THE EFFECTS OF SPRING DEBARKING AND DEFOLIATION BY GOATS ON *ACACIA KARROO* TREES IN THE FALSE THORNVELD OF THE EASTERN CAPE, SOUTH AFRICA

By
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Declaration

This thesis is the results of the author's own original work, unless specifically indicated by citation in the text; and it has never been submitted to other institution.

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Dedication

This work is dedicated to my family, Zukiswa (Mom), Andisa (Sister) and Ambesa (Daughter).

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Abstract

In the study the early flush phenophase induced response of *A. karroo* were investigated. The investigation was carried out in the False Thornveld of the Eastern Cape, a vegetation type that is dominated by *A. karroo* species and herbaceous layer dominated by Increaser II grass species. In the study two treatments were investigated; debarking and defoliation. A simple randomized block design, with 6 treatments; replicated three times was set up. Debarking was done manually by hand and defoliation by 12 goats for two weeks in October 2004. Defoliation was preceding debarking in a plot were the combination of the two would be applied. Goats were allowed to remove 70 to 80 % of forage within browsing height before moving to the next camp.

Spring defoliation did not have any detectable effect on shoot length, spine, length, internode length, number of pods, numbers of seeds per pod, condensed tannins, nitrogen and cell wall contents. The defoliation resulted in higher number of shoots produce within 1.5 m ($p < 0.05$), and basally ringed trees caused topkill, resulting in reduction in tree height (40%), basal circumference (17%), decreased number of shoots produced, number pods ($p < 0.01$) and seeds per pod ($p < 0.01$). However basal ringing increased NDF ($p < 0.01$), ADF ($p < 0.05$), there was a decrease in nitrogen content of leaves ($p < 0.05$) also there was a slight increase in shoot length but this was not significant ($p > 0.05$). Debarking did not have an effect on spine length, internode length, ADL, ADC, condensed tannin and phosphorus. Period after treatment application determines the resource allocation to defenses, mature tree in the second season allocated resources to growth. Young trees in the second season produced more tannin than older trees ($p < 0.05$).

In semi-arid environments growth takes first preference over defense mechanisms. Trees in this environment responded to debarking by growth more than defense. The defoliated trees showed the ability to overcompensate for the lost tissue. The young trees in the first season had less chemical defense and more fiber, while in the second season they had more chemical defense and fiber making it less digestible. The structural defense of the trees was not affected by defoliation but was reduced by basal ringed trees. Young trees are poor defendants as they invest in growth more than defense. An investment on structural defense will require that the attack be carried out for a longer periods than was the case in this study. I concluded that defoliated *A. karroo* trees survived lower canopy defoliation by tolerance and debarked trees by resistance.

Chapter 1

General Introduction

The False Thornveld of the Eastern Cape is a typical savanna vegetation which consists of two layers of vegetation (Acocks 1975). The availability of resources and disturbance regimes are important in this biome for the existence of grasses and bushes (Sankaran *et al.* 2005). The upper layer of trees provide browse and lower the grass layer that dominates the vegetation allowing it to be utilized by browsers and grazers (Tainton 1999). Savannas cover a fifth of the earth's surface supporting most of the rangeland, livestock and wildlife biomass (Sankaran *et al.* 2005). The most ecologically acceptable way of managing this vegetation, in an agricultural system, is by stocking with both grazers and browsers (Teague & Trollope 1981). It has been argued that this type of vegetation can be utilized most economically for cattle farming, with goat farming used as a secondary enterprise (Aucamp *et al.* 1984).

The phenomenon of bush encroachment is defined as the proliferation of woody plants which negatively affects herbaceous production and results in reduced grazing capacity (Smit *et al.* 1996). The causes of this phenomenon are diverse, but include climate change, soils and the exclusion of fire (Smit *et al.* 1999). The complexity of bush encroachment problem has resulted in the development of many models in an attempt to explain the cause of this phenomenon in southern Africa (Ward 2005). The coexistence of grass and bush can be described as the separation of rooting niche of this form of vegetation, assuming that water is the limiting resource (Weigand *et al.* 2005). This model led to the conclusion that overgrazing was the cause of bush encroachment. More models were developed due to inadequacy of the above model to establish the cause of bush encroachment (Ward 2005). The model that was proposed by Weigand *et al.* (2005) concluded that bush encroachment can best be understood as a cyclical succession between open savanna and woody dominance that is controlled by (i) rainfall variability in space and time and (ii) competition for resources by the neighbouring trees. Another model that has been developed described tree-grass interaction in the ecological buffering mechanism, which regards savanna regions as boundaries between pure grasslands and tropical forest (Jeltsch *et al.* 2000).

The bush community is natural to the environment of the Eastern Cape (Aucamp *et al.* 1984). *A karroo* occurs in great stands across this Province. Utilization by goats not only increases the saleable product off the range, but goats are also utilized as the biological control agents of this bush (Aucamp *et al.* 1984; Stuart-Hill 1987). Although, goats are used as control agents, little is known about the response of woody plants to browsing in the African savannas (Scogings 1998). Results from a previous study in the same veld type, indicated that the growing phenophase and the intensity of defoliation determine the response of *A. karroo* to disturbance (Teague & Walker 1988). Repeated browsing affects tree canopy by increasing regrowth, high annual branch growth, extensive tree branching but it does not affect plant population (Scogings 1998; Fornara & du Toit 2007).

Bark stripping is common in the forests caused by rodents and browsers, where it can cause serious financial losses (Gill 1992; Welch & Scott 1998; Faber 1996). Studies done on the impact of the bark stripping in different trees and by different animals indicate that recordings of significant reductions in production are rare (Welch & Scott. 1998). Even though the *Acacia* species are the most studied bush in Africa (Bergström 1992; O'Connor 1996), there is only one known study of bark stripping (Scogings & Macanda 2005).

Plant responses to herbivory or fire are important as they affect the feeding behavior of browsers (Bergström *et al.* 2000). The responses might come in the form of morphology or herbage chemistry (Karban & Myers 1989). The response of plants to herbivory of any form is termed induced response (Karban & Myers 1989; Agrawal 2000). The responses vary from increased resistance to tolerance of plant to herbivore attack (Karban & Myers 1989). The herbage chemistry change has been variable in studies but when it occurs it is measured in terms of the carbon nutrient balance (CNB) of the plant (Scogings 1998). The interest in CNB arose from the attempts to explain plant resistance to herbivory (Bryant *et al.* 1983). The CNB was used to explain the results in many studies but its success in predicting results was very limited. (Hamilton *et al.* 2001).

African *Acacias* were intensively studied but little is known about their responses to defoliation (Scogings 1998). The studies have not come up with similar results to understand the responses due to variability of these results. The results of the studies in African savannas have been explained using Resource Availability (RA) model (Scogings 1999). RA models states that plants growing in the fertile soils are fast growing and have less carbon based secondary metabolites and have more spines (Bryant *et al.* 1989). Plants from resource poor environments are slow growing and are more efficient chemical defenders than fast growing plant from resource rich environment (Bryant *et al.* 1989).

1.1 Problem statement

While *Acacias* are the most studied group of African woody plants in terms of responses to browsing, only one study is known of the effects of bark stripping in *Acacias*, it was done in the False Thornveld of the Eastern Cape by Scogings & Macanda (2005). It was an opportunistic study whereby goats were observed utilizing bark of *A. karroo*. A controlled trial was established to study the response of *A. karroo* to two factors debarking and heavy defoliation. The current interest of plant-herbivore interaction to study tolerance and resistance together as resistance has been studied (Juenger & Lennartsson 2000).

1.2 Objectives

The objective of the study was to investigat[illegible]ponse of *A. karroo* trees to spring debarking and browsing.

1.3 Key questions

1. Does browsing, with or without bark stripping, increase new shoot size?
2. Does browsing, with or without bark-stripping, reduce the reproduction?
3. Does browsing, with or without bark stripping, increase the physical defenses by either (i) reducing internode length (thus more spines/length) or (ii) increasing spine length?
4. Does browsing, with or without bark-stripping, increase chemical defences by increasing foliar tannin/nitrogen and fibre/nitrogen ratios?
5. Is complete ringing more effective than simple bark stripping inducing the responses?

1.4 Hypothesis

Debarking and defoliation will result in compensatory growth, increased physical defense and less chemical defense.

Chapter 2

Literature Review

2.1 Introduction

Browse forms an integral part of savanna production systems, therefore, the understanding of animal plant interactions becomes important. Browse of the bushes are tender shoots, twigs, leaves, fruits and pods (Aganga & Tshwenyane 2003). Grime (1977) has classified the external factors that limit forage production into stress and disturbance. Stress in plants is caused by shortage of light, water, minerals and suboptimal temperature. Disturbance that is considered is caused by herbivory, pathogens, wind damag[illegible]re. The effects of herbivores on plants vary and these may change the structure of plant communities, as they affect reproduction, growth, defense and dispersion (Martinez & López-Portillo 2003). Changes in the forage may affect the future utilization of forage and performance of herbivores (du Toit *et al.* 1990). The morphological changes that are inflicted by herbivory on plants may change the preference and performance of animals (Bryant *et al.* 1991). The responses to defoliation may be chemical or morphological (Cooper *et al.* 2003). Chemical changes are short lived and morphological change are more permanent (Cooper *et al.* 2003). In the review section the induced responses of bushes following browsing and debarking, will be discussed.

The ecological optimal way of managing the savanna areas of southern Africa is through the utilization of both the herbaceous layer and the woody layer of the vegetation (Teague & Trollope 1981). Applying herbivory and withholding disturbance are the main functions of vegetation management, therefore, the understanding of vegetation responses is important (Vesk *et al.* 2004). The impact of herbivory is important in this vegetation type as it impacts on the forage preference and performance of animals (Bryant *et al.* 1991). Damage to the vegetation can, therefore, have significant influence on plant response, which could include morphology, chemical composition, phenology, photosynthesis and growth (Nykänen & Korecheva 2004; De Nagy Kovë Hrabar 2006). Induced responses can either increase resistance to herbivores or increase defenses (Karban & Myers 1989). Teague *et al.* (1990) in the study of browse production and responses of *A. karroo* to defoliation found that the response is closely related to the following parameters; moisture, soil depth, magnitude and duration growth following defoliation.

The dominant hypothesis is that induced plant responses are a cost saving strategy, the costly nature of allocation of resource to defense in the absence of herbivory rather than in the presence of herbivory (Agrawal 2000 & 2005). This kind of adaptation enhances plant fitness in the presence of herbivory. This hypothesis shows that herbivory is costly to plants as they divert resources to defense instead of growth in the presence of herbivores. Induced plant response are categorized into (i) plant resistance traits that reduce herbivore performance (ii) tolerance traits (iii) phenological escape that reduces plant availability when herbivores are most active (Agrawal 2000; Fornara & du Toit 2007). Few studies have shown that herbivory benefits plants and response differs according to seasons (Rohner & Ward 1997). *A. karroo* trees are positively affected by early-flush defoliation, which is also when carbohydrate reserves were at their lowest (Teague & Walker 1988). Defoliation by goats affects the total non-structural carbohydrates (TNC), which are reduced by up to 50% with severe defoliation (Teague 1987), however reduction was short lived. Plants have the ability to respond to browsing both with above ground compensation and with increased defense (Gadd *et al.* 2001). The response of semi-arid bushes is categorized into sprouters and non-sprouters. Sprouters are associated with disturbances that cause topkill in the bushes (Vesk *et al.* 2004).

Plants can respond to herbivore attack via tolerance, compensation or increased defense (Gadd *et al* 2001). Earlier studies of plant response have focused on the plant resistance traits ignoring tolerance (Juenger & Lennartsson 2000). Tolerance is the degree to which plant fitness is affected by herbivory (Strauss & Agrawal 1999). Compensation is the ability of a plant to grow after it has been defoliated (Gadd *et al.* 2001), Strauss & Agrawal (1999) describe compensation as another form of tolerance. Defence is the trait that confers fitness benefit to a plant in the presence of herbivory (Strauss & Agrawal 1999). Plant resistance to browsing comes in two forms defense and tolerance (Haukioja & Koricheva 2000). It is imperative that both forms of resistance be considered when studying plant response as they affect the plant-herbivore interaction in different ways. The co-evolution of plant-herbivore makes it necessary that tolerance and resistance traits are studied together as they do not affect co-evolution in the same way (Juenger & Lennartsson 2000).

2.2 Herbivore resistant traits

Plants have co-evolved with the herbivore population that enable them to developed defense mechanisms (Aganga & Tshwenyane 2003). Leguminous plants usually have thorns, fibrous foliage growth form that protect canopy from browsing. Induced defense are differentiated from constitutive defense by the way in which they are manifested. Defense starts once the herbivores begin feeding on the plant (Pointrineau *et al.* 2004; Gowda & Palo 2003). Induced plant responses that render the plants unacceptable or reduce animal performance are more effective in terms of defense mechanisms (Karban & Baldwin 1997). Induced defenses are triggered by the attack from the herbivores (Harvell 1990). Even limited herbivory can trigger plant responses, which can affect herbivore selection of host choice, growth and rate of attack by herbivores (Agrawal 2005). The defense against herbivory is triggered when the benefits of defense out compete that of production (Ward & Young 2002). The inducibility of defense is determined by the level of attack. The defence and inducibility are regulated by rate of attack, low attack results in low defence/low inducibility, moderate attack high defence/high inducibility and high attack high defence/moderate to low indicibility (Pointrineau *et al.* 2004).

The defense traits have been studied and results of the studies have led to the development of defense theories (Zangerl & Rutledge 1996; Gowda & Palo 2003). The optimum defense theory predicts that plant parts that are likely to be attacked constitute more of constitutive defense rather that induced defenses while those that are unlikely to be attacked have more induced defenses (Zangerl & Rutledge 1996). The theory of defence states that investments in any form of defense is driven by the risk of being eaten and limited to the cost of producing that particular defense trait in terms of available resource that can be utilized for growth or reproduction (Gowda & Palo 2003). Induced defenses are differentiated from constitutive defense by the mode of expression. The success of induced defense can be viewed in three ways: (i) inducibility is cost reducing whereby defending only occurs when the bush is threatened by the enemy; (ii) inducible defense allows more efficient defense against multiple enemies through resource reallocation to different modes of defense mechanisms thereby plants invest morphological and chemical defense simultaneously (iii) differing defense might limit damage to plants as the enemy will have adapted to the changing quality of the victim bush in the case of herbivory (Karban & Myers 1989 & Pointrineau *et al.* 2004). The evolutionary flexibility and inducibility provides for more effective and less costly defenses against natural enemies (Pointrineau *et al.* 2004). The optimal defense theory is often explained and categorized into two components, that it has constitutive and induced defense. Induced defense is mostly used by those plant parts that are not under constant threat of attack (Zangerl & Rutledge 1996). Defense mechanisms in plants come in the forms of chemicals, thorns and spines (Juenger & Lennartsson 2000). The traits that are responsible for defense in the African *Acacias* are spines and tannin concentration (Gadd *et al.* 2001; Cooper & Owen-Smith 1985; 1986).

2.2.1 Forage chemical defense

Generally, plants that grow in nutrient-poor soils contain a relatively high content of secondary metabolites than plants found in nutrient-rich soils (Bryant *et al* 1989; Rohner & Ward 1997). Chemical defense has been classified according to its effect after ingestion, they either inhibit digestion or become toxic (Bryant *et al.* 1991; Bergström 1992). The condensed tannin has been accepted as chemical defense tool in plants. This chemical is known to reduce protein availability in leaves once they are ingested (Robbins *et al.* 1987). The inhibitory effect of tannin on protein molecules in the animal gut has been scrutinized due to its big molecular size that renders it easily polarized by acid (Bryant *et al.* 1991). In Kruger National Park condensed tannin has been found to influence the nutritional value of feed for giraffes (Furstenburg & van Hoven 1994). The deterrence of herbivores by tannins is not totally as the result of protein and carbohydrate inhibition. This avoidance by herbivores can be caused by the toxicity that results in animal getting malaise (Bryant *et al.* 1991). The effectiveness of condensed tannin as the defense amour for plants is basically dependent on tannin structure (Bryant *et al.* 1991). Bryant *et al.* (1991) found that plants depend on wide range of chemical substance for chemical defense rather than a class of secondary metabolites and effectiveness of these is based on toxicity rather than digestion inhibition.

It is documented that *Acacia* trees have a higher content of tannins which are known for the ability to deter browsing (Rohner & Ward 1997). Changes in total tannins and phenols in the plant are not common, but changes in nitrogen rich secondary metabolites were found (Scogings 1998). Tannin changes cannot always be attributed to herbivory as it has been found that they are also changed by climatic conditions and phenophase (Fursteburg & van Hoven 1994). In the study of *Acacia tortilis* conducted in Tanzania there were no significance differences in concentrations of phenols, condensed tannin and nitrogen in leaves (Gowda 1997). Tannin levels have been proven to decrease digestibility as concentration of tannin increases following browsing (Teague 1989b). The increase in tannin content of *A. karroo* plants is mainly affected by season. The rapid responses of *A. karroo* to defoliation in the early dormant season showed no increase in tannin content of leaves in a study by Scogings (2005). The no increase in tannin content of leaves after browsing may be attributed to the metabolism of mature leaves and dormancy stage of growth (Scogings 2005). In the study conducted in Kenya on *A. drepanolobium* the tannin level where not affected by defoliation by mega-herbivores (Gadd *et al.* 2001). In the Kruger National Park trees where browsed by giraffe for 12 months the level of condensed tannins increased (Furstenburg & van Hoven 1994). Plants have shown variable response to herbivory but the increase in carbon and phenolics has been recorded while terpene decreases (Nykänen & Koricheva 2004). The carbohydrate requirements for growth take preference thereby reducing the carbon-based metabolites synthesis, which are important in chemical defences (du Toit *et al.* 1990). It has always been postulated that there is a trade-off between tannin and growth, however, this has not be scientifically proven (Ward & Young 2002; Gadd *et al* 2001).

The arid environment plants are expected to invest more in anti-herbivore defense but for *Acacias* there is no clear allocation of resources to chemical defense in the form of polyphenols, condensed tannins and protein-precipitating tannins (Rohner & Ward 1997). In *A. karroo* the concentration of condensed tannins was found to differ according to plant size, age of the shoot and leaf (Teague 1989a). Teague (1989b) showed that *A. karroo* increased their chemical defense after browsing, by the digestibility of young leaves compared to older leaves. The studies have shown that there are in fact no trade-offs between the physical and chemical defense with *A. karroo* trees, which contrast with other trees which do not invest in both defenses (Rohner & Ward 1997). In the available literature there is little understanding of the chemical defense as there has not been much research done on other plant chemicals in terms of response and their toxicity levels. It is clear that trees and bushes rely on a wide range of chemicals rather than tannins for their defense (Bryant *et al.* 1991).

2.2.2 Physical defense

Physical defenses are required by the plants to withstand environmental pressure, be it attacks by browsers or damage by wind (Lucas *et al.* 2000). This kind of defense can be in the form of total prevention of herbivory by hardiness in form of seed shells, spines and thorns. Also this can be in the form of toughness, whereby, herbivory takes place but the part that is defoliated develops resistance. (Lucas *et al.* 2000). In the study of *Populus* leaves, the sink strength increased with insect wounding, this was more explicit in young growing plants (Arnold & Schultz 2002).The resource availability (RA) hypothesis states that plants growing in nutrient rich soils have more thorns or spines for defense than those growing in nutrient poor soils (Bryant *et al.* 1989). In a fertilizer study of *A. tortilis* conducted in Kenya, it was found that larger mass of long spine come with high fertilizer treatments (Gowda *et al.* 2003). This study of *A. tortilis* supported RA hypothesis that states that plants growing in nutrient rich soils invest on constitutive defense like thorns and these are also induced by browsing.

It is generally accepted that herbivory can change plant structures by inducing the increase in density of spines, hairs and sprickles (Karban & Myers 1989). The physical defenses of *Acacia* species, i.e. thorns, have shown an increase in length and density, specifically on the branches that are accessible to browsing (Midgley & Ward 1996; Young & Okello 1998). *A. berlandiere, A. greggii and A. scaffneri* have responded to browsing by increasing the spine and leaf density (Cooper *et al.* 2003). Midgley and Ward (1996) in their study of *A. karroo* and *Z. mucronata* reported that thorn length increased with decrease in tree height. Young (1987), studying *A. depranolobium,* recorded a significant increase of up to 27 % in thorn length in browsed trees as compared to unbrowsed trees. In the same study the thorn length of lower branches was up to 44 % longer as compare to those of higher branches. It was found that herbivores limit the extent of annual growth thus preventing the development of small thorns characteristic of late season growth (Midgley & Ward 1996). Browsing of *A. depranolobium* by large herbivores has resulted in increase spine length (Young & Okello 1998). The exclusion of browsers for three years in *Hormantophylla spinnosa* vegetation resulted in the reduction in length and density of spines (Gómez & Zamora 2002).

Spines have been regarded as defense weapons for trees that grow in nutrient-rich soil (Gowda *et al.* 2003). Trees browsed by large mammals e.g. elephants and those browsed by goats have shown increased shoot length after browsing (Gowda 1997; Young 1997). Branches of *A. seyal* that are within reach of giraffe produced longer thorns and at higher density than those out of reach (Milewske *et al.* 1991). A study of the thorns of *Damnacanthus indicus* in Japan, was found that they deterred deer browsing successfully (Takada *et al.* 2003). Gowda (1997), reported on research conducted in Tanzania on *A. tortilis*, that spine density had a negative effect on intake rate of goats. The same study found that the spines affected feeding behaviour from twig removal to leaf removal thereby reducing the amount of biomass removed (Gowda 1997). In the study of *A. seyal*, it was shown that trees that had their thorns removed suffered strong biomass removal than those that have their thorns intact (Milewske *et al.* 1991). The role of thorns of *Acacias* were studied to establish their part in plant defense, it was concluded that they protect stems not leaves. The leaves of *A. karroo* were longer than thorns and also the nodes were sparsely distributed (Midgley *et al.* 2001).

Lucas *et al.* (2000) categorize physical defense into toughness and hardiness, with toughness being the organized mixture of components and hardiness being what is generally referred to as elastic or plastic resistance. The physical defense is there to protect plants against detachment; the mechanisms work in two different ways to prevent crack from developing and other prevent cracks from continuing. The toughness of the plant is the results increased fibre contents of leaves after defoliation. Hardiness in plant requires high density tissue, which prevents the plant from reaching the stress levels where it could break under the pressure applied by herbivores. The theory of toughness and hardiness has not been really tested in real environments; rather it has been the subject of laboratory-based chemistry (Lucas *et al.* 2000).

2.2.3 The cell wall contents

The plant uses two mechanisms to withstand disturbance from environmental factors, hardiness and toughness. Toughness in the plant tissue is generally composed of cell wall contents like cellulosic microfibrils, hemicellulose and lignin matrix; toughness is the composite construction of these contents. Hardiness is just elasticity or plasticity of the plant tissue it is not regarded as property but mechanical test (Lucas *et al.* 2000). In the humid areas of Nigeria the neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL) contents increased with the increase in age of coppice growth (Larbi *et al.* 2005). The increase in the cell wall contents was coupled with the decrease in crude protein content of the leaves. In the savanna of East Africa grass fiber content showed increase with the progression of season but reached peak in areas where herbivory was highest (Georgiadis & McNaughton 1990). The NDF, ADF and lignin were found to be positively correlated with shearing strength of *Bracharia* pasture ecotypes, the shearing strength is force required to split leaves (Hughes *et al.* 2000). The cell wall contents play a pivotal role in the plant defense strategies. The two strategies employed by the plant in defense, first is to make structural components that limit the degree of detachment. The second one is where plants make structural components that break at higher force than herbivore can achieve without its own structural failings (Lucas *et al.* 2000).

2.3 Tree tolerance strategies to herbivory

When plants cannot avoid herbivory either by defence or escape, tolerance is the only option to utilized (Lehtilä 2000). Tolerance of woody plants should be understood as it is an important part of resistance given that their defense ability does not totally exclude browsing (Haukioja & Koricheva 2000). Plant tolerance deals with the ability of plants to respond to defoliation either by regrowth or temporarily mantains reduced regrowth. Tolerance is expressed through the ability of plant to maintain fitness through growth and reproduction after the plant has been attacked by herbivore (Boege 2005). These two survival strategies that are used by plants to resist defoliation may have different effects in plant-herbivore interaction. Tolerance effect on foliage is not similar to the effects of defense, as the tolerance does not alter plant acceptability and availability to herbivores (Juenger & Lennartsson 2000). At the same time highly tolerant plants have little defense traits. Tolerance usually includes regrowth by production of new shoot through activation of dormant buds (Lehtilä 2000).

2.3.1 Growth of trees after browsing

Plants have the ability to respond to defoliation or disturbance through regrowth, increased defense and saving energy (Gadd *et al.* 2001; Rohner & Ward 1997). With the understanding of growth and defence hypothesis there is no clear trade-offs between growth and defense (Rohner & Ward 1997). Certain plants are known for their ability to respond to browsing by replacing lost somatic cell over and above what was lost through browsing. This phenomenon is known as overcompensation (Dangerfield & Modukanele 1996). In the study by Pellew (1983) in the Serengeti ecosystem browsing by giraffe stimulated shoot production of *Acacias*. Heavily browsed *A. nigrescens* over-compensated for the leaf or twig removal as there was no significant difference between heavy and lightly browsed trees (du Toit *et al.* 1990). *A. karroo* trees also have the ability to produce more forage after defoliation, as found by Teague & Walker (1988). Pruning of *A. tortilis* resulted in significant increase in new shoot and spine biomass production as compared to unbrowsed plants (Gowda 1997). Simulated shoot and leaf defoliation of *A. drepanolobium* showed no negative correlation between growth and plant defense (Gadd *et al.* 2001).

A number of plants have bud banks, these can be mobilized to compensate for herbivore damage, but this may be costly as they need herbivory before they start to produce (Lehtilä 2000). Many woody plants respond to defoliation by increasing shoot production (Cooper *et al.* 2003). In one trial in Lorugum moderate intensity of browsing increased shoot production of *A. tortilis* (Oba 1998). Removal of the apical meristem reduces inter-shoot competition, thereby allocating resources to foliage enrichment and shoot regrowth (du Toit *et al.* 1990). The removal of the apical meristem reduces the apical dormancy and this activates the dormant buds (Bergström *et al.* 2000). Trees respond to defoliation differently where three species of *Acacias* responded by increasing the leaf component of twigs (Cooper *et al.* 2003). High utilization of African *Acacia* has not resulted in lowered productivity but clipping of new shoots increased shoot production after one year (Bergström 1992). The growth rate of *Lepus californicus* was increased up to 2.5 times on shrubs that where exposed to browsing than those not browsed (Martìnez & López-Portillo 2003).

Compensatory shoot regrowth response has been reported in many species of African *Acacias* (Cooper *et al.* 2003). As well as in trees that have had their shoots clipped. *A. drepanolobium*, for example, can fully compensate the loss of shoot length (Gadd *et al.* 2001). Another evident form of compensatory response in trees was an increase in leaf density (Cooper *et al.* 2003). The leaf compensatory growth in African *Acacias* is activated when defoliation is only restricted to leaves but when shoots are damaged the response is an increase in shoot production (Cooper *et al.* 2003). In the study where regrowth was measured for heavily and lightly browsed trees, results showed that heavily browsed trees compensated for the lost tissue as there was no difference between regrowth of the trees (du Toit *et al.* 1990)

In the study of *Acacia* trees in South Africa the theory of browsing lawns was investigated and found that trees exposed to browsing developed tolerance and resistance traits (Fornara & du Toit 2007). According to Fornara & du Toit (2007) the tolerance traits are regrowth ability in shoots and leaves, branch growth rate, extensive tree branching and internal N translocation. Certain plants like *P. glandulosa* change the architecture when exposed to serve defoliation by growing short dense shoots, also grew few tall shoots to escape browsing (Martìnez & López-Portillo 2003). Oba (1998) studying *A. tortilis* recorded shorter shoots in the browsed trees compared to unbrowsed trees with higher forage production. The distribution of many short spiny stems tends to protect root, crown and genet survival and the development of one long stem is the way to escape browsing and allowing the plant to reproduce (Martìnez & López-Portillo 2003). Heavy browsing did not affect leaf:shoot ratio as it was similar in browsed and unbrowsed, this can be attributed to compensatory growth of shoots after clipping (Fornara & du Toit 2007).

2.3.2 Reproduction as affected by disturbance

There are two different views in plant ecology about herbivory. One view maintains that herbivory is detrimental to plant growth and reproduction, the other view states that plants benefit from being eaten as they respond by overcompensation (Paige & Whitham 1987). Reproduction may be defined as the ability of mature trees to flower and produce viable seeds, and for the seeds to disperse and germinate (Smit *et al.* 1996). Plants adapt to severe disturbance in different ways. Some plants have adopted the annual or short-lived perennial cycle, the feature of annuals is production of high biomass that helps the completion of their short life cycle and the maximizing of seed production (Grime 1977). Studies have shown that herbivory results in increased biomass production, but how seed production is related to biomass is not explicit (Paige & Whitham 1987). For the ruderal plants during stress time, more photosynthate is directed towards seed production, which [illegible] seed production at the expense of vegetative development (Grime 1977). Seeds of some woody plants have seasonal dormancy which prevents the development under unfavourable conditions (Smit *et al.* 1996).

Herbivores have the ability to reduce population survival, growth and reproduction of plants (Goheen *et al.* 2007). The impact of herbivory on plant reproduction in African savannas is still not well understood, but the big mammals have been shown to decrease survival growth of plants of genus *Acacia* (Goheen *et al.* 2007). In the study of reproduction in *Indigofera spinosa*, it was shown that clipping reduced reproduction causing clipped plants to remain in a vegetative state, and under heavy clipping; regrowth never reached maturity (Keya 1997). A study by Paige & Whitham (1987) supports the idea of overcompensation by plants that were eaten by animal here, plants that were browsed produced two inflorescences and those that were unbrowsed produced only one. A long-term field experiment demonstrated that herbivory in *A. drepanolobium* reduced seed biomass and increased spine length (Goheen *et al.* 2007). There is experimental evidence that mammalian herbivores kill and suppress growth of *Acacia*, this shows they can suppress *Acacia* reproduction (Goheen *et al.* 2007). Lowenberg (1994) showed that for *Sanicula arctopoides* when clipped in flowers, it will shift seed production to earlier or later maturing umbels. Repeated clipping of actual flowers resulted in the reduction of seed production relative to controls but single clipping of same intensity resulted full compensation (Lowenberg 1994).

2.4 Effects of debarking on trees

Certain browsers are known for their ability to debark the trees in tropical and temperate forests (van Rooyen & du Toit 1993; Faber & Thorson 1996; Gill 1992; Vospernik 2006; Gref & Stål 1994) Bark striping is common in forest of Britain where different species of deer are known to remove the bark (Gill 1992). The bark is usually removed from the main stem at a height of 50-100 cm from the ground but it is often removed from the root buttress (Gill 1992). This debarking causes the premature death of poplar, syringe, *Pinus sylvestris,* trees (Gill 1992; van Rooyen & du Toit 1993; Faber 1996; Welch & Scott 1998). The bark stripping has been recognized as the most serious damage that can occur in a forest as compared to browsing and fraying as the trees do not readily recover (Vospernik 2006). Bark damage by porcupines (*Hystrix africaeaustralis*) and African elephant (*Loxodonta africana*) can interact with fire to cause the mortality of *Dombeya rotundifolia* and *Burkea africana* (Yeaton 1988). Porcupines however, are known to gradually kill large *Cordyla africana* trees by removing only half the bark around their boles (Thomson 1974). In contrast, incomplete girdling, or bark stripping, does not usually kill many trees as the damaged bark can easily regrow (Gref & Stål 1994; Faber & Thornson 1996).

The species that have been studied, debarking of trees were done by the deer but the reason for the bark removal is not known; considering the selective ability of this species many factors would have to be investigated (Gill 1992). The moose that utilize the bark of *Pinus sylvestris*, the incidence of debarking increases during April and May. This period corresponds with the increase in fibre, potasium, starch and total carbohydrate and a decrease in crude protein, phosphorus and magnasium content (Faber 1996). With moose, on the one hand, bark stripping is a form of behavioral expression, not the search of high nutrient source (Faber 1996). Porcupines, on the other hand, utilize the syringa instead of the stinkwood that has smooth soft bark, and because the cork of syringa is high in phenolic compounds (van Rooyen & du Toit 1993). In Britain the removal of bark is common in winter, in spring and summer the bark can be easily be removed (Gill 1992). In the areas w[illegible]ark stripping has been studied it has been found that following factors are affecting the probability of bark removal, bark thickness, roughness, stem branchiness and ease of bark removal (Gill 1992).

Total girdling has proven to totally disrupt phloem transportation and soon depletes root photosynthates, resulting in death (Gref & Stål 1994). Bark-stripping reduces photosynthetic efficiency of cork-oak (Werner & Correia 1996). The large amounts of water lost through the stripped area affects water balance and, directly or indirectly, limits physiological processes (Werner & Correia 1996). Girdling of *Vitis vinifera* L has been used extensively to increase the size of the seedless grape but this resulted in fruit that are rich in carbohydrates as the result of interruption in the phloem transportation (Williams *et al.* 2000). This practice will decrease CO_2 assimilation, stomatal conductance and change the carbohydrate distribution (Williams *et al.*

2000). Werner & Correia (1996) have recorded low disturbance in water potential and stomatal conductance of bark stripped Quercus *suber L* in Portugal. The stomatal closure occurs as a short term response and recovery was quicker (Williams *et al.* 2000). The immediate response of poplar bark to girdling was an increase of deposition of starch and a rise in soluble-protein level which occurred in the bark tissue (Stepien & Sauter 1994).

It is understood that bark stripping has little effect on timber production as well as tree survival. This is supported by the findings of Welch & Scot (1998) where there was little increment in girth of trees. Complete bark-stripping i.e. girdling, is effective in killing the trees (Negreros-Castillo & Hall 1994). In the forest of *P. sylvestris*, light bark stripping is less detrimental than stem breakage, while severe striping can cause stem deformation, weaknesses in timber, development of stain and rot, as well as top breakage (Faber & Thornson 1996).

Chapter 3

Materials and Methods

3.1 Site location

The trial was conducted on Adelaide Experimental farm, 32°40'S, 26°17'E. The farm is in the Nxuba Local Municipality, which falls under the Amatole District Municipality of the Eastern Cape in South Africa (Figure 1). The experimental farm covers an area of 525 ha. It has been utilized by cattle and goats under controlled conditions for 30 years. The farm was taken away from commercial farmers by government 30 years ago because of degradation concerns from farming practices. The site selected was in the camp not part of a grazing experiment and was selected based on the basis of density and [illegible] the *A. karroo.* The site is situated at the foot of a mountain. On a flat area 600 m above sea level. The 1.62 ha area was fenced and divided into 18 plots.

3.2 Climate and soils

The Adelaide Experimental Farm is in the semi-arid region with the average rainfall of 486 mm.annum^{-1}. The area receives summer rainfall that peaks in November/December (Figure 2). Midsummer (December and January) droughts are common and the winters (May to August) are generally dry (Figure 2). Rainfall during the study period was as 516mm in 2004/05 and 597mm in 20005/06, above average for the area. The summers are hot and winters are cold with an average temperature of 18 °C (Figure 2).

The soil form of the site was derived from dolerite and is classified as of Herschell / Valsrivier (Dept. Agriculture Development 1991). Soil depth is about 600 mm, a clay content of about 15 – 35 %. The eroded topsoil might be due to herbivory, leaving the upper surface dominated by gravel.

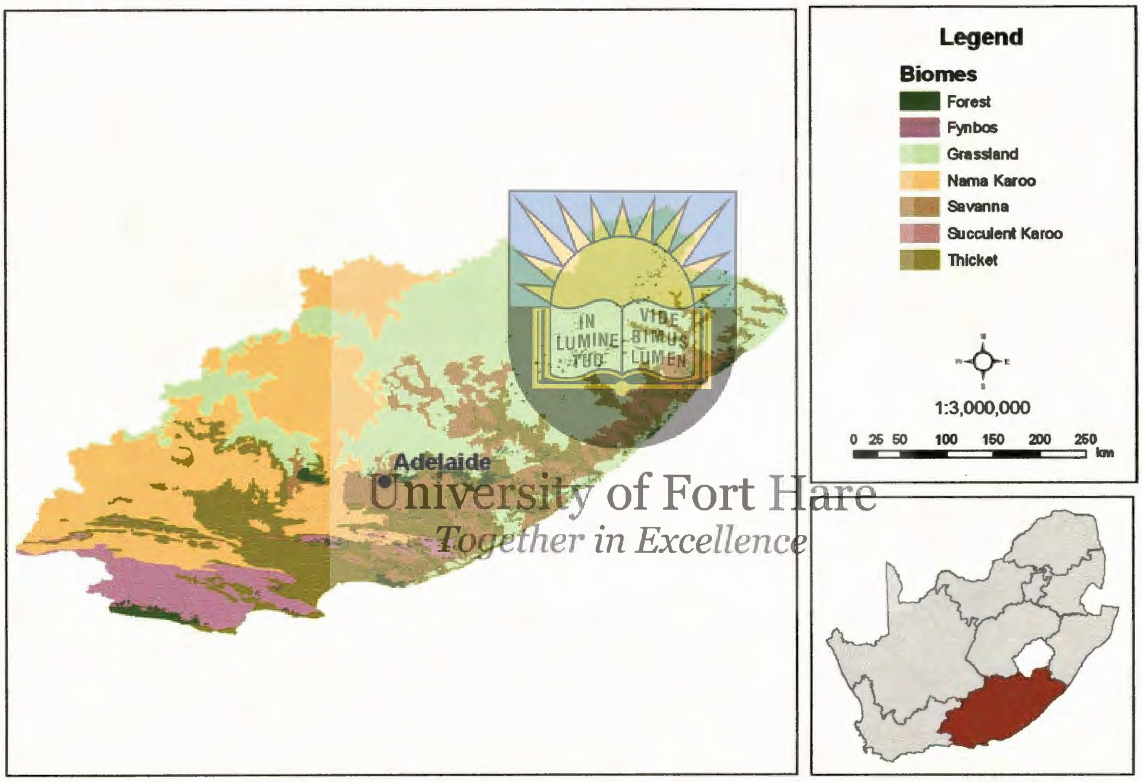

Figure 1: Biomes of the Eastern Cape (Source: Low & Robelo, 1996)

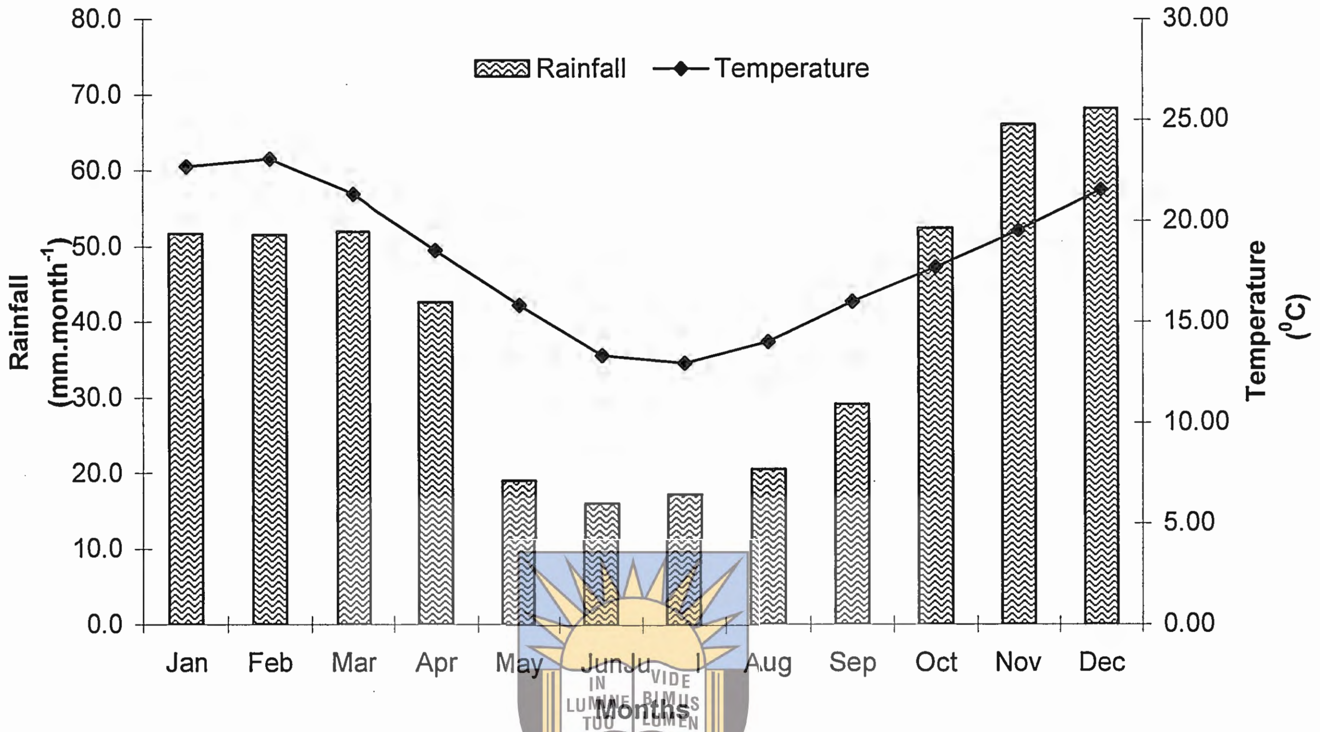

Figure 2: 30 years monthly rainfall and temperature averages for the Adelaide Experimental Farm.

3.3 Vegetation

The study area falls in the dry grass-bush communities of the Eastern Cape Province in the vegetation type known as the False Thornveld of the Eastern Cape (Acocks 1975). This veld type occurs in the region starting from Debe Nek in the east, Middledrift, Alice, Fort Beaufort, Adelaide and Bedford in the west (Acocks 1975). This veld type is part of the savanna biome (Low & Rebelo 1996) (Figure 1). The tree component on the Experimental Farm varies from open *Acacia karroo* to dense bushclumps of *Scutia Maytenus* and *Cassine* species (O'Reagain & Hobson 1989). Where the bushclumps exist they are formed by a variety of species which coexist in close proximity.

A. karroo is the pioneer bush species, and constitutes about 80 % of the vegetation on the farm and about 72 % of experimental area (Appendix A). The remainder of the bush component is made up of palatable bushes like *Ehritia rigida*, *Grewia occidentalis*, and unpalatable bushes like *Azima tetracantha* and shrubs such as *Lippia javanica*. The trees on the site were still young, 49 % of the bush community was ≤ 1m, only 11 % of trees >3 m in height (Appendix B). As the bushes are still young, 100% of the bush component was on the available height of goats. That is, they browse within 1.5 m height. Tree density in the plots varied from 583 to 3000 trees per hectare. The general tree density of the site was 1920 trees per hectare.

The herbaceous sward consists of perennial tufted grasses, including *Seteria neglecta Panicum maximum, Sporobolus frimbiatus* and *Cynodon dactylon*. The decreaser grasses constituted 37.11 % of herbaceous layer represented by *S. neglecta, P. maximum* and *P. stapfiunum* (Appendix C). The herbaceous cover of soil varied from a minimum number of 11 strikes and a maximum of 36; average percentage cover was 21 % (Appendix D).

3.4 Treatments

The experimental design was a simple randomized block design with six treatments. Each treatment was replicated three times in 30m x 30m plots. The plots were divided by a fence to control browsing. In each plot all the trees that were within the required height class were marked by numbered metal tags. The treatments were allocated to a plot randomly (Figure 3).

NORTH

DBS 1	DBS 2	DNB 3			
DBR 4	NDBS 5	NDBR 6	NDNB 7		
DBR 8	NDBR 9	DBR 10	NDBR 11	DNB 12	DBS 13
			NDNB 14	NDNB 15	NDBS 16
				NDBS 17	DNB 18

Figure 3: Diagrammatic representation of experimental layout and treatment

Two treatments were investigated during this study the effects of defoliation and debarking. The treatments were applied in the experiment as treatment combinations that derived from three levels of debarking and two levels of defoliation. The levels of debarking are (i) no debarking, (ii) bark stripping and (iii) basal ringing. The defoliation was divided into (i) no defoliation and (ii) heavy defoliation. The different levels of treatments were mixed to give six treatment combinations. The combinations are as follows:

1.No defoliation + No debarking (NDNS) 2.No defoliation + Bark stripping (NDBS) 3.No defoliation + Basal ringing (NDBR) 4.Defoliation + No debarking (DNS) 5.Defoliation + Bark stripping (DBS) 6. Defoliation + Basal ringing (DBR)

The plots were heavily browsed by 6 virgin does and 6 bucks. The goats were divided equally into two groups according to the sex. All defoliation plots were browsed by goats for two weeks. The goats where moved out when they had utilized about 85% of the leaf material within 1.5 m. The goats were move out of the plot once they move around the plot without browsing or once they grazed more that they browsed. During the first week 12 goats were used to browse. At the end of the first week the bucks were again moved into the experiment plots to apply more pressure on the debarked and defoliated trees. Debarking was carried out on the first week for three days in all nine plots.

According to Scogings & Macanda (2005) the most susceptible trees to debarking are the trees at a height 1-3 m and with a basal circumference ≤ 31 cm. The trees that were used for the experiment were of height class of 1.5 m to 2.5 m, this being the dominant height class in the experimental site. Trees of the required height were identified and marked in the experimental site in all the plots. Six trees were selected randomly and marked using wooden pegs. The debarking was done manually using a knife; this was due to management considerations. The trees were debarked from ground level up to 50 cm above the ground and this was done on the main stem of the tree (Figure 4). For bark stripping, 30 cm long bark strip was removed in the north-facing side of the stem (Figure 4). The width of the scars varied according to the stem thickness. The rule of thumb was that only half of the stem bark could be removed for bark striping treatment. For bark ringing, the length of the scar was 15 cm, achieved by removing the bark around the stem (Figure 4).

1. Trees first day of treatment application 2. Goats browsing in the trial

3. Bark stripped tree with multi stem 4. Heavily defoliated trees

5. Basally ringed and defoliated tree 6. No defoliation no debarking plot

Figure 4: Photographs showing different treatments and application on trees

The treatments were applied immediately after the first spring rain of 2004. After the rains, the trees were afforded the opportunity to fully grow, after the treatments were applied (Figure 4). Since early growth of plants is dependent mainly on the plant energy reserve, heavily damaging the tree at this stage could weaken the tree. Teague & Walker (1988) found that *A. karroo* is very sensitive to browsing during early flush-phenophase when carbohydrate reserves are low.

The parameters that were measured were growth, physical defense, reproduction and forage quality. All the parameters were measured on current season shoots that were ≤ 3 mm diameter. In each tree, four shoots within 1,5m above the ground were selected randomly. The shoots were selected from north, east, south and west sides of the tree. For each shoot selected the following variables were measured shoot length, basal internode length, length of longest spine. On each side of the tree, the largest bunches of seed pods were randomly selected and the number of seed pods in that batch was counted. From that batch, the longest pod was selected and the number of seeds inside was counted. The numbers of shoots ≤ 3 mm within 1.5 m were counted on each tree. All these variables were measured at the end of the growing seasons on the last week of April in 2005 and 2006. After the treatment application in October 2004 the trial was closed for browsing and grazing until June 2006.

Leaf samples were collected for forage quality analysis. The leaf samples were collected in the period 8h00 to 10h00. Sampling was done at the end of growing season in the first week of May. The samples were air dried indoors at room temperature for a period of 5 days. After the samples were dry they were ground through 1mm sieve. Grounded samples were then taken to the laboratory where they were analyzed for Acid Detergent Fibre (ADF), Neutral Detergent Fibre

(NDF), Acid Detergent Lignin (ADL), Acid Detergent Cellulose (ADC), Nitrogen, Phosphorus, and Hemicellulose was determined from the samples (Goering & van Soest 1970; AOAC 2004). Condensed tannin were analysed by acid butanol assay method (Porter *et al* 1986). The method uses 50% methanol and 5% hydrochloric acid butanol. In the method the pine bark was used as the calibration standard.

3.5 Statistical analysis

The data was analyzed for induced response of the *A. karroo*. Before the data was analysed for the effect of treatment it was tested for normality. The normality test that was performed in the data is Shapiro-Wilk's test (SPSS 2006). Other variables were normally distributed and others were not, those that were not could not be transformed as they could not change even though transformation was performed (Appendix E). The variables that are not normally distributed are number of pods, seeds per pod, phosphorus, ADF, ADL and ADC. The data was analyzed by parametric and non-parametric methods. All the values that were normally distributed were analysed with a two-way analysis of variance (ANOVA) using General Linear Model (GLM). Those that failed normality test were analysed with Kruskal-Wallis test SPSS (2006). Factors used in the analysis of data were defoliation, debarking and season. Pearson correlation was used to determine the relationship between different parameters (SPSS 2006).

Initial tree size was used as the co-variant; variable that represent tree size i.e. the tree height and basal circumference. The values of the trees before the treatments were applied were used for the purpose of covariant. The impact of treatments on tree size was assessed by analysis of the difference between initial data and post treatment data. The actual difference and percentage change were analyzed by two-way ANOVA. The physical defense was the spine length in relation to internode length and cell wall contents. Chemical defense was the concentration of condensed tannins and abundance of fibre. The means of the variables were tested for difference using Bonfferroni test. Growth parameters are number of shoots, shoot length, tree height and basal circumference. The forage quality of the leaves will be determined by regression and Pearson's correlation between nutrients i.e. nitrogen/phosphorus and condensed tannins, and cell wall constituents. The induced responses of all the variables were analyzed by two-way ANOVA, using tree size and year as the covariates. The model for the ANOVA:

$$Y_{ijklmn} = \mu + a_{ijk} + b_{ijk} + C_{ijk} + D_{lmn} + E_{ijk} + (C_{ijk} * D_{lmn}) + (C_{ijk}*E_{ijk}) + (D_{lmn}*E_{ijk}) + (C_{ijk}*D_{ijk}*E_{ijk}) + e$$

Y_{ijklm} = effect of treatment on variables, μ = Intercept, a_{ijk} = tree height, b_{ijk} = basal circumference, C_{ijk} = level of defoliation, D_{lmn} = level of debarking, E_{ijk} = season, $C_{ijk} * D_{lmn}$ = level of defoliation * level of debarking, $C_{ijk}*E_{ijk}$ = level defoliation * season, $D_{lmn}*E_{ijk}$ level of debarking*season, $C_{ijk}*D_{ijk}*E_{ijk}$ = level of defoliation*level of debarking*season and e = error

Chapter 4

Results

4.1 Growth factors

After two seasons, defoliation did not significantly affect tree height ($p > 0.05$) while debarking was significantly affected ($p < 0.01$). The defoliated and bark stripped trees did not change in height but the basally ringed trees the height was reduced, their canopies died and the trees coppiced from the based. The mean reduction in tree height of the basally ringed trees was -1 m. (Table 1). A combination of both factors, debarking and defoliation, had an effect on height ($p < 0.05$), the mean change for defoliated and basally ringed trees was -0.76 m, and -1.2 m for no defoliation and basal ringing (Table 1). Basa[illegible]ees are kept available to browsers, in the vegetative stage for longer.

Debarking had an effect on basal circumference ($p < 0.05$) while defoliation did not ($p > 0.05$). Basal ringing reduced basal circumference by 3 cm, average growth of non stripped trees was -0.3 cm, and while bark stripped trees increased their basal circumference by 3 cm (Table 1). The combination of both factors did not significantly change basal circumference ($p > 0.05$) therefore there was no interaction between treatments. The reduction of height and basal circumference is the result of canopy death in all basally ringed trees. Basal ringing had resulted in serious damages in tree size as it actually reduced it in all aspects. The basal ringing completely killed 4 trees (7 %).

The number of shoots was significantly affected by defoliation (p = 0.03). The number of browseable shoots within 1.5 m height was significantly increased by defoliation; the defoliated trees had an average of 124 shoots compared to 105 of non defoliated trees (Table 2). In the debarked trees the average number of shoots was significantly affected by debarking (p = 0.00). Basal ringing significantly decreased the number of shoots produced by trees; basally ringed trees produced an average of 85 shoots and those non debarked producing 131 shoots (Table 2). Bark stripped trees were not significantly different with non debarked trees. The combination of defoliation and debarking had no effect in shoot numbers (p > 0.05). The season had and effect in number of shoots produced (p = 0.03). The first season (2005) after treatment application had a significantly lower number of shoots than second season (2006) (Figure 5). The numbers of shoots produced did not vary because of the treatment combination; the variation on the means was as the results individual treatments (Tab[illegible]). The defoliated trees produced more shoots than the non defoliated trees, showing that defoliation is beneficial to the trees. Basal ringing in these trees reduced growth as the number of shoots produced in both seasons was low in these trees. The season and treatment did not have significant effect on number of shoot produced (p > 0.05).

Shoot length was not affected by debarking and defoliation (p>0.05), however, basally ringed trees had longer shoots than other classes of debarking with a mean of 23 cm; 20 cm and 19 cm for bark stripped and non stripped trees respectively. The longest shoots were found on coppice growth. Also season after treatment application did not change shoot growth.

Table 1: Change in tree height and basal circumference ± SE during two seasons (2004/5 and 2005/6).(±SE).

Treatments & Treatment Combination	**Height (m)**		**Basal Circumference (cm)**	
	Difference in Height	**Percentage Change**	**Difference in Circumference**	**Percentage Change**
Debarking				
Basal Ringing	-1.0(0.11) ^{a}	-50.8(5.80)^{a}	-3.2(1.14)^{a}	-20.9(6.78)^{a}
Bark Stripping	0.2(0.12)^{b}	[illegible]1.6(6.56)^{b}	3.2(1.29)^{b}	21.5(6.78)^{b}
No Debarking	0.2(0.12)^{b}	[illegible].9(6.30)^{b}	-0.4(1.24)^{ab}	-1.8(6.78)^{ab}
Defoliation				
Defoliation	-0.2(0.09) ^{a}	[illegible]1.3([illegible]8)^{a}	-0.2(0.92)^{a}	-1.8(5.62)^{a}
No Defoliation	-0.2(0.09) ^{a}	-[illegible].5(4[illegible])^{a}	0.05(0.92)^{a}	0.9(5.62)^{a}
Defoliation + Debarking				
Defoliation + Basal Ringing	-0.8(0.16)^{a}	-39.9(8.03)^{a}	-2.3(1.53)^{a}	-16.2(9.59)^{a}
Defoliation + Bark Stripping	0.3(0.16)^{a}	[illegible].2(8.03)^{a}	1.0(1.53)^{b}	5.5(9.59)^{b}
Defoliation + No Debarking	0.7(0.16)^{a}	3.7(8.03)^{a}	0.5(1.53)^{b}	3.7(9.59)^{b}

^{a,b,c} Mean values with different superscripts within the same column are significantly different ($P < 0.05$)

Table 2: Effects defoliation and debarking on physical response of *A. karroo*.(±SE)

Treatments & Treatment Combination	No Shoots	Shoot length	Internode Length	Spine Length	Number of Pods	Number of Seeds/pod
Debarking						
Basal Ringing	85.26(7.139)^{a}	21.92(1.053)^{a}	1.15(0.06)^{a}	1.95(0.196)^{a}	0.41(0.222)^{a}	0.81(0.361)^{a}
Bark Stripping	127.70(8.094)^{b}	21.11(1.194)^{a}	1.37(0.068)^{a}	2.98(0.222)^{b}	2.91(0.252)^{b}	4.52(0.409)^{b}
No Debarking	131.29(7.763)^{b}	19.58(1.145)^{a}	1.24(0.065)^{a}	3.00(0.213)^{b}	1.66(0.241)^{c}	3.07(0.392)^{b}
Defoliation						
Defoliation	124.22(8.814)^{a}	21.91(0.851)^{a}	1.32(0.048)^{a}	2.83(0.158)^{a}	1.75(0.179)^{a}	2.86(0.291)^{a}
No Defoliation	105.28(8.814)^{b}	19.83(0.881)^{a}	1.19(0.048)^{a}	2.46(0.158)^{a}	1.57(0.179)^{a}	2.74(0.291)^{a}
Defoliation + Debarking						
Defoliation Basal Ringing	98.69(10.703)^{a}	23.81(1.579)^{a}	1.26(0.09)^{a}	2.14(0.294)^{a}	0.13(0.333)^{a}	0.35(0.541)^{a}
Defoliation Bark Stripping	136.69(12.888)^{a}	21.99(1.961)^{a}	1.46(0.108)^{a}	3.35(0.354)^{a}	3.20(0.401)^{b}	4.51(0.651)^{b}
Defoliation No Debarking	137.27(10.341)^{a}	19.94(1.526)^{a}	1.24(0.086)^{a}	3.01(0.284)^{a}	1.94(0.321)^{b}	3.71(0.523)^{b}

^{a,b,c} Means with different superscripts within the same column are significantly different ($P < 0.05$)

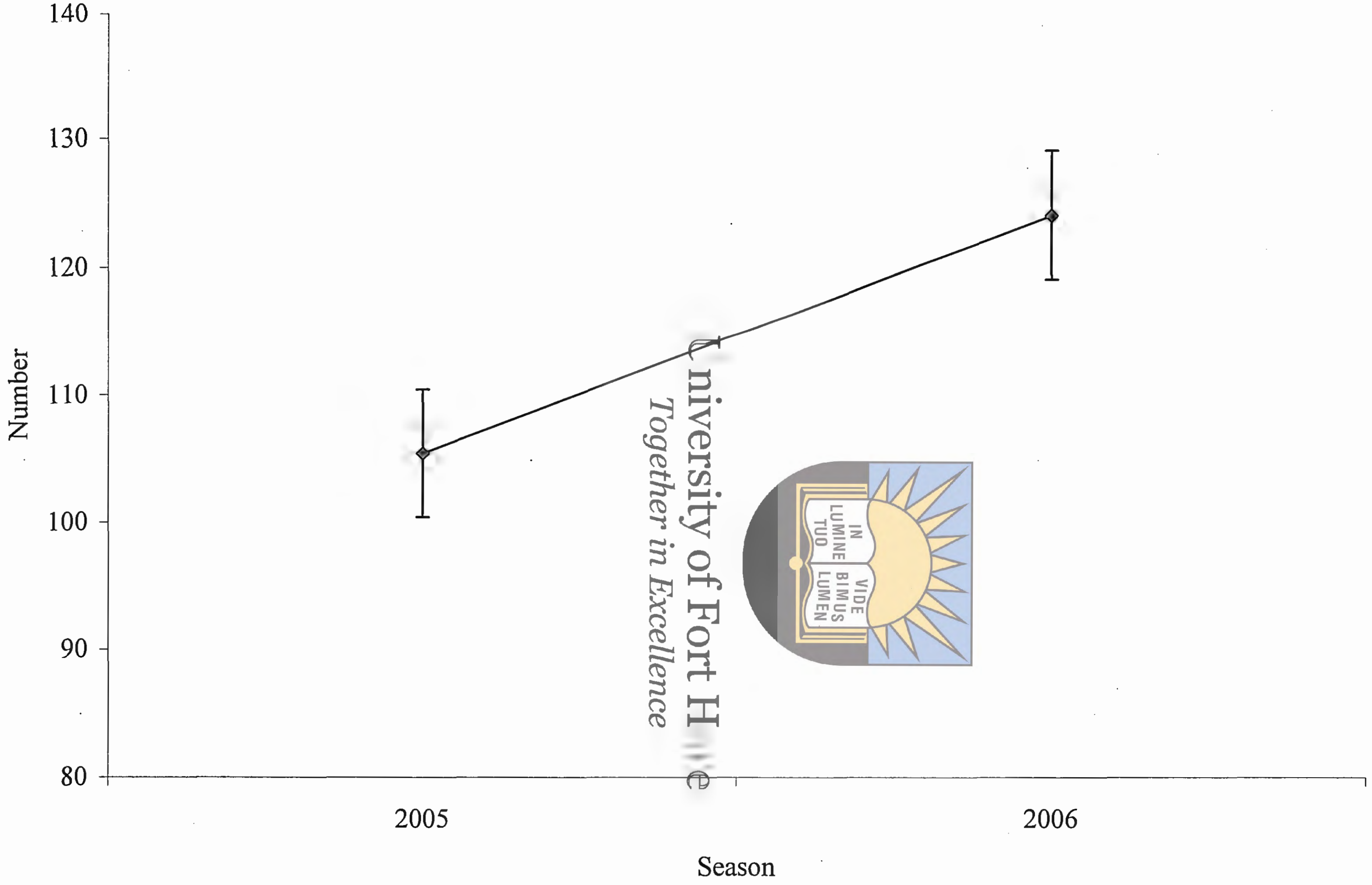

Figure 5: Number of shoots of *A. karroo* produced in two growing seasons. Error bars denote SE

4.2 Reproductive factors

Defoliation had no significant effect ($p > 0.05$) on the reproductive ability measured by number of seeds per pod and number of pods respectively. Defoliated trees had equal numbers (2) of pods with those not defoliated; and equal number of seeds per pod (3) (Table 2).

Number of pods and number of seeds per pod in the first season were counted on the dying canopy and on the second season on the new growth. Debarking affected seed and pod production significantly ($p < 0.00$). Basal ringing resulted in the lowest number of pods of (0.4) and seeds per pod (0.8) (Table 2). The numbers of pods on basally ringed trees were significantly lower from both levels of debarking while between bark stripping and no stripping there was no significant difference. Seeds per pod on basally ringed trees were significantly lower than the other levels of debarking while stripping was not different from no stripping. Bark stripping promoted seed production as it had the highest number of pods (3) and seeds per pod (4) amongst the different treatments (Table 2). There was no significant difference due to combination of treatments (debarking and defoliation) on reproduction ($p > 0.05$). Time since treatment application did not influence pod and seed production over the period of two seasons. The basally ringed trees were relying on coppice growth and remain in vegetative state for longer. Basal ringing prevents trees to rich maturity so that they can produce seeds to increase tree population.

4.3 Physical defense

The internode length was not affected by both defoliation and debarking ($p > 0.05$). There was no difference in internode length amongst the treatments; therefore, numbers of spines per unit, length were not different between the levels of defoliation and debarking. Spine length was not affected by defoliation ($p > 0.05$). Defoliated trees did not change their physical defense investment as is evidenced by no significant change in length and numbers of spines per unit length.

Debarking had a significant effect on the spine length ($p < 0.05$). Debarked trees had the shortest spine (2 cm) compared to non stripped trees (3 cm) (Table 2). The basally ringed trees spine length was not different from those of stripped trees but significantly lower from those of non stripped (Table 2). There was no interaction between debarking and defoliation on internode and spine length ($p < 0.05$). The general trend was that basally ringed trees had shorter spines compared to non stripped trees (Table 2). This means that mature trees are better armed against browsers than young trees. The spine length to internode length ratio for the debarked trees is higher than that of no debarked trees. Internode length ($p = 0.049$) and spine length ($p = 0.275$) did not change over seasons after treatments. Therefore physical defense did not increase over the period of two years after treatment application.

4.4 Relationship between tolerance variables

Tree height and basal circumference where significantly correlated ($p < 0.01$; $\rho = 0.66$) (Table 3); an increase in tree height occured concurrently with basal circumference. Tree height was positively related to number of shoots produced ($p < 0.01$; $\rho = 0.46$). Number of shoots produced were also positively related to basal circumference ($p < 0.01$; $\rho = 0.60$). Numbers of shoots produced is strongly related to tree size, coppicing trees have fewer numbers of shoots than bigger trees. The bigger trees produced more shoots after defoliation than smaller trees. Shoot length was not significantly related to any variable but it had weak negative relationship with number of shoots ($p > 0.05$; $\rho = -0.15$).

The relation between seeds produced per pod and number of pods was positively related and was significant ($p < 0.01$; $\rho = 0.971$) (Table 3). The linear regression model of number of seeds per pod and pods were used to calculate the number of seeds produced with the equation $y = 1.385x + 0.5003$, this has high coefficient of determination ($p < 0.01$; $R^2 > 0.90$) (Figure 6). Number of shoots were positively and significantly related to number of pods and seeds ($p < 0.01$) and ($\rho = 0.6$). Tree height was positively correlated to number of seeds and pods ($p < 0.01$; $\rho = 0.6$ and 0.5 respectively). The tree size had a very good relation with the numbers of pods produced ($p < 0.01$, $R^2 > 0.90$ tree height and $R^2 = 0.80$ basal circumference) (Figure 6). The linear regression model produced by relationship were used to estimate the number of pods using the equation $y = 2.8752x - 3.7965$. Shoot length had poor negative correlation with reproductive parameters, but this was not significant ($p > 0.05$) (Table 3). This means pods are produced at the expense of shoot length. The growth factors and tree size are in positively related to plant reproduction. This relationship means that bigger trees produce more seeds than young trees. The number of seeds and pods are closely related and pods related to growth parameters, therefore, reproduction does not take place at the expense of growth or vice versa. The younger trees were producing fewer pods and seeds; and thus reduce recruitment of new plants.

Table 3: Pearson's correlation table of growth and physical defense parameters in *A. karroo* trees (n = 36)

Parameters	Tree Height (m)	Basal Circumference (cm)	Number Shoots	Shoot Length (cm)	Internode Length (cm)	Spine Length (cm)	Number Pods	Number Seeds/Pod
Tree Height (m)		0.663*	0.464*	0.05^{ns}	0.393**	0.494*	0.540*	0.576*
Basal Circumference (cm)			0.598*	0.01^{ns}	0.409**	0.427**	0.633*	0.639*
Number of Shoots				-0.15^{ns}	0.416**	0.504*	0.599*	0.597*
Shoot Length (cm)					0.552*	0.412**	-0.21^{ns}	-0.24^{ns}
Internode Length (cm)						0.760*	0.340**	0.351**
Spine Length (cm)							0.368**	0.378**
Number of Pods								0.971*
Number of Seeds / Pod								

^{ns} not significant $p > 0.05$; * significant at $p < 0.05$; ** significant at $p < 0.01$

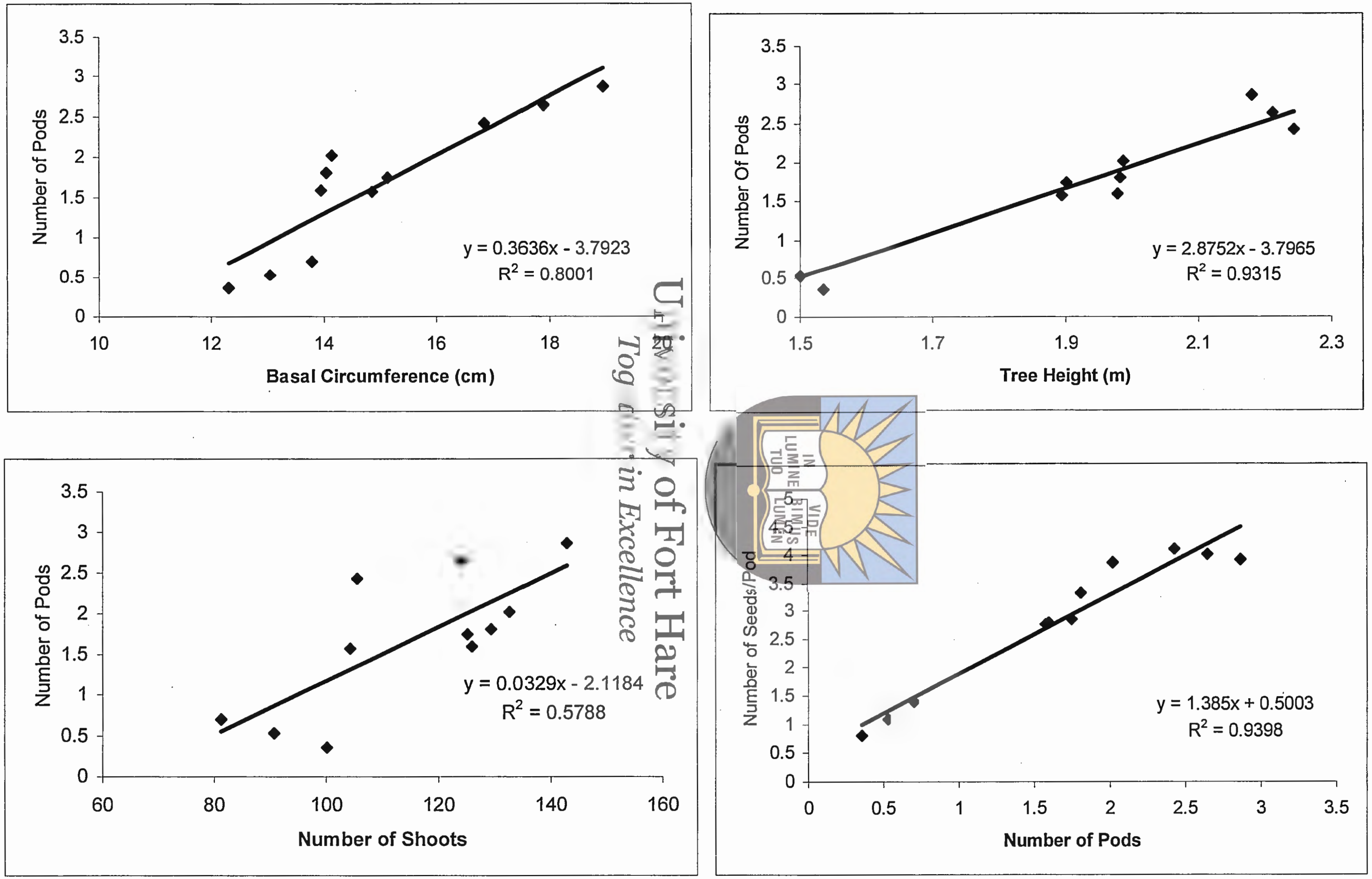

Figure 6: Regression between the tolerance parameters of *A. karroo* trees.

4.5. Forage quality

Phosphorus and nitrogen were the nutritional elements that were analyzed from the leaf samples. The phosphorus content of the leaves was not significantly affected by the debarking and defoliation ($p > 0.05$) (Table 4). Defoliation did not have a significant impact on nitrogen content ($p > 0.05$). Nitrogen was significantly reduced by basal ringing ($p = 0.03$). Nitrogen content of basally ringed (1.6%) trees was significantly lower than that of bark stripped (1.96%) and non debarked (1.8%) (Table 4). The allocation on nutrients is not influenced by disturbance.

Spring defoliation had no effect on the fiber content of the trees ($p > 0.05$). The means of both NDF and ADF are almost equal to those of the non defoliated plants (Table 4). The debarking had significant effect on NDF ($p < 0.01$) and ADF ($p = 0.036$). Basally ringed trees had a significantly higher content of NDF (23%) compared to stripped trees (21%) and non stripped trees (21%) (Table 4). Basal ringing increased their production of ADF as they had significantly higher content (22%) than both stripped and non debarked trees (21%) (Table 4). Generally the fiber content of leaves was higher on the coppice growth than in the old trees. There was no interactive effect of both factors on fiber contents ($p > 0.05$). NDF and ADF have increased from the first to second season ($p = 0.00$ and 0.036 respectively). NDF was lower in the first season than in the second season (19% and 23%), same pattern was evident for ADF (20% and 22%) (Figure 7). The increase of fiber contents was not proportional from the first to the second season, NDF increased at higher rate than ADF (Figure 7). There was a no significant interaction between defoliation and season for fiber contents.

The ADL content was not altered by both defoliation and debarking ($p>0.05$). Defoliation had no significant effect on ADC contents ($p>0.05$) and debarking had a slight effect ($p = 0.049$). Basally ringed trees produced higher content of lignin than stripped and non debarked trees (Table 4). The interaction between debarking and year was not significant ($p = 0.05$). Basally ringed trees produced more lignin in their second season of growth (Figure 7). Production of lignin resulted in reduction in ADC (Figure 7). ADC content in the second season was less than in the first season ($p = 0.02$) (Figure 7).

Generally defoliated trees had higher tannin concentration, however, the difference was not significant ($p > 0.05$) (Table 4). Debarking also did not significantly affect condensed tannin concentration ($p> 0.05$). In the debarking levels, basally ringed trees had lower tannin concentration (159 mg/g) as compared to bark stripped (183 mg/g) and non debarked (164 mg/g) (Table 4). The time since treatment show significant difference ($p = 0.027$). Trees in the first season had higher tannin concentration than in the second season (182 mg/g and 155 mg/g) (Figure 9). There was no significant interaction between the treatments; however, there was a significant interaction ($p < 0.05$) between the season and debarking. In the first season basally ringed trees had lower levels (143 mg/g) while in the second season they had the highest level 174 mg/g (Figure 10). Shoots from bark stripped trees had highest concentration of tannin in the first season (212 mg/g) and in the second season it was lower (155 mg/g) (). Bark stripped trees and defoliated trees responded to disturbance in the first season by producing more condensed tannin. In the absence of disturbance in the second season resulted in the relaxation of defense. The new growth sustained its defense strategy for longer periods than in the older trees.

Table 4: Effect of defoliation and debarking on forage quality variables of the *A. karroo* trees. (±SE)

Treatments	Phosphorus (%)	Nitrogen (%)	NDF (%)	ADF (%)	ADL (%)	ADC (%)	Condensed Tannin (mg/g)
Debarking							
Basal Ringing	0.09(0.005)^{a}	1.60(0.088)^{a}	22.95(0.411)^{a}	22.97(0.435)^{a}	9.75(0.316)^{a}	14.86(0.418)^{a}	159.78(10.1)^{a}
Bark Stripping	0.11(0.006)^{a}	1.96(0.099)^{b}	20.61(0.466)^{b}	20.81(0.494)^{b}	8.58(0.359)^{a}	13.75(0.474)^{b}	183.70(11.452)^{a}
No Debarking	0.10(0.006)^{a}	1.84(0.095)^{b}	21.10(0.447)^{b}	20.86(0.473)^{b}	9.02(0.344)^{a}	13.34(0.454)^{b}	164.50(10.984)^{a}
Defoliation							
Defoliation	0.01(0.004)^{a}	1.75(0.071)^{a}	21.51(0.332)^{a}	21.69(0.352)^{a}	9.20(0.256)^{a}	13.86(0.337)^{a}	177.70(8.157)^{a}
No Defoliation	0.10(0.004)^{a}	1.84(0.071)^{a}	21.60(0.332)^{a}	21.41(0.352)^{a}	9.03(0.256)^{a}	14.10(0.337)^{a}	160.49(8.157)^{a}
Defoliation + Debarking							
Defoliation + Basal Ringing	0.10(0.008)^{a}	1.54(0.131)^{a}	23.74(0.616)^{a}	22.50(0.653)^{a}	9.67(0.474)^{a}	14.12(0.626)^{a}	155.13(15.143)^{a}
Defoliation + Bark Stripping	0.11(0.009)^{a}	1.78(0.158)^{a}	19.60(0.742)^{a}	21.10(0.786)^{a}	8.75(0.571)^{a}	13.63(0.754)^{a}	200.19(18.234)^{a}
Defoliation + No Debarking	0.10(0.007)^{a}	1.92(0.127)^{a}	21.20(0.595)^{a}	21.45(0.631)^{a}	9.18(0.458)^{a}	13.83(0.605)^{a}	177.78(14.631)^{a}

^{a,b,c} Means with different superscripts within the same column are significantly different ($P < 0.05$)

NDF – Neutral Detergent Fibre, ADF - Acid Detergent Fibre, ADL – Acid Detergent Lignin, ADC – Acid Detergent Cellulose

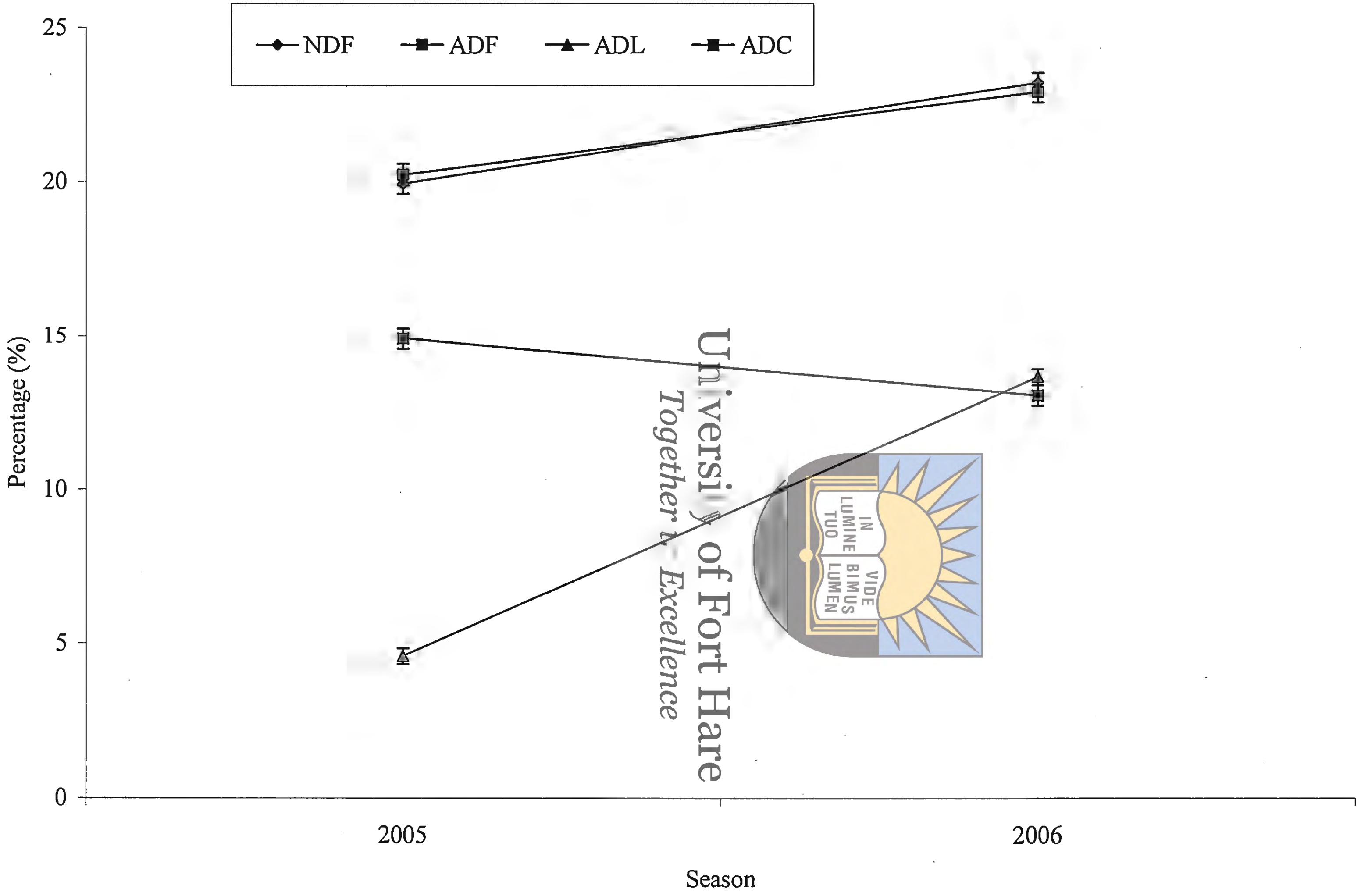

Figure 7: Percentage composition of cell wall contents of *A. karroo* leaves over two seasons

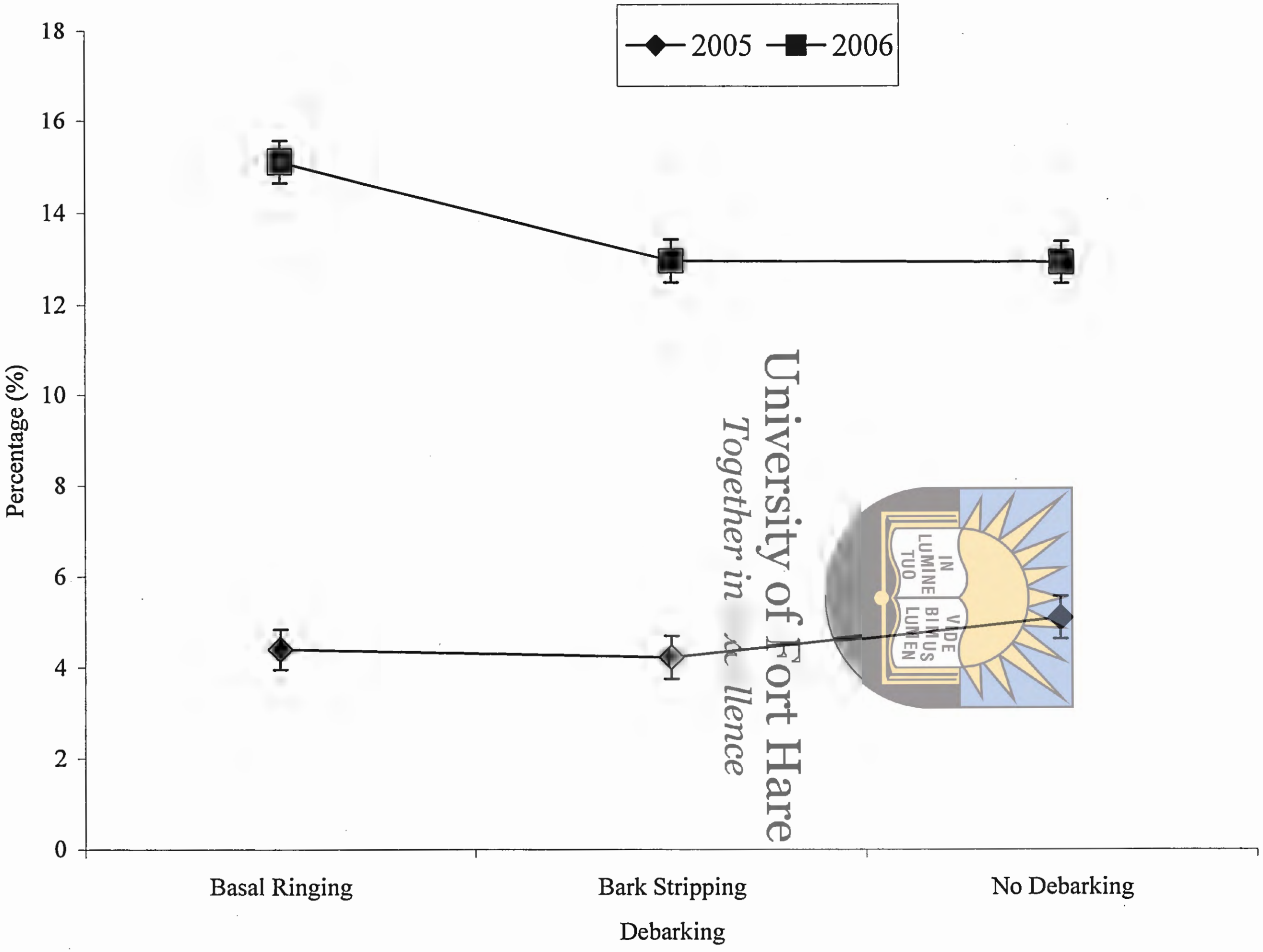

Figure 8: Percentage composition of ADL in the *A. karroo* trees for two seasons

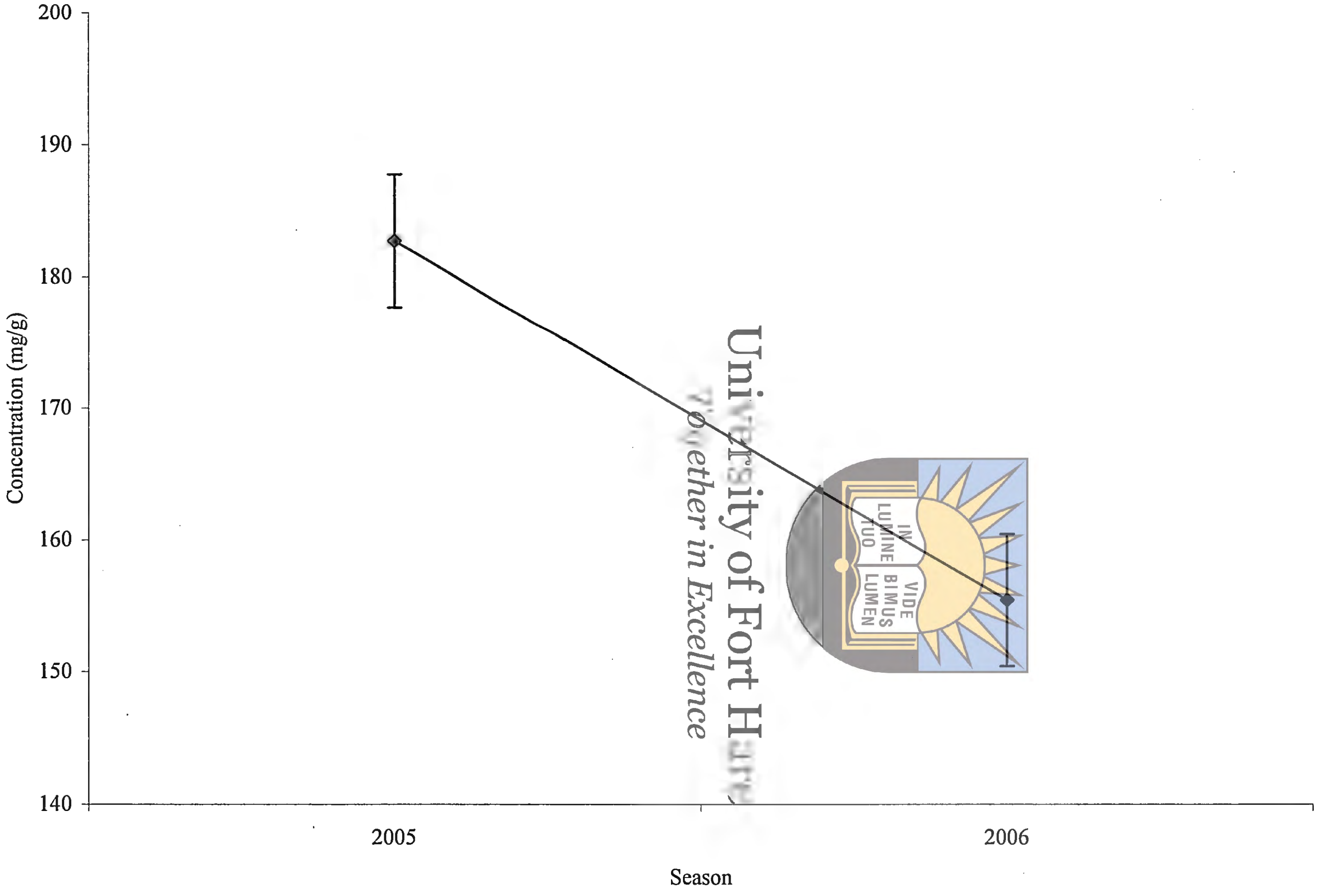

Figure 9: Average condensed tannin concentration of *A. karroo* leaves over two seasons. Error bars denote SE.

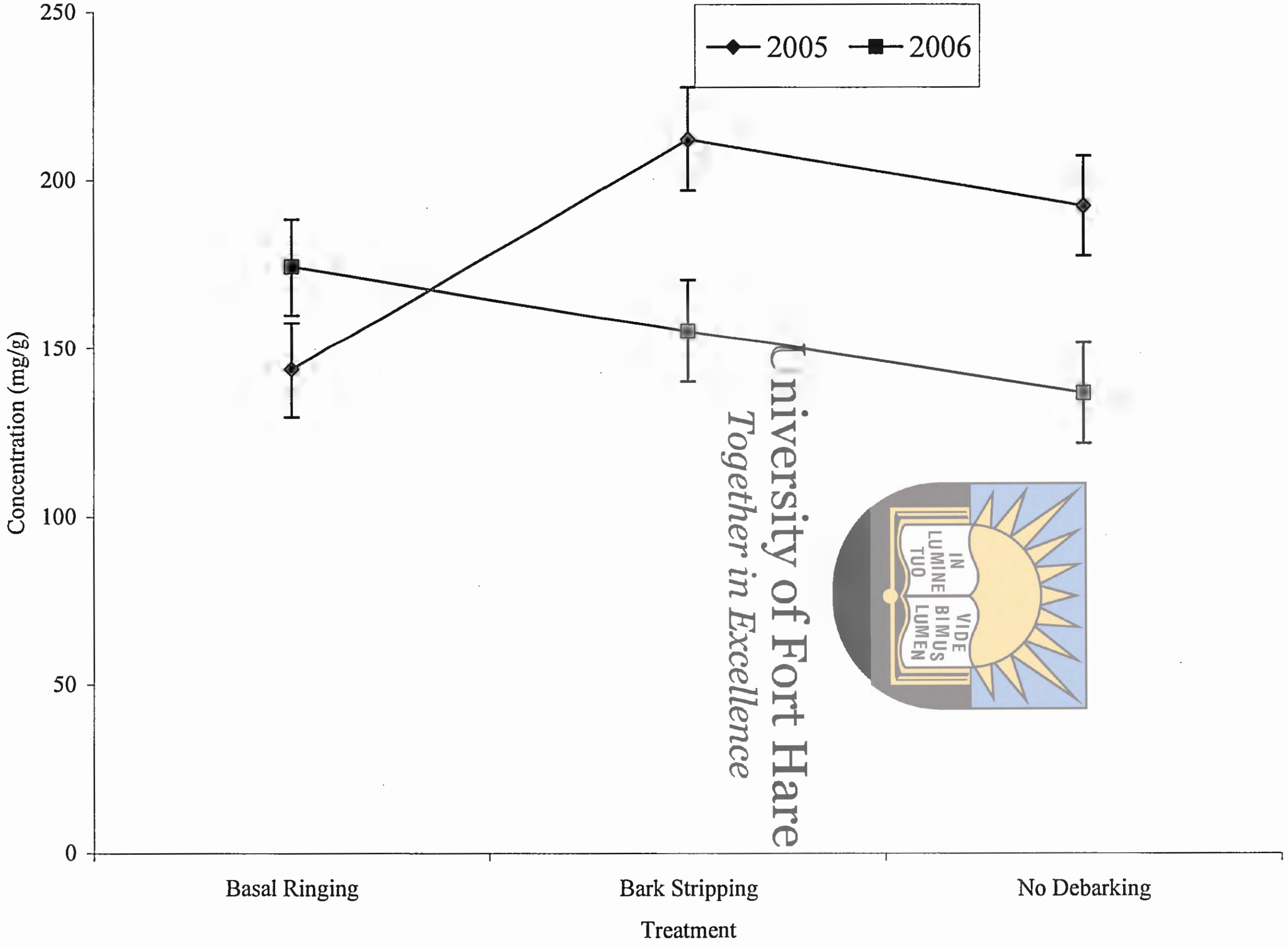

Figure 10: Condensed tannin concentration interaction between the levels of debarking and season in the *A. karroo* trees.

4.6 Forage quality variables correlations

Phosphorus content of the leaves is highly correlated with the nitrogen and this relationship is significantly related ($p < 0.01$; $\rho = 0.864$) (Table 5). NDF was significantly negatively correlated to nutrients and the relationship was negative ($p = 0.05$; $\rho = -0.4$) (Table 5). ADF was significantly negatively correlated to nutrients (P: $p < 0.01$; $\rho = -0.5$; N: $p < 0.01$; $\rho = -0.6$) (Table 5). Fiber increases with decrease in levels nutrients, thus coppice growth leaves were less digestible than new leaves of older trees, as evidence by higher NDF content. The increase of fiber in forage results in the decrease in forage quality. Condensed tannin had no significant correlation with the nutrients. Condensed tannin concentration was independent of any nutrient. Hemicellulose only showed significant correlation with the nitrogen ($p < 0.05$) but no significant relation with phosphorus (Table 5).

Cell wall contents showed strong positive correlations (Table 5). NDF had a strong positive correlation with the ADF ($p < 0.05$; $\rho = 0.553$) (Table 5). The fiber contents (NDF and ADF) of forages increase concurrently. NDF was positive correlated to the ADC ($p < 0.05$; $\rho = 0.7$). Increase in cell wall contents renders forage less digestible. NDF was negatively correlated to condensed tannin ($p < 0.05$; $\rho = 0.546$). Linear regression model of NDF and condensed tannin showed strong relation ($p < 0.05$; $R^2 > 0.70$) (Figure 11). The investment of young trees to defense was low, they survive disturbance by increasing fiber. Young trees invested in fiber rather than tannins as the strategy to survive disturbance. The ADF was positively and significantly correlated to ADL ($p < 0.01$; $\rho = 0.756$) and hemicellulose was negatively correlated to ADF ($p < 0.01$; $\rho = -0.444$). The ADL was significantly correlated to the ADC ($p < 0.05$; $\rho = -0.378$) and ADC was negatively correlated to hemicellulose ($p = 0.01$; $\rho = -0.428$).

Condensed tannin was not significantly correlated to ADL and ADC of the leaf ($p > 0.05$) (Table 5).

Table 5: Pearson's correlation table of forage quality parameters of *A. karroo* trees (n=36)

Parameters	P(%)	Nitrogen (%)	NDF (%)	ADF (%)	ADL (%)	ADC (%)	Condensed Tannin (mg/g)	Hemicellulose (%)
P (%)		0.864**	-0.401*	-0.515**	-0.462*	-0.05 ^{ns}	0.194 ^{ns}	0.191 ^{ns}
TKN (%)			-0.401*	-0.619**	-0.583**	0.03 ^{ns}	0.201 ^{ns}	0.343 ^{ns}
NDF (%)				0.553**	0.675**	-0.29 ^{ns}	-0.546**	0.169 ^{ns}
ADF (%)					0.756**	0.25 ^{ns}	0 ^{ns}	-0.444*
ADL (%)						-0.378**	-0.243 ^{ns}	-0.159 ^{ns}
ADC (%)							0.315 ^{ns}	-0.428**
Tannin (mg/g)								-0.265 ^{ns}
Hemicellulose (%)								

^{ns} not significant $p > 0.05$; * significant at $p < 0.05$; ** significant at $p < 0.01$

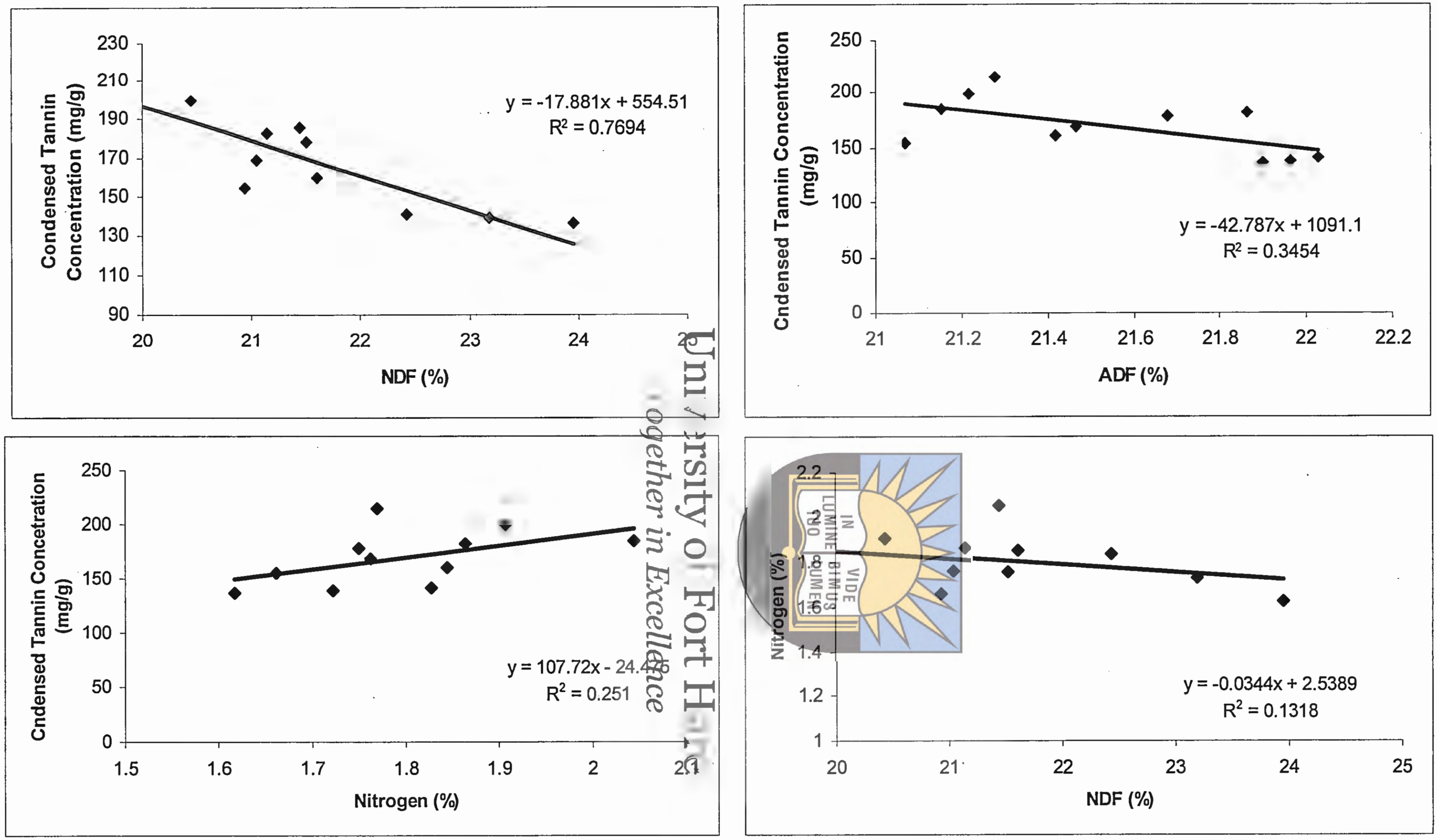

Figure 11: Relationship between the forage quality parameters of *A. karroo* trees.

Chapter 5

Discussion and Conclusions

The shoot length and number of shoots produced are the evidence of compensatory growth. In this study lack of difference in shoot length of defoliated and non-defoliated trees is an indication that the defoliated trees compensated for the lost tissue. The number of shoots produced over-compensated as the number of shoots produced exceeded those in the non-defoliated trees. Lower canopy defoliation had stimulatory effects on shoot production. These results contradict findings by Teague (1988) that early-flush period is the most delicate period of the growth phases (Teague 1988). In this study browsing was beneficial to the tree. The trees produced more shoots after defoliation confirms the findi[illegible]gue (1989). The lack difference in shoot length and higher numbers of browseable shoots produced support the findings that the absence of goats during the growing season results in recovery (Teague & Walker 1988). Basal circumference and height are not affected by lower canopy defoliation. Lack of difference in tree height demonstrates the recovery of tree in the absence of hebivory during growing seasons. One spring seasons defoliation followed by period of rest would not have a detrimental effect on growth of trees. Mature *A. karroo* trees survive defoliation by producing more shoots.

Debarking of *A. karroo* has not been widely studied as defoliation. Complete girdling is known for its ability to cause premature death while incomplete girdling does not. Incomplete girdling allows bark to regrow (Gill 1992 and Vospernik 2006). In this study bark ringing was more detrimental to the plant than bark stripping. Basally ringed trees canopies died resulting in reduced tree height and trees coppiced from the base. This result was similar to findings from other studies (Gill 1992 and Vospernik 2006). Shoot length was not significantly different between basally ringed and non-ringed trees but the shoots from the coppice growth were 15% longer than other treatments. This is in agreement with the compensatory growth studies that found resources are allocated to growth after the tree has been defoliated (Pellew 1988; Teague & Walker 1988 and du Toit *et al.* 1990). Bark stripping increased the basal circumference; the bigger basal circumference may be the result of the growing bark after debarking (Gill 1992). Basal ringing is more detrimental to trees as it retarded growth of trees even in the absence of browsers for two seasons.

The reproductive ability of the trees has been studied and different results were found depending on the species studied (Paige & Witham 1987 and Goheen *et al.* 2007). In this study defoliation of the lower canopy did not influence seed and pod production. This may be attributed to the fact that pod production normally takes place on the upper canopy of the tree. Early-flush basal ringing significantly reduced the number of seeds per pod and number of pods produced. The numbers of seeds in a pod are positively related to number of pods produced. The strong positive correlation of reproduction parameters and tree height and basal circumference shows that young trees produce less seeds, reducing recruitment. The basally ringed trees were in the vegetative stage and survive by coppice growth. The pod production was also reduced by early season dormant debarking (Scogings & Macanda 2005). In the study of *Acacias* by Goheen *et al.* (2007) it was found that heavy defoliation decreased reproduction to benefit physical defense in the form of spines. The basally ringed trees showed tolerance traits in the form of increased shoot length and lesser reproductive ability, therefore, growth was at the expense of reproduction, a result supported by the work of Fornara & du Toit (2007). The allocation for reproduction was not increased over the period of two seasons whilst trees were still growing.

Herbivory can influence morphology of forage by increasing the density of spines, hairs and prickles (Karban & Myers 1989). The physical defense traits also include cell wall contents (Lucas *et al* 2000). In this study defoliated trees were not different to non-defoliated trees in terms of spine length. These results did not support the finding by Midgley & Ward (1996) that indicated branches that are within reach of herbivores produce longer thorns. The internode length never changed because of defoliation. This was because defoliation was only for one season it might not have justified the investment on structural defense as there was no constant threat of defoliation.

The coppice growth had the shortest spines and internode length was not different amongst the debarked trees. Coppice growth was poorly armed for browsing as compare to mature trees. The spine length showed no relationship to internode but had a positive relationship with number of shoots. The relation between spine length and number of shoots concurs with the findings that tolerance traits and resistance traits could occur together (Fornara & du Toit 2007). Bark stripped trees did not produce longer spines and shorter internodes than non-debarked trees, these findings are supported by those of Karban & Myers (1989). Cell wall contents were not significantly affected by defoliation and debarking except for NDF and ADF that were significantly higher on basally ringed trees. Young trees showed their resistance traits by increasing their fiber contents of forage which increases the toughness of leaves and twigs. During the second year of growth, young trees invested more on growth as their ADF and ADL contents increased significantly during 2006 growing season. The increase of cell wall contents in the second year was expected as explained by Larbi *et al.* (2005). The relationship that exist between nutrient and cell wall contents in leaves of young trees shows that they are less digestible. The higher fiber content of the forage means that it is hard to break and will not be the first to be ingested. Cell wall contents improve plants hardiness or toughness (Lucas *et al.* 2000). The younger trees invested physical defense as they increased their cell wall contents.

Condensed tannins have been studied in dry savannas and variable results have been recorded (Teague 1989, du Toit *et al.* 1990, Furstenburg & van Hoven 1994, Macanda & Scogings 2003 and Scogings 2005). In the study by Scogings (2005) browsing in early dormant season of *A. karroo* showed no change in the concentration of condensed tannins after 10 days of browsing (Scogings 2005). Macanda & Scogings (2003) found that concentration of condensed tannin to be higher on heavily browsed trees a year after early dormant season browsing. In Teague (1989) *A. karroo* showed an immediate increase in condensed tannin levels after browsing, Furstenburg & van Hoven (1994) also found that plants browsed throughout the year showed an increase condensed tannin concentration after browsing. Condensed tannin levels vary according to tree size, temperature, light intensity and phonological status of foliage (Furstenburg & van Hoven 1994). In this study contrary to early dormant season defoliation early flush defoliation did not have impact in condensed tannin concentration. The debarking did not affect condensed tannin concentration. These results of no change due to defoliation were also found in *A tortilis* in Tanzania (Gowda 1997). Change in condensed tannin concentration is also affected by climatic conditions and phenophase (Furstenburg & van Hoven 1994). Coppice growth had lower condensed tannin concentration in the first year and this concurred with early dormant defoliation (Macanda & Scogings 2003) while bark stripping increased condensed tannin level. Condensed tannins concentration responded to absence of defoliation during the growing season. In the second season after treatment application tannins were lowest for bark stripped and non debarked trees. The basally ringed trees in the second season had higher tannin than in the first year of growth. Mature trees invested in growth in the absence of herbivory. This concurs with the theory of induced defence (Karban & Myers 1989, Harval 1990 and Karban & Baldwin 1997). Condensed tannins are negatively correlated to NDF. These two are resistance traits therefore young plants only use one of the two to resist herbivory. The nutrient content of leaves was not altered by defoliation and debarking, therefore, it was not dependent on disturbance.

In unbrowsed situation birch species increased protein content during spring and reaches maximum in early summer (Palo *et al.* 1985). [illegible] fodders in semi-arid areas of Botswana are known to maintain higher protein and mineral content during growth than grasses as they reach maturity (Aganga & Tshwenyane 2003). In the studies by Macanda & Scogings (2003) and Scogings (2005) that were conducted to investigate response of *A. karroo* nutrients to browsing, they have shown no response. The younger trees allocation of resource to growth and reducing allocation to secondary metabolites renders new shoots to be palatable to herbivores (du Toit *et al.* 1990). The allocation to growth results in more cell wall contents in leaves of coppice growth. In this research fiber content of new shoots of coppice growth was higher making forage less digestible. The fact that fiber is negatively related to nutrients renders the young shoots to be less palatable to browsers. Defoliation and debarking had no effect on the concentration of nutrients of the leaves.

Lower canopy defoliation had no effect in on tree height, basal circumference and shoot length. Complete ringing reduced growth by reducing height, basal circumference and number of browseable shoots produced, and tended to increase shoot length. Spring browsing of lower canopy resulted in overcompensation of shoot production. Also for shoot length there was compensatory growth.

I conclude that basal ringing is detrimental to growth as it reduced most number of shoots produced, tree height and basal circumference; and that defoliation alone does not result in canopy death while basal ringing alone does cause topkill. Based on two seasons of research, defoliation did not affect the reproductive ability of the trees, evidenced by lack of differences between browsed and non-browsed trees. Basal ringing reduced reproduction by turning tree to vegetative stage. Only mature trees are able to produce seeds. The tolerance traits that were strongly demonstrated by the trees were shoot production and shoot length.

It is further concluded that spring defoliation does not result in increased physical defense as evidenced by no changes in internode and spine length. Basal ringing also did not induce physical defense in form of spines rather it reduced it by reducing spine length. Basal ringing increases its physical defense by increasing hardiness as it produces more fibre and lignin. The chemical defense was not increased by lower canopy defoliation. Bark stripping induced the chemical defense by increasing condensed tannin concentration, and basal ringing reduced concentration. Chemical defense is more dependent on the growing stage of the tree, as shown by higher concentration of condensed tannin in second season of growth after basal ringing. The allocation to defense was affected by the stage of growth as younger trees invested in growth rather than defense. The nature of inductivity of defense explains the adaptive nature of allocation to defense. In this study it shown that coppice growth is less nutritious than mature trees. Spring debarking resulted in induction of more resistance traits as bark stripped trees result in increased chemical defense and basally ringed trees in more NDF, ADF and ADL content. Spring defoliated trees did not exhibit any form of resistance because there where no induced defense, therefore, mature trees survive browsing through tolerance. Mature defoliated trees survived spring browsing by compensatory growth which is a tolerance trait.

Spring lower canopy defoliation is good for forage production as it results in compensatory growth. To control density increase browsing should be continuous and not for short periods of heavy browsing. Basal ringing brings the trees to the available height and it can also be effective in killing trees this reducing bush encroachm[illegible]e coppice growth could not be regarded as forage of good quality because of high fiber content as compared to older trees growth. The older trees, therefore, produce better forage than young trees. Management of trees for forage production should keep trees at the available height but not as juvenile trees. To control bush encroachment spring basal ring can be used as it can cause complete death of trees without chemical application. I recommend further investigation comparing basal ringing and bush chopping as method of bush encroachment.

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Appendices

Appendix A: Tree species composition in the experimental site in Adelaide Experimental Farm

PLOT NUMBER	*A. karroo*	*Aloe ferox*	*Azima Teteracantha*	*Ehretia rigida*	*Grewia Occidentalis*	*Maytenous Heterophyla*	*Maytenous polycantha*	*Lippia javanica*	*Rhus undulata*	*Tecomania Capensis*	**TOTAL**
PLOT 1	13			8				2	1		**24**
PLOT 2	17				1			3			**21**
PLOT 3	18		3		1			1	1		**24**
PLOT 4	11										**11**
PLOT 5	14			7				4	1		**6**
PLOT 6	18			2				10		1	**1**
PLOT 7	21		11					2	2		**36**
PLOT 8	23							2			**25**
PLOT 9	5							2			**7**
PLOT 10	10	1					1	6			**18**
PLOT 11	23		2	4			1	4			**34**
PLOT 12	21		1	2	1						**25**
PLOT 13	28		1								**29**
PLOT 14	8		1			1		3			**13**
PLOT 15	21		1	5				1			**28**
PLOT 16	21		2					2			**26**
PLOT 17	15					1		2			**18**
PLOT 18	9		1		2			3			**15**
TOTAL	**296**	**1**	**23**	**28**	**6**	**2**	**2**	**47**	**5**	**1**	**411**
% Composition	**72.02**	**0.24**	**5.60**	**6.81**	**1.46**	**0.49**	**0.49**	**11.44**	**1.22**	**0.24**	**100**

Appendix B: Bush structure in the experimental site in the Adelaide Experimental Farm

PLOT NUMBER	0 - 0.5	0.51 - 1	1.01 - 1.5	1.51- 2.0	2.01 - 2.5	2.51 - 3.0	3.01 - 3.5	3.51 - 4.0	4.01 - 4.5	4.51 - 5.0	TOTAL
PLOT 1	9	5	4	2	2	2					24
PLOT 2	4	8	1	3	2	2				1	21
PLOT 3	6	5	5	2	2	4					24
PLOT 4	2	3	1	2			2		1		11
PLOT 5	3	8	9	2	1	2		1			26
PLOT 6	13	4	5	1	1	7					31
PLOT 7	12	8	3	3		4	3	3			36
PLOT 8	12	2	3	1	1	4		2			25
PLOT 9	2	2				2	1				7
PLOT 10	6	5	3	1	1				1	1	18
PLOT 11	3	8	9	2	3	0	3	3	3	0	34
PLOT 12	5	4	6	2	4	2	1	1			25
PLOT 13	10	6	4	2		2	3	1	1		29
PLOT 14	5	2	1	2					3		13
PLOT 15	1	3	5	3	4	5	2	3	1	1	28
PLOT 16	9	12	1			2	1		1		26
PLOT 17	3	5	2	1	4	1	1	1			18
PLOT 18	4	3	2	2	3	1					15
TOTAL	109	93	64	31	28	40	17	15	11	3	411
% Composition	26.52	22.63	15.57	7.54	6.81	9.73	4.14	3.65	2.68	0.73	100

Appendix C: Herbaceous layer composition in the experimental site in Adelaide Experimental Farm

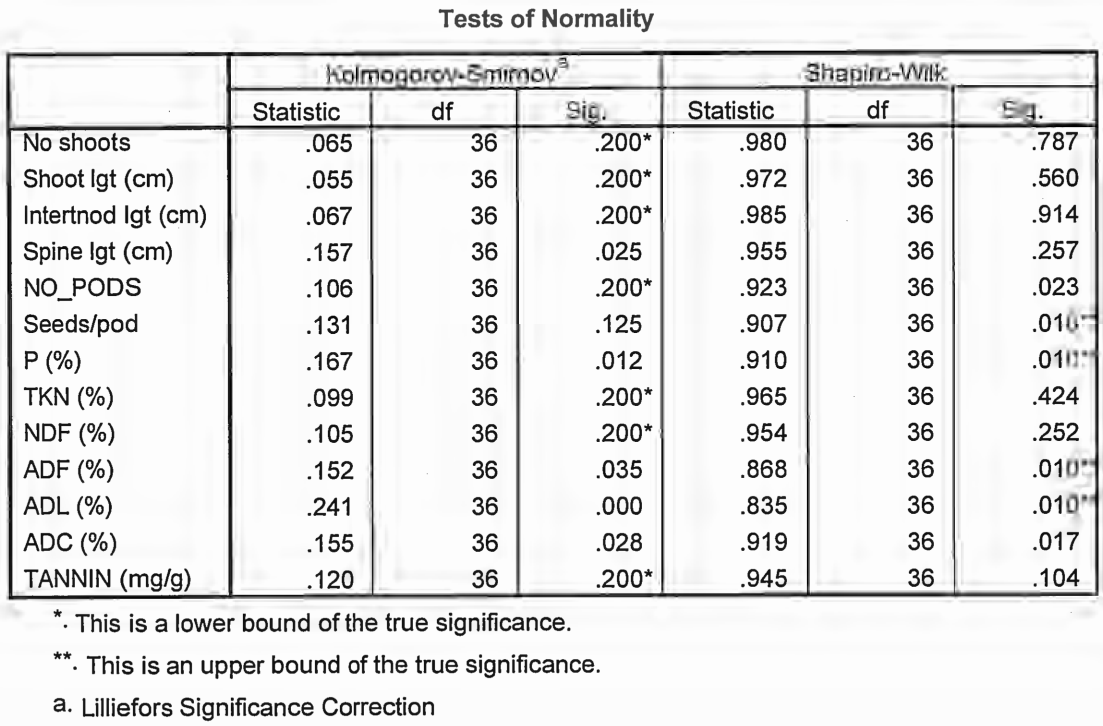
PLOT NUMBERS	ARCO	CYDA	CYPL	DIER	ERCU	EROB	FORB	PAMA	PAST	SENE	SPAF	SPFI	SPNI	TOTALS
PLOT 1	1		1			6	3	1		3		27	8	50
PLOT 2	11			3		4	1	3	2	5		8	13	50
PLOT 3		3		7	1	2	4	10	3	6		11	3	50
PLOT 4		1			2	6	3	7	2			27	2	50
PLOT 5				5	1	3	4	7		14		12	4	50
PLOT 6				3	1	1	1	10	3	17	1	3	10	50
PLOT 7				5	1	1	1	3	1	19		9	10	50
PLOT 8					5	1	1	6	1	7		27	2	50
PLOT 9				5		2	3	6	1	8		22	3	50
PLOT 10				2			4	12	3	11		12	6	50
PLOT 11		3		4		5	2	5		14		11	6	50
PLOT 12	1	2		13		1	1	4	3	12		10	3	50
PLOT 13				5	3	3	5	11	1	13		4	5	50
PLOT 14		2		3		1	4	4		11		13	2	50
PLOT 15	1			2	5	10	2	6	2	8		11	3	50
PLOT 16	2			3	4	2	5	4		19		6	5	50
PLOT 17		6		4		3	6	7	3	9		12		50
PLOT 18		2		4	2	8	3	9	2	16		2	2	50
Total	**16**	**19**	**1**	**68**	**25**	**69**	**53**	**115**	**27**	**192**	**1**	**227**	**87**	**900**
% Composition	**1.78**	**2.11**	**0.11**	**7.56**	**2.78**	**7.67**	**5.89**	**12.78**	**3.00**	**21.33**	**0.11**	**25.22**	**9.67**	**100.00**

ARCO – *Aristida conjesta*
CYDA – *Cynodon dactylon*
CYPL – *Cymbopogon plurinodis*
DIER – *Digitaria eriantha*
ERCU – *Eragrostis curvula*
EROB – *Eragrostis obtuse*
PAMA – *Panicum maximum*
PAST – *Panicum stapfianum*
SENE – *Setaria neglecta*
SPAF – *Sporobolus africanus*
SPFI – *Sporobolus frimbiatus*
SPNI – *Sporobolus nitens*

Appendix D: The table showing the basal cover of the experimental site using Swiftsynd method

Plot Number	Total Strikes	Total points	Percentage (%)
PLOT 1	23	100	23
PLOT 2	22	100	22
PLOT 3	22	100	22
PLOT 4	37	100	37
PLOT 5	26	100	26
PLOT 6	22	100	22
PLOT 7	14	100	14
PLOT 8	26	100	26
PLOT 9	20	100	20
PLOT 10	26	100	26
PLOT 11	20	100	20
PLOT 12	14	100	14
PLOT 13	15	100	15
PLOT 14	19	100	19
PLOT 15	21	100	21
PLOT 16	17	100	17
PLOT 17	11	100	11
PLOT 18	22	100	22
Average	21	100	21

Appendix E: Normality test for response variable



Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
No shoots	.065	36	.200*	.980	36	.787
Shoot lgt (cm)	.055	36	.200*	.972	36	.560
Internod lgt (cm)	.067	36	.200*	.985	36	.914
Spine lgt (cm)	.157	36	.025	.955	36	.257
NO_PODS	.106	36	.200*	.923	36	.023
Seeds/pod	.131	36	.125	.907	36	.010**
P (%)	.167	36	.012	.910	36	.010**
TKN (%)	.099	36	.200*	.965	36	.424
NDF (%)	.105	36	.200*	.954	36	.252
ADF (%)	.152	36	.035	.868	36	.010**
ADL (%)	.241	36	.000	.835	36	.010**
ADC (%)	.155	36	.028	.919	36	.017
TANNIN (mg/g)	.120	36	.200*	.945	36	.104

*. This is a lower bound of the true significance.

**. This is an upper bound of the true significance.

a. Lilliefors Significance Correction

Appendix F: Debarking

Test Statistics^{a,b}

	NO_PODS	Seeds/pod	P (%)	ADF (%)	ADL (%)	ADC (%)	Hemicellulose
Chi-Square	24.620	21.742	3.039	6.641	1.272	6.020	3.564
df	2	2	2	2	2	2	2
Asymp. Sig.	.000	.000	.219	.036	.529	.049	.168

a. Kruskal Wallis Test

b. Grouping Variable: Debarking

Appendix G: Defoliation

Test Statistics^{a,b}

	NO_PODS	Seeds/pod	P (%)	ADF (%)	ADL (%)	ADC (%)	Hemicellulose
Chi-Square	.157	.073	.009	.025	.144	.169	1.449
df	1	1	1	1	1	1	1
Asymp. Sig.	.692	.787	.924	.874	.704	.681	.229

a. Kruskal Wallis Test

b. Grouping Variable: Defoliation

Appendix H: Treatment Combination

Test Statistics^{a,b}

	NO_PODS	Seeds/pod	P (%)	ADF (%)	ADL (%)	ADC (%)	Hemicellulose
Chi-Square	11.665	11.439	6.187	4.257	1.626	1.298	5.289
df	2	2	2	2	2	2	2
Asymp. Sig.	.003	.003	.045	.119	.444	.523	.071

a. Kruskal Wallis Test

b. Grouping Variable: TREATMEN

Appendix I: Season

Test Statistics^{a,b}

	NO_PODS	Seeds/pod	P (%)	ADF (%)	ADL (%)	ADC (%)	Hemicellulose
Chi-Square	.036	.157	2.605	10.827	26.270	9.811	.000
df	1	1	1	1	1	1	1
Asymp. Sig.	.849	.692	.107	.001	.000	.002	1.000

a. Kruskal Wallis Test

b. Grouping Variable: season

Appendix J: Number of Shoots

Tests of Between-Subjects Effects

Dependent Variable: No shoots

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	41854.702[a]	13	3219.592	5.421	.000
Intercept	343.064	1	343.064	.578	.455
TREE_HGT	588.336	1	588.336	.991	.330
BASALCIR	6747.740	1	6747.740	11.361	.003
DEFOLIAT	3178.512	1	3178.512	5.352	.030
DEBARKIN	15243.412	2	7621.706	12.832	.000
YEAR	3123.629	1	3123.629	5.259	.032
DEFOLIAT * DEBARKIN	288.595	2	144.297	.243	.786
DEFOLIAT * YEAR	84.038	1	84.038	.141	.710
DEBARKIN * YEAR	1290.791	2	645.396	1.087	.355
DEFOLIAT * DEBARKIN * YEAR	1237.932	2	618.966	1.042	.369
Error	13066.662	22	593.939		
Total	528954.387	36			
Corrected Total	54921.364	35			

a. R Squared = .762 (Adjusted R Squared = .621)

Appendix K: Shoot Length

Tests of Between-Subjects Effects

Dependent Variable: Shoot lg. (cm)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	205.799[a]	13	15.831	1.224	.327
Intercept	36.619	1	36.619	2.832	.107
TREE_HGT	28.705	1	28.705	2.220	.150
BASALCIR	51.028	1	51.028	3.947	.060
DEFOLIAT	38.565	1	38.565	2.983	.098
DEBARKIN	30.253	2	15.126	1.170	.329
YEAR	10.107	1	10.107	.782	.386
DEFOLIAT * DEBARKIN	12.043	2	6.022	.466	.634
DEFOLIAT * YEAR	14.447	1	14.447	1.117	.302
DEBARKIN * YEAR	15.086	2	7.543	.583	.566
DEFOLIAT * DEBARKIN * YEAR	9.305	2	4.653	.360	.702
Error	284.445	22	12.929		
Total	16167.151	36			
Corrected Total	490.244	35			

a. R Squared = .420 (Adjusted R Squared = .077)

Appendix L: Internode Length

Tests of Between-Subjects Effects

Dependent Variable: Intertnod lgt (cm)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.833[a]	13	6.406E-02	1.542	.179
Intercept	9.583E-02	1	9.583E-02	2.307	.143
TREE_HGT	.101	1	.101	2.422	.134
BASALCIR	.113	1	.113	2.718	.113
DEFOLIAT	.143	1	.143	3.453	.077
DEBARKIN	.232	2	.116	2.798	.083
YEAR	.181	1	.181	4.362	.049
DEFOLIAT * DEBARKIN	6.992E-02	2	3.496E-02	.842	.444
DEFOLIAT * YEAR	3.619E-04	1	3.619E-04	.009	.926
DEBARKIN * YEAR	4.273E-02	2	2.136E-02	.514	.605
DEFOLIAT * DEBARKIN * YEAR	6.333E-02	2	3.167E-02	.762	.479
Error	.914	22	4.154E-02		
Total	58.312	36			
Corrected Total	1.747	35			

a. R Squared = .477 (Adjusted R Squared = .168)

Appendix M: Spine Length

Tests of Between-Subjects Effects

Dependent Variable: Spine lgt (cm)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	11.331[a]	13	.872	1.949	.081
Intercept	.259	1	.259	.579	.455
TREE_HGT	.844	1	.844	1.888	.183
BASALCIR	.882	1	.882	1.972	.174
DEFOLIAT	1.253	1	1.253	2.801	.108
DEBARKIN	8.382	2	4.191	9.372	.001
YEAR	.560	1	.560	1.252	.275
DEFOLIAT * DEBARKIN	.617	2	.308	.689	.512
DEFOLIAT * YEAR	8.132E-03	1	8.132E-03	.018	.894
DEBARKIN * YEAR	.367	2	.184	.411	.668
DEFOLIAT * DEBARKIN * YEAR	.272	2	.136	.305	.740
Error	9.838	22	.447		
Total	272.976	36			
Corrected Total	21.169	35			

a. R Squared = .535 (Adjusted R Squared = .261)

Appendix N: Nitrogen

Tests of Between-Subjects Effects

Dependent Variable: TKN (%)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	3.197[a]	13	.246	2.752	.018
Intercept	5.082E-02	1	5.082E-02	.569	.459
TREE_HGT	.194	1	.194	2.169	.155
BASALCIR	1.264E-02	1	1.264E-02	.141	.710
DEFOLIAT	8.252E-02	1	8.252E-02	.923	.347
DEBARKIN	.724	2	.362	4.052	.032
YEAR	1.122	1	1.122	12.552	.002
DEFOLIAT * DEBARKIN	.304	2	.152	1.703	.205
DEFOLIAT * YEAR	1.170E-03	1	1.170E-03	.013	.910
DEBARKIN * YEAR	5.173E-02	2	2.587E-02	.289	.752
DEFOLIAT * DEBARKIN * YEAR	.327	2	.164	1.831	.184
Error	1.966	22	8.937E-02		
Total	121.426	36			
Corrected Total	5.163	35			

a. R Squared = .619 (Adjusted R Squared = .394)

Appendix O: Neutral Detergent Fibre

Tests of Between-Subjects Effects

Dependent Variable: NDF (%)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	160.198[a]	13	12.323	6.257	.000
Intercept	62.810	1	62.810	31.892	.000
TREE_HGT	9.394E-03	1	9.394E-03	.005	.946
BASALCIR	3.712E-03	1	3.712E-03	.002	.966
DEFOLIAT	6.280E-02	1	6.280E-02	.032	.860
DEBARKIN	34.000	2	17.000	8.632	.002
YEAR	95.422	1	95.422	48.452	.000
DEFOLIAT * DEBARKIN	12.960	2	6.480	3.290	.056
DEFOLIAT * YEAR	6.171	1	6.171	3.133	.091
DEBARKIN * YEAR	.115	2	5.750E-02	.029	.971
DEFOLIAT * DEBARKIN * YEAR	1.896	2	.948	.481	.624
Error	43.328	22	1.969		
Total	16929.719	36			
Corrected Total	203.526	35			

a. R Squared = .787 (Adjusted R Squared = .661)

Appendix P: Condensed Tannin Concentration

Tests of Between-Subjects Effects

Dependent Variable: TANNIN (mg/g)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	33921.421[a]	13	2609.340	2.195	.050
Intercept	3694.335	1	3694.335	3.107	.092
TREE_HGT	3.331	1	3.331	.003	.958
BASALCIR	5.894E-02	1	5.894E-02	.000	.994
DEFOLIAT	2627.621	1	2627.621	2.210	.151
DEBARKIN	2961.636	2	1480.818	1.245	.307
YEAR	6693.123	1	6693.123	5.629	.027
DEFOLIAT * DEBARKIN	2070.105	2	1035.052	.871	.433
DEFOLIAT * YEAR	161.012	1	161.012	.135	.716
DEBARKIN * YEAR	15133.911	2	7566.955	6.364	.007
DEFOLIAT * DEBARKIN * YEAR	2128.321	2	1064.161	.895	.423
Error	26157.195	22	1188.963		
Total	1089400.788	36			
Corrected Total	60078.616	35			

a. R Squared = .565 (Adjusted R Squared = .307)

Appendix Q Tree height and basal circumference

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	HGT_DIFF	6.336[a]	7	.905	13.392	.000
	PER_HGT	15391.061[b]	7	2198.723	11.230	.001
	BCIRC_DI	125.203[c]	7	17.886	2.357	.106
	PER_BCIR	5294.780[d]	7	756.397	2.677	.077
Intercept	HGT_DIFF	7.765E-02	1	7.765E-02	1.149	.309
	PER_HGT	106.223	1	106.223	.543	.478
	BCIRC_DI	5.116	1	5.116	.674	.431
	PER_BCIR	299.836	1	299.836	1.061	.327
TRHGHT_0	HGT_DIFF	.140	1	.140	2.068	.181
	PER_HGT	252.668	1	252.668	1.290	.282
	BCIRC_DI	1.062	1	1.062	.140	.716
	PER_BCIR	53.229	1	53.229	.188	.674
BCIRC_05	HGT_DIFF	.110	1	.110	1.632	.230
	PER_HGT	294.310	1	294.310	1.503	.248
	BCIRC_DI	2.873	1	2.873	.379	.552
	PER_BCIR	191.833	1	191.833	.679	.429
DEFOLIAT	HGT_DIFF	1.789E-04	1	1.789E-04	.003	.960
	PER_HGT	15.435	1	15.435	.079	.785
	BCIRC_DI	8.689E-02	1	8.689E-02	.011	.917
	PER_BCIR	32.263	1	32.263	.114	.742
DEBARKIN	HGT_DIFF	5.659	2	2.829	41.863	.000
	PER_HGT	14003.362	2	7001.681	35.761	.000
	BCIRC_DI	102.700	2	51.350	6.766	.014
	PER_BCIR	4430.804	2	2215.402	7.840	.009
DEFOLIAT * DEBARKIN	HGT_DIFF	.371	2	.186	2.747	.112
	PER_HGT	691.376	2	345.688	1.766	.220
	BCIRC_DI	4.908	2	2.454	.323	.731
	PER_BCIR	147.377	2	73.689	.261	.776
Error	HGT_DIFF	.676	10	6.759E-02		
	PER_HGT	1957.924	10	195.792		
	BCIRC_DI	75.891	10	7.589		
	PER_BCIR	2825.932	10	282.593		
Total	HGT_DIFF	7.793	18			
	PER_HGT	19298.153	18			
	BCIRC_DI	201.344	18			
	PER_BCIR	8123.624	18			
Corrected Total	HGT_DIFF	7.012	17			
	PER_HGT	17348.984	17			
	BCIRC_DI	201.094	17			
	PER_BCIR	8120.712	17			

a. R Squared = .904 (Adjusted R Squared = .836)

b. R Squared = .887 (Adjusted R Squared = .808)

c. R Squared = .623 (Adjusted R Squared = .358)

d. R Squared = .652 (Adjusted R Squared = .408)