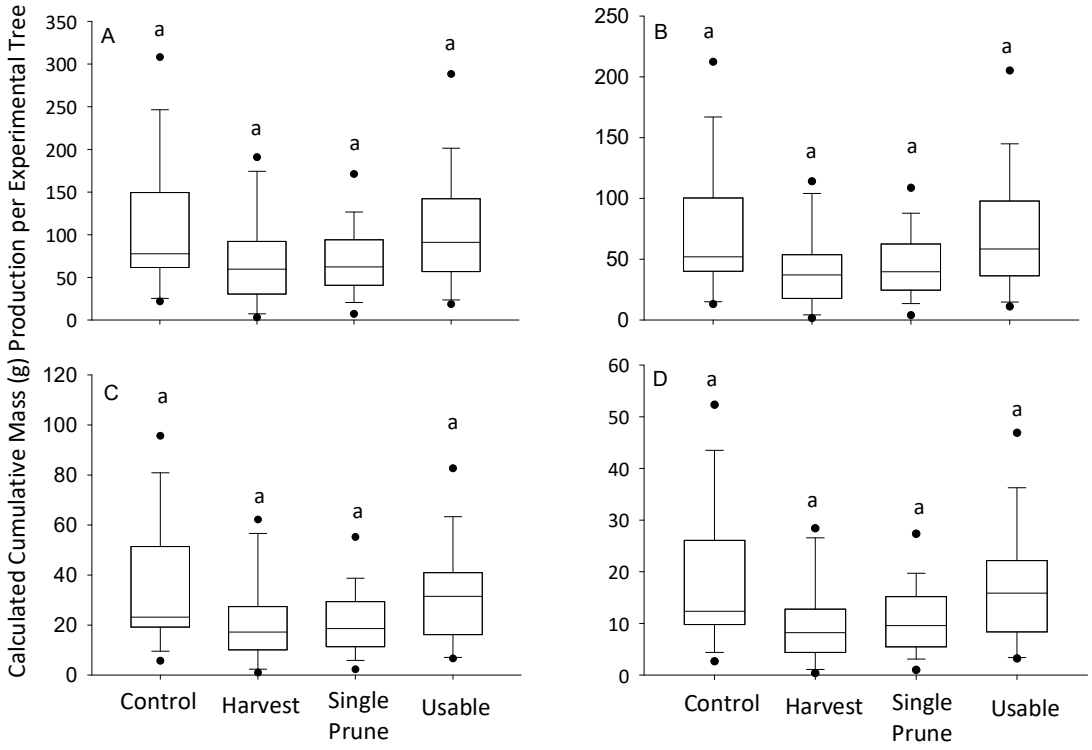

Figure 4.8: Calculation of cumulative biomass (g) production per *Dichrostachys cinerea* experimental tree through the study year of four mass categories, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

The harvest and single prune treatments produced similar percentages of calculated cumulative biomass production through the year relative to the control treatment (Figure 4.9). The percentage of calculated cumulative biomass production for the harvest treatment varied from approximately 60 - 71% of the control treatment while the single prune treatment calculated cumulative biomass production relative to the control treatment varied from approximately 63 - 68% (Figure 4.9). The usable treatment had the highest percentage of calculated cumulative biomass production relative to the control and even surpassing the control treatment in the total shoot wet mass and wood wet mass categories, approximately 102% and 104% respectively (Figure 4.9).

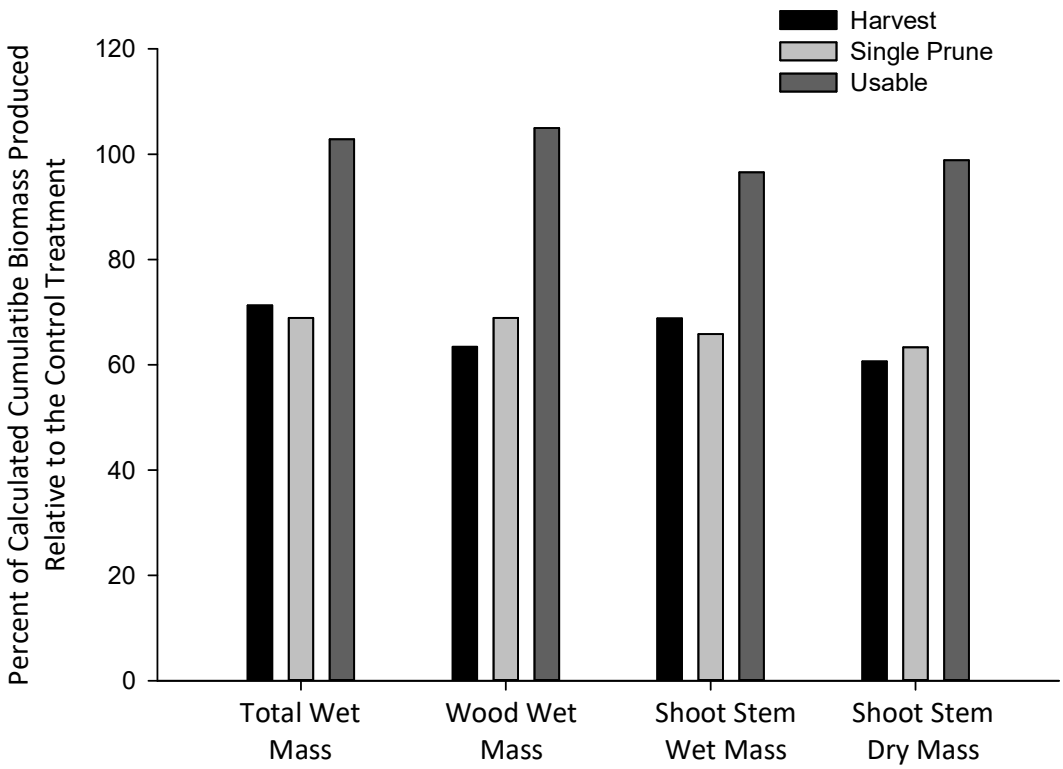

Figure 4.9: Calculated cumulative biomass produced by post-harvest treatments of *Dichrostachys cinerea* as a percentage of the predicted cumulative biomass produced by the control treatment.

Calculated cumulative biomass production per unit area differed significantly in all mass categories (Figure 4.10 A-D). However, further post-hoc analyses found no differences between treatments in the total shoot wet mass and shoot stem wet mass categories. Significant differences between the control and harvest treatments as well as between the harvest and usable treatments were found in the wood wet mass and shoot stem dry mass categories (Figure 4.10 A-D). The harvest and single prune treatments did not differ significantly in the wood wet mass and shoot stem dry mass categories (Figure 4.10B and 4.10D).

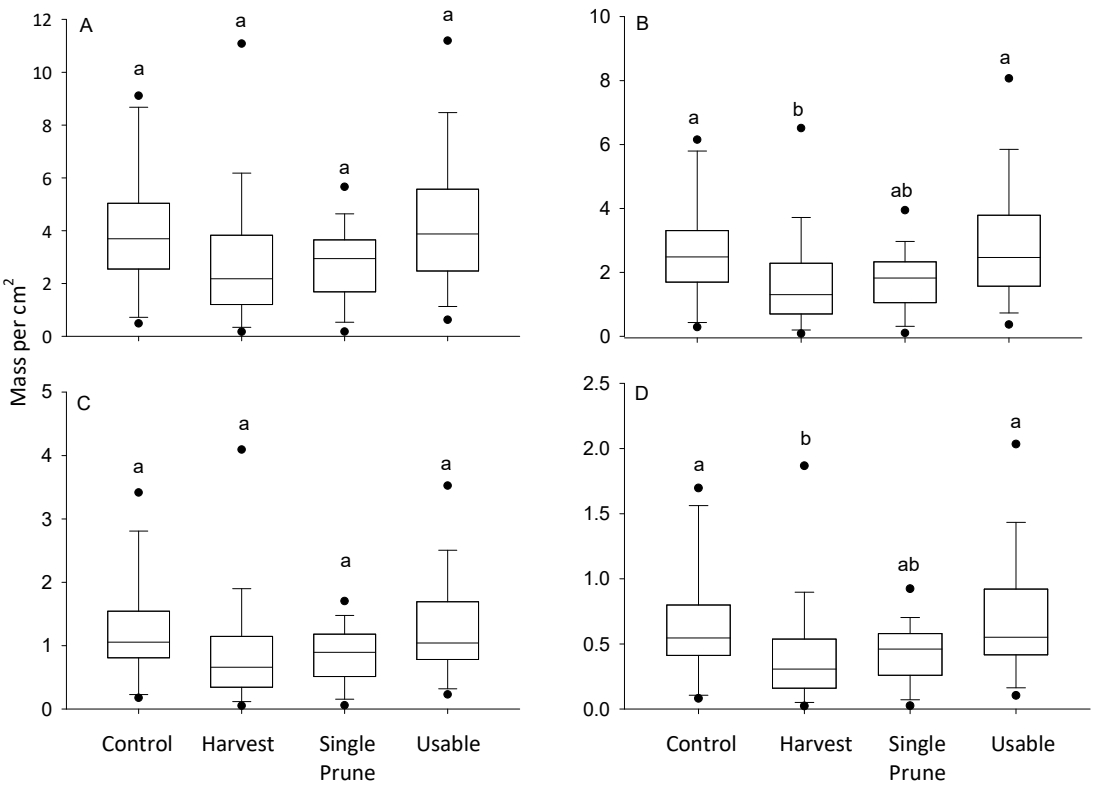

Figure 4.10: Calculation of cumulative biomass production per unit basal (g/cm^2) per *Dichrostachys cinerea* experimental stump through the study year of four mass categories, (A) Total shoot wet mass; (B) Wood wet mass; (C) Shoot stem wet mass; and (D) Shoot stem dry mass. Differing superscript letters indicate a significant difference between treatments ($p < 0.05$). Outliers presented were restricted to the 5th and 95th percentiles.

4.4 Discussion

4.4.1 *Proportion of mass categories*

There was no significant difference found in the proportion that a mass category contributed to the sum of all mass categories per treatment for either species. Moyo *et al*. (2015b) found that *T. sericea* produces significantly less leaves per coppice shoots when stumps have been previously exposed to multiple cutting events compared to stumps which experienced fewer cutting events. Considering the number of leaves per coppice shoot was not measured, it is difficult to compare if the post-harvest treatments had a similar influence in the current study. With that in mind, it is assumed that the number of leaves produced per coppice shoot did not differ significantly between post-harvest treatments as there was no significant difference found in the contribution of the proportion leaf wet mass to the total shoot wet mass. A study conducted on the influence of browsing on the

leaf characteristics of coppice shoots found no difference between the average dry mass (g), the area (cm^2) or the specific leaf area ($cm^2\ g^{-1}$) of coppicing *T. sericea* shoots (Moyo *et al*. 2015a). If browsing is compared to a frequent harvesting regime then it stands to reason that frequent harvesting will not affect the contribution leaves make to the overall mass of a coppice shoot which is what occurred in the current study. Moyo *et al*. (2015b) did expose the stumps to the cutting regimes for a two year period while the stumps in the current study were only exposed to the post-harvest treatments for one year, thus after time these post-harvest treatments may influence the number of leaves per coppice shoot and therefore the contribution of the relevant mass categories for both species.

4.4.2 *Standing Biomass*

The single prune treatment produced a significantly lower standing biomass prediction when compared to the control and usable treatments after one growing season (Harvest treatment was not included as no coppice shoots were produced in July 2016). The comparatively high number of coppice shoots present in July 2016 in the control and usable treatments, even though significantly smaller (Chapter 2), produce more biomass than a single large coppice shoot produced by the single prune treatment for both species. This was the case for all mass categories. The high number of coppice shoots produced in the control and usable treatments would eventually decrease as previous studies have found the number of coppice shoots per stump decreases through time (Shackleton 2001; Moyo *et al*. 2015a). This decrease in number of coppice shoots can be due to either self-thinning or resprout shoot dieback (Moyo *et al*. 2015a). Neke *et al*. (2006) found a third of coppice shoots across species had died five months after felling, with *T. sericea* having the highest (± 38%) and *D. cinerea* (± 27%) the lowest coppice shoot dieback rate. Self-thinning is a process which promotes a trees height gain by means of reallocating resources (Moyo *et al*. 2015a). The single prune treatment accelerates this process as coppice shoots produced by the single prune treatment may receive important resources (carbohydrates and starch) which would have been previously disseminated to other coppice shoots (Forrester *et al*. 2003; Latt *et al*. 2000), resulting in significantly longer coppice shoots than in other post-harvest treatments (Chapter 2). Even though the predicted standing biomass was lower in the single prune treatment after one growing season, in subsequent seasons this may

change as coppice shoots of the control and usable treatments start to compete with each other, resulting in shoot deaths.

4.4.3 *Cumulative Biomass*

In terms of cumulative biomass produced through the growing season per experimental tree, the control and usable treatments generally produced the highest amounts of biomass as few coppice shoots reached the desired 2 cm size. The combination of having numerous coppice shoots and adequate time for growth would result in overall higher cumulative biomass production (Laureysens *et al*. 2003). The high number of coppice shoots in the control and usable treatments leads to a rapid leaf area development and better utilisation of space than treatments that remove coppice shoots (Laureysens *et al*. 20003). A previous study conducted on *T. sericea* found that a no prune treatment (i.e. control) resulted in the highest biomass productivity when compared to single (leaving one shoot) and double (leaving two shoots) treatments (Shackleton 2001). The harvest and single prune treatments produced less biomass through the study period regardless of producing more coppice shoots than the control and usable treatments (Chapter 2). The stumps of the harvest and single prune treatments were exposed to a disturbance (cutting of all coppice shoots) which would result in the mobilization of resources to the production of new coppice shoots (Bellingham and Sparrow 2000; Clarke *et al*. 2010). However, these coppice shoots did not have the same amount of time as the control and usable coppice shoots to accumulate mass resulting in lower productivity.

4.4.4 *Biomass relative to control*

The harvest treatment produced approximately 50 - 65% biomass of the control treatment in *T*. *sericea* and increased to approximately 60 – 70% for *D*. *cinerea*. The total shoot wet mass of the harvest treatment was the highest percent across mass categories for *D*. *cinerea* (71%) while shoot stem wet mass had the highest percent of biomass produced relative to the control for *T*. *sericea* (64%). This suggests that the two species allocate resources to differing shoot components when exposed to frequent disturbances. *Dichrostachys cinerea* seems to allocate more resources to leaves and side branches (including spines) creating a complex shrub like structure protecting the stump from further damage while *T*. *sericea*

seems to allocate resources to the shoot stem increasing shoot growth to escape a "damage" zone by growing tall (Shackleton 2000). A switch in resource allocation appeared in *T. sericea* in the single prune treatment. The wood wet mass category had the highest percent of biomass produced (74%) relative to the control treatment. This increase in percent to wood wet mass suggests that with an established coppice shoot, resources are then allocated to expanding the canopy by means of additional side branches.

4.4.5 *Mass per unit area*

As stump basal area was found not to have a significant influence on the coppicing metrics of *T. sericea* or *D. cinerea* (Chapter 2), it stands to reason that the control and usable treatments produced the highest biomass per unit area. Interestingly, converting cumulative biomass production to cumulative biomass produced per unit area resulted in a significant difference between treatments for *D. cinerea*. The inclusion of basal area as a normalising factor allows for the understanding of how much biomass is being produced dependent on the size of the stump. Shackleton (2001) found that larger stumps of *T. sericea* produced a greater number, as well as longer coppice shoots which would lead to higher productivity after four growing seasons.

4.4.6 *Management options*

The management of coppice shoots is an intensive action and requires repeated application (Shackleton 2001). Considering this study was conducted for one year and a difference in standing biomass as well as cumulative biomass production through a growing season was already prominent, adaptive management systems would be able to promote growth and biomass production of coppice shoots. An idea to enhance biomass production of coppice shoots would be to allow stumps to coppice for a year unmanaged and then apply pruning treatments to leave either one or two of the largest shoots. The removal of some of the coppice shoots will contribute to earlier apical dominance of the remaining shoot(s) (Shackleton 2000). The adaptive management system would be a manipulation of natural systems as coppice shoot numbers have been recorded to decrease with time (Laureysens *et al*. 2003; Moyo *et al*. 2015a). There is a need to keep one or two shoots per stump to enhance coppice shoot production as a previous study has found the repeat removal of

coppice shoots causes a decrease in shoot diameter and length (Moyo *et al*. 2015b). The retention of one or two coppice shoots without the competition of smaller coppice shoots should promote quicker growth as there will be less competition for light and valuable resources (Latt *et al*. 2000; Shackleton 2000).

4.5 Conclusion

Post-harvest treatments can influence the cumulative biomass production of an experimental tree. The manipulation of coppice shoot production is dependent upon management objectives. If the management objective is to maximise biomass production (which is often the case) from a coppicing tree then the control treatment would be the most beneficial after one year of growth. Coppice shoots did not reach the desired size for the usable treatment and therefore this treatment could not be effective.

Chapter 5

SYNTHESIS AND OVERALL CONCLUSION

5.1 Overview

The aim of this study was to investigate the influence four different post-harvest treatments would have on the coppice response and production of two savanna species. The overall findings suggest that post-harvest management can be an effective management tool in manipulating coppice response and production of *T*. *sericea* and *D*. *cinerea*. This has been previously proposed by Hosier (1993). The application of a single prune treatment resulted in thicker as well as longer coppice shoots when compared to the control treatment for both species (Chapter 2). This coincides with findings by Shackleton (2001). The single prune treatment seemed to have the greatest effect on the diameter of coppice shoots of *D*. *cinerea*, as coppice shoots produced by the single prune treatment were over 1.5 times the thickness of the control treatment while only being 1.2 times the length of the control treatment. The treatments did not seem to affect the growth pattern of *T*. *sericea* coppice shoots as the single prune treatment produced coppice shoots 1.6 times longer and wider than the control treatment.

Either diameter or length, can be used in the prediction of coppice shoot biomass (Chapter 3). The linear equations could then be used in calculating the biomass of coppice shoots removed and even more importantly the coppice shoots which remained on the stump. The use of allometry in estimating biomass at a landscape level is common when a general equation can be used. This study highlights the importance of specific allometric equations as differing variables had more influence on the equations. For both species *T*. *sericea* and *D*. *cinerea*, diameter was more influential in the estimation of biomass for the more complex mass categories while length was the more influential variable in estimating the simpler biomass categories (Chapter 3). However, predictions of mass for measurements which exceed the range of the data used to derive the equations should be done with caution, as the relationship between these variable is not fully understood.

The biomass estimates show that the after 12 months of growth that a control treatment would produce more biomass than a single prune treatment (Table 5.1). This estimation is

Table 5.1: Post-harvest treatment effects on the coppice production of experimental trees relative to the control. Differences considered significant at 95% confidence.

Species	Treatment	Cumulative Number of coppice shoots	Diameter (cm)	Length (cm)	Cumulative Total Shoot Wet Mass (g)	Cumulative Wood Wet Mass (g)	Cumulative Shoot Stem Wet Mass (g)	Cumulative Shoot Stem Dry Mass (g)
T. sericea	Harvest	Increase	Decrease	Decrease	Decrease	Decrease	Decrease	Decrease
	Single Prune	Increase	Increase	Increase	Decrease	Decrease	Decrease	Decrease
	Usable	No difference	No difference	No difference	No difference	No difference	No difference	No difference
D. cinerea	Harvest	Increase	Decrease	Decrease	No difference	No difference	No difference	No difference
	Single Prune	Increase	Increase	Increase	No difference	No difference	No difference	No difference
	Usable	No difference	No difference	No difference	No difference	No difference	No difference	No difference

at stump level, where more coppice shoots in the control treatment have had the opportunity to grow and accumulate mass for 12 months compared to a single coppice shoot as is in the single prune treatment (Chapter 4). However, at shoot level the single prune coppice shoot would weigh more than individual coppice shoots in the control treatment. This is a result of the single prune treatment being larger than coppice shoots produced by the control treatment (Table 5.1) (Chapter 2).

Based on the findings in this study, and assuming a constant growth rate over time, it would take coppice shoots in the control treatment less than three years to reach the minimum desired size of 2cm, for both species. To reach the preferred size of 4 cm by harvesters (Shackleton 2001; Neke *et al*. 2006 Matsika *et al*. 2012), it would take *T. sericea* coppice shoots 5.5 years, while taking *D. cinerea* a little longer at 5.8 years. The coppice shoots produced in the single prune treatment of both species would reach the desired size of 2 cm in 1.7 years, and the preferred harvesting size of 4 cm in 3.3 years. These rotation times are quicker than scenarios developed by Twine (2011) from data collected by Shackleton (2001), but the desired harvesting size in the scenarios was set at 6 cm. The scenarios suggest that a "no prune" treatment would take seven years while a single prune treatment would take four years for coppice shoots to reach a size of 6 cm (Shackleton 2001; Twine 2011). From the results in the current study, it would take 4.8 years for coppice shoots produced in the single prune treatment and 8.5 years for coppice shoots produced in the control treatment to reach the size of 6 cm. The difference in rotational time needed may be due to the severe drought that was experienced in 2015/2016 which would have caused plants to be water stressed.

The use of the allometric equations derived from measurements taken in this study (Chapter 3) to determine length from diameter for *T. sericea* and *D. cinerea*, shows that at a diameter of 4 cm, the length of *T. sericea* coppice shoots would be 250.88 cm while *D. cinerea* coppice shoots would reach a length of 245.76 cm. The length of coppice shoots derived from the allometric equations in this study far exceeds the average length of poles found in fuelwood bundles cut by harvesters (Shackleton 2001). Shackleton (2001) found that the average length of *T. sericea* poles was 194 cm while the average length of other species, which may have included *D. cinerea*, was 171 cm. It would take 3.4 years for the

coppice shoots produced by the control treatment to reach the average length of 171 cm for all species found in fuelwood bundles while taking only 2.8 years for the single prune coppice shoots to reach the same size. Coppice shoots produced by *T. sericea* in the control treatment would take 3.9 years to reach the average length, 194 cm, of *T. sericea* fuelwood poles found in bundles (Shackleton 2001). The coppice shoots of *T. sericea* produced in the single treatment would only need 2.4 years to reach the average length of 194 cm. The shorter predicted time to reach the desired lengths suggests that coppice shoots in this study are allocating resources to grow tall instead of wide. This may be as apical dominance has not yet established and shoots are competing for light.

Applying the predicted lengths calculated previously (Chapter 3) to the allometric equations derived to determine shoot dry mass, *T. sericea* coppice shoots would have a biomass of 114.60 g while *D. cinerea* coppice shoots would weigh 95.88 g after the approximately 5.5 year rotation needed to reach a diameter of 4 cm (Chapter 2). The time required for coppice shoots to reach this mass would decrease to 3.3 years in the single prune treatment. These calculated values are surprisingly low for stems of 4 cm. If a diameter of 4 cm was to be used in allometric equations derived by Nickless *et al*. (2011) or Shackleton and Scholes (2011) the calculated mass values are much higher. The equations derived for *T. sericea* by Nickless *et al*. (2011) calculate mass to be 1.28 kg and the calculated value for *D. cinerea* to be 2.02 kg while Shackleton and Scholes equations calculate the wood mass of coppice shoots to be 223.96 g and 311.11 g respectively. These mass calculations from other allometric equations are higher than the calculations from this study as they focus on calculating total wood biomass. Nickless *et al*. (2011) derived equations for calculating biomass of an entire tree while Shackleton and Scholes (2011) equations can be used to calculate total wood biomass of coppice shoots. The calculations used in the current study focus on calculating the dry biomass of the main stem of the coppice shoot. The main stem is the part of the coppice shoot which would be used for fuelwood as side branches would be cut off in the collecting process making the stem easier for transportation. If wood mass was calculated from the current study, the calculations would be of wet wood mass which is not useful in calculation potential fuelwood biomass as dry mass is what is important. The difference in biomass calculations between other allometric equations and the equations derived in the current study highlight the importance of deriving equations for the exact

mass to be calculated. Allometric equations that predict for total wood biomass may be overestimating the potential fuelwood availability as harvesters may not utilise all the side branches of a coppice shoot.

Coppice shoots are known to have a quicker growth rate than that of seedlings and saplings as coppice shoots have access to stored reserves and water through a well developed root system of the established stump. This rapid growth rate of coppice shoots may negatively influence the density of the wood being produced. The slower growing stems usually produce denser and therefore heavier wood (Twine 2011). Both, *T. sericea* and *D. cinerea* are considered to be dense wooded plants with densities of 720 kg/cm^3 and 800 kg/cm^3 respectively (Van Wyk 1974). Thus even though coppice shoots grow quicker than saplings the wood being produced may be of inferior quality to harvesters when compared to sapling wood.

Combining the calculations of coppice shoot mass to the number of shoots produced per stump (Chapter 2) it can be assumed that the control treatment of *T. sericea* would produce harvestable size shoots of 687.6 g in 5.5 years while *D. cinerea* would produce 671.6 g of harvestable size shoots in the same amount of time. This will most likely be an overestimation as coppice shoot numbers are known to decrease with time and therefore the coppice shoot number after 5.5 years will not be the same as after one year of measurements (Shackleton 2001; Moyo *et al*. 2015a).

This study has provided useful insight on the coppice response and production of these two savanna species once being exposed to post-harvest treatments for 12 months. The allometric equations derived in this study can be applied to dynamic global vegetation models and aid in the estimation of biomass where *T. sericea* and *D. cinerea* are common. Through the extrapolation of the data rotational harvest times can be predicted and potentially applied in rural communities.

5.2 Conclusion and Recommendations

In conclusion, the implementation of managerial post-harvest treatments can be utilised to manipulate the morphology of coppice shoots and the coppice shoot biomass production of two savanna species. The selection of post-harvest treatment will depend on the desired outcome. If the desired outcome is to maximise the growth of a coppice shoot to reach a particular size, then the single prune treatment would be preferred while if the desired outcome is to maximise biomass production after a disturbance and removal of aboveground biomass then the control or usable treatment would be the most appropriate post-harvest treatment.

The current study is continuing which will create a larger dataset over numerous seasons. As coppice regrowth has been previously underestimated in biomass predictions the results of this study are important with regards to understanding coppicing strategies and production of two savanna species as well as aiding in vegetation modelling. In terms of future research, the following recommendations could be taken into consideration:

- The allometric equations derived in the current study should be tested and validated by cutting, drying and weighing coppice shoots once they reach a diameter of 4 cm.
- The application and confirmation of allometric equations developed in this study on any other coppicing studies done on *T*. *sericea* or *D*. *cinerea*. Coppicing studies done in differing area could indicate the need for not only species-specific but also site-specific allometric equations.
- The wood density of coppice shoots should be compared to the wood density of similar sized saplings, as to gain an understanding of the difference between the two growth forms.
- The leader shoot (shoot with highest diameter from first month) in the control treatment should be tracked and compared monthly with the coppice shoots in the single prune treatment as to gain an understanding of how competition influences growth rates of coppice shoots.
- The number of leaves produced per coppice shoot should be considered and compared between treatments to gain an understanding of resource allocation between treatments.

- The stored reserves (TNC) of experimental trees should be analysed before and after any post-harvest treatments, as to gain an understanding of how the treatments are influencing the mobilization of resources.
- If rural communities are willing to implement and monitor the management of coppice regrowth as a potential sustainable method of harvesting fuelwood.

REFERENCES

Aerts, R., November, E., Maes, W., Van der Borght, I., Negussie, A., Aynekulu, E., Hermy, M. and Muys, B. 2008. In situ persistence of African wild olive and forest restoration in degraded semiarid savanna. *Journal of Arid Environments* 73: 1131-1136

Araújo, T.M., Higuchi, N. and de Carvalho Júnior, J.A. 1999. Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Pará, Brazil. *Forest Ecology and Management* 117: 43-52

Archibald, S. and Bond, W.J. 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karoo* in forests, savnna, and arid environments. *Oikos* 102: 3-14

Banks, D.I., Griffin, N.J., Shackleton, C.M., Shackleton, S.E. and Mavrandonis, J.M. 1996. Wood supply and demand around two rural settlements in a semi-arid savanna, South Africa. *Biomass and Bioenergy* 11(4): 319-331

Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forestry* 2: 49-53

Bellingham, P.J. and Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89(2): 409-416

Bembridge, T.J. and Tarlton, J.E. 1990. Woodfuel in Ciskei: a headload study. *South African Forestry Journal* 154: 88-93

Bond, W.J. and Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *TRENDS in Ecology and Evolution* 16(1): 45-51

Bowersox, T.W., Schubert, T.H., Strand, R.F. and Whitesell, C.D. 1990. Coppicing success of young *Eucalyptus salinga* in Hawaii. *Biomass* 23: 137-148

Burnham, K.P and Anderson, D.R. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods Research* 33: 261-304

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H.,

Riéra, B. and Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87-99

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C. and Henry, M. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20(10): 3177-3190

Chirwa, P.W., Syampungani, S. and Geldenhuys, C.J. 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(3): 237-245

Chidumayo, E.N., Gambiza, J. and Grundy, I. 1996. Managing Miombo woodlands. In Campbell B (ed) *The Miombo in transition: woodlands and welfare in Africa*. Centre for International Forestry Research, Cifor 175-194

Clarke, P.J., Lawes, M.J. and Midgley, J.J. 2010. Resprouting as a key functional trait in woody plants-challenges to developing new organizing principles. *New Phytologist* 188(3): 651-654

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

Colgan, M.S., Swemmer, T. and Asner, G.P. 2014. Structural relationships between form factor, wood density, and biomass in African savanna woodlands. *Trees* 28(1): 91-102

Egoh, B.N., O'Farrell, P.J., Charef, A., Gurney, L.J., Koellner, T., Abi, H.N., Egoh, M. and Willemen, L. 2012. An African account of ecosystem service provision: Use, threats and policy options for sustainable livelihoods. *Ecosystem Services* 2: 71-81

Fisher, J.T., Witkowski, E.T.F., Erasmus, B.F.N., van Aardt, J., Asner, G.P., Wessels, K.J. and Mathieu, R. 2011. Human-modified landscapes: patterns of fine-scale woody vegetation structure in communal savannah rangelands. *Environmental Conservation* 39(1): 72-82

Forrester, D., Bauhus, J. and Connell, M. 2003. Competiton in thinned Silvertop Ash (*Eucalyptus sieberi* L. Johnson) stands from early coppice growth. *Forest Ecology and Management* 174: 459-475

Gehring, C., Park, S. and Denich, M. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management* 195: 69-83

Gignoux, J., Clobert, J. and Menault, J.C. 1997. Alternative fire resistance strategies in Savanna trees. *Oecologia* 110: 576-583

Griffiths, M.E. 1959. A revision of the African Species of *Terminalia*. *Journal of the Linnean Society of London Botany* 55(364): 818-907

Handavu, F., Syampungani, S. and Chisanga, E. 2011. The influence of stump diameter and height on coppicing ability of selected key Miombo woodland tree species of Zambia: A guide for harvesting for charcoal production. *Journal of Ecology and the Natural Environment* 3(14): 461-468

Hara, T., Kimura, M. and Kikuzawa, K. 1991. Growth patterns of tree height and stem diameter in populations of *Abies veitchii*, *A. mariessii* and *Betula ermanii*. *Journal of Ecology* 79: 1085-1098

Harrington, R.A. and Fownes, J.H. 1995. Radiation interception and growth of planted and coppice stands of four fast-growing tropical trees. *Journal of Applied Ecology* 32(1): 1-8

Henry, H.A.L. and Aarseen, L.W. 1999. The interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbour effects, or biased regression? *Ecology Letters* 2: 89-97

Higgins, S.I., Bond, W.J. and Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence. *Journal of Ecology* 88: 213-229

Hofstad, O. 2005. Review of biomass and volume functions for individual trees and shrubs in Southeast Africa. *Journal of Tropical Forest Science* 17(1): 151-162

Holdo, R.M. 2006. Tree growth in an African woodland savanna affected by disturbance. *Journal of Vegetation Science* 17(3): 369-378

Hosier, R.H. 1993. Charcoal production and environmental degradation. *Energy Policy* 21: 491-509

Kaschula, S.A., Twine, W.C. and Scholes, M.C. 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(3): 387-418

Kaschula, S.A., Twine, W.C. and Scholes, M.C. 2005b. The effect of catena position and stump characteristics on the coppice response of three savannah fuelwood species. *Environmental Conservation* 32(1): 76-84

Kennedy, A.D. 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: 148-158

Kerkhoff, A.J. and Enquist, B.J. 2009. Multiplicative by nature: why logarithmic transformation is necessary in allometry. *Journal of Theoretical Biology* 257(3): 519-521

Khan, M.L. and Tripathi, R.S. 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

Kirkland, T., Hunter, L.M. and Twine, W. 2007. "The Bush is No More": Insights on institutional change and natural resource availability in rural South Africa. *Society and Natural Resources* 20: 337-350

Komiyama, A., Jintana, V., Sangtiean, T. and Kato, S. 2002. A common allometric equation for predicting stem weight of mangroves growing in secondary forests. *Ecological Research* 17: 415-418

Latt, C.R., Nair, P.K.R. and Kang, B.T. 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. and Ceulemans, R. 2003. Population dynamics in a 6-year old coppice culture of popular. I. Clonal differences in stool mortality, shoot dynamics and shoot diameter distribution in relation to biomass production. *Biomass and Bioenergy* 24: 81-95

Litton, C.M. and Kauffman, J.B. 2008. Allometric models for predicting aboveground biomass in two widespread woody plants in Hawaii. *Association for Tropical Biology and Conservation* 40(3): 313-320

Lowore, J.D. and Abbott, P.G. 1995. Initial regeneration of Miombo woodland under three silvicultural systems. In: Lowore, J., Abbott, P.G. and Khofi, C.F. (eds) *Management of Miombo woodland by local communities: proceedings of a workshop for technical forestry staff, Kasungu, 24-26 January 1995*. Forest Research Institute of Malawi, Zomba; University of Aberdeen, Aberdeen. pp 6-17

Luoga, E.J., Witkowski, E.F.T. and Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35

MacDonald, J.E. and Powell, G.R. 1983. Relationships between stump sprouting and parent-tree diameter in sugar maple in the 1st year following clear-cutting. *Canadian Journal of Forest Research* 390-394

Madubansi, M. and Shackleton, C.M. 2007. Changes in fuelwood use and selection following electrification in the Bushbuckridge lowveld, South Africa. *Journal of Environmental Management* 83: 416-426

Malimbwi, R.E., Solberg, B. and Luoga, E. 1994. Estimation of biomass and volume in miombo woodland at Kitulangalo Forest Reserve, Tanzania. *Journal of Tropical Forest Science* 17(2): 230-242

Mascaro, J., Litton, C.M., Hughes, R.F., Uowolo, A. and Schnitzer, S.A. 2011. Minimizing bias in biomass allometry: Model selection and log-transformation of data. *Biotropica* 43(6): 649-653

Matsika, R., Erasmus, B.F.N. and Twine, W.C. 2012. A tale of two villages: assessing the dynamics of fuelwood supply in communal landscapes in South Africa. *Environmental Conservation* 40(1): 71-83

Miyanishi, K. and Kellman, M. 1986. The role of root nutrient reserves in regrowth of two savanna shrubs. *Canadian Journal of Botany* 64(6): 1244-1248

Moyo, H. 2013. The coppicing of a savanna tree species (*Terminalia sericea*) in relation to resource manipulation and disturbance. PhD thesis. University of the Witwatersrand, Johannesburg, South Africa

Moyo,H., Scholes, M.C. and Twine, W. 2015a. Resprouting after coppicing is negatively influenced by browsing in *Terminalia sericea*. *Ecological research* 30(5): 899-907

Moyo, H., Scholes, M.C. and Twine, W. 2015b. The effects of repeated cutting on coppice response of *Terminalia sericea*. *Trees* 29: 161-169

Mwavu, E.N. and Witkowski, E.T.F. 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

Navar, J. 2009. Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. *Forest Ecology and Management* 257: 427-434

Neke, K.S. 2004. Savanna woodlands in relation to human utilisation. PhD thesis. University of the Witwatersrand, Johannesburg, South Africa

Neke, K.S., Owen-Smith, N. and Witkowski, E.T.F. 2006. Comparative resprouting response of savanna woody plant species following harvesting: the value of persistence. *Forest Ecology and Management* 232: 114-123

Netshiluvhi, T.R. and Scholes, R.J. 2001. Allometry of South African woodland trees. *Council for Scientific and Industrial Research (CSIR), South Africa, Report: ENV-P-I, 7*

Nickless, A., Scholes, R.J. and Archibald, S. 2011. A method for calculating the variance and confidence intervals for tree biomass estimates obtained from allometric equations. *South African Journal of Science* 107: 86-95

Niklas, K.J. 1994. The allometry of safety-factors for plant height. *American Journal of Botany* 81(3): 345-351

Okello, B.D., O'Connor, T.G. and Young, T.P. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *Forest Ecology and Manangement* 142: 143-153

Oker-Blom, P., Pukkala, T. and Kuuluvainen, T. 1989. Relationship between radiation interception and photosynthesis in forest canopies: Effect of stand structure and latitude. *Ecological Modelling* 49: 73-87

Packard, G.C., Birchard, G.F. and Boardman, T.J. 2011. Fitting statistical models in bivariate allometry. *Biological Reviews* 86: 549-563

Paumgarten, F. 2005. The Role of non-timber forest products as safety-nets: A review of evidence with a focus on South Africa. *GeoJournal* 64: 189-197

Pouliot, M. and Treue, T. 2013. Rural people's reliance on forests and the non-forest environment in West Africa: evidence from Ghana and Burkina Faso. *World Development* 43: 180-193

Rutherford, M.C. 1979. Aboveground biomass subdivision in woody species of the savanna ecosystem project study area, Nylsvley. Cooperative Scientific Programmes: CSIR

Sawadogo, L., Savadogo, P., Tiveau, D., Dayamba, S.D., Zida, D., Nouvellet, Y., Oden, P.C. and Guinko, S. 2010. Allometric predictions of above-ground biomass of eleven woody tree species in the Sudanian savanna-woodland of West Africa. *Journal of Forestry Research* 21(4): 475-481

Scholes, R.J. 1997. Savanna. In: Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds.), *Vegetation of southern Africa*. Cambridge University Press

Scholes, R.J. and Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review Ecological Systems* 28: 517-544

Scholes, R.J. and Walker, B.H. 1993. An African savanna; synthesis of the Nylsvley Study. UK, Cambridge

Scroth, G., D'Angelo, S.A., Teixeira, W., Haag, D. and Lieberei, R. 2002. Conversion of secondary forest in agroforestry and monoculture plantations in Amazonia: consequences for biomass, litter and soil carbon stocks after seven years. *Forest Ecology and Management* 163: 131-150

Shackleton, C.M. 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, C.M. 1997. The prediction of woody plant productivity in the savanna biome, South Africa. PhD thesis. University of the Witwatersrand, Johannesburg, South Africa.

Shackleton, C.M. 1998. Annual production of harvestable deadwood in semi-arid savannas, South Africa. *Forest Ecology and Management* 112: 139-144

Shackleton, C.M. 2000. Stump size and the number of coppice shots for selected savanna tree species. *South African Journal of Botany* 66(2): 124-127

Shackleton, C.M. 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, C.M., Buiten, E., Annecke, W., Banks, D., Bester, J., Everson, T., Fabricius, C., Ham, C., Kees, M., Modise, M. and Phago, M. 2007. Exploring the options for fuelwood policies to support poverty alleviation policies: evolving dimensions in South Africa. *Forests, Trees and Livelihoods* 17(4): 269-292

Shackleton, C.M. and Clarke, J.M. 2007. Research and management of Miombo woodlands for products in support of local livelihoods. Johannesburg, World Bank

Shackleton, C.M., Griffin, N.J., Banks, D.I., Mavrandonis, J.M. and Shackleton, S.E. 1994. Community structure and species composition along a disturbance gradient in a communally managed South African savanna. *Vegetatio* 115: 157-167

Shackleton, C.M. and Scholes, R.J. 2011. Above ground woody community attributes, biomass and carbon stocks along a rainfall gradient in the savannas of the central lowveld, South Africa. *South African Journal of Botany* 77: 184-192

Shackleton, C. and Shackleton, S. 2004. The importance of non-timber forest products in rural livelihood security and as safety-nets: a review of evidence from South Africa. *South African Journal of Science* 100: 658-664

Shackleton, S.E., Shackleton, C.M., Netshiluvhi, T.R., Geach, B.S., Balance, A. and Fairbanks, D.H.K. 2002. Use patterns and values of savanna resources in three rural villages in South Africa. *Economic Botany* 56: 130-146

Strauss, S.Y. and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14(5): 179-185

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communites*. Princeton University Press

Twine, W. 2011. Harvesting of Coppice, Final Report. Eskom Holding Limited. South Africa

Twine, W., Moshe, D., Netshiluvhi, T. and 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

Van Wyk, P. 1974. *Trees of the Kruger National Park*. Cape Town: Purnell and Sons

Van Wyk, B. and Van Wyk, P. 1997. *Field Guide to Trees of Southern Africa*. Cape Town, South Africa: Struik Publishers

Wang, C. 2006. Biomass allometric equations for 10 co-occuring tree species in Chinese temperate forests. *Forest Ecology and Management* 222: 9-16

Wessels, K.J., Colgan, M.S., Erasmus, B.F.N., Asner, G.P., Twine, W.C., Mathieu, R., van Aardt, J.A.N., Fischer, J.T. and Smit, I.P.J. 2013. Unsustainable fuelwood extraction from South African savannas. *Environmental Research Letters* 8: 014007 [online 10pp]

Wigley, B.J., Cramer, M.D. and Bond, W.J. 2009. Sapling survival in a frequently burnt Savanna: Mobilisation of carbon reserves in *Acacia karroo*. *Plant Ecology* 203(1): 1-11

Williams, A. and Shackleton, C.M. 2002. Fuel wood use in South Africa: Where to in the 21st Century? *The South African Forestry Journal* 196(1): 1-7

Williams, R.J., Zerihum, A., Montagu, K.D., Hoffman, M., Hutley, L.B. and Chen, X. 2005. Allometry for estimating aboveground tree biomass in tropical and subtropical eucalypt woodlands: towards general predictive equations. *Australian Journal of Botany* 53: 607-619

Zhao, J. and Chen, J. 2012. Interspecific variation in compensatory regrowth to herbivory associated with soil nutrients in three Ficus (Moraceae) saplings. *PloS one* 7(9), p.e45092