

**THE EFFECT OF FIRE ON THE ROOT CARBOHYDRATE CONCENTRATION AND
GROWTH OF ENCROACHING *Terminalia sericea* IN A SEMI-ARID SAVANNA
WOODLAND IN THE WATERBERG PLATEAU PARK, CENTRAL NAMIBIA**

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OF

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ABSTRACT

Fire is an ecological disturbance that may kill or topkill woody plants and control the biomass of woody species in disturbance prone areas, thus maintaining the co-existence of trees and grasses in savanna ecosystems. Relatively recently, savannas have been altered worldwide by a phenomenon known as bush encroachment, which is the suppression of grasses by woody species due to the increase in woody biomass. *Terminalia sericea* is a woody encroaching species which occurs in woodland savannas on dystrophic sandy soils; it often forms dense thickets and is considered as an encroacher on the Waterberg Plateau Park. The ability of encroaching woody species to resprout after topkill by fire, particularly in savanna ecosystems, is due to the already established and functioning carbohydrate reserves stored in the roots. From a management perspective, fire may be used as a preventative measure to combat encroachment of woody plants or less successfully as a symptom treatment. It may be possible to reduce the regrowth of woody encroaching species through the more frequent use of fire, if it is known how fast the root carbohydrate concentrations of resprouts return to pre-fire concentrations. The aim of the study was to investigate how time since last burn, in a semi-arid savanna woodland at the Waterberg Plateau Park, influences the growth of the encroaching *T. sericea*, in particular the replenishment of root carbohydrates subsequent to fire. The Waterberg Plateau Park is on the south-western side of the woodland to the north of the country on deep Kalahari sands. The study used the space for time substitution approach as described by Pickett (1989), to investigate the effect of fire on the resprouting ability, growth rate and the replenishment of root total non-structural carbohydrates of *T. sericea*.

In October 2014, thirty *T. sericea* resprouts were collected from each of the four fire treatment blocks which were last burned 1, 2, 14 and 24 years ago, respectively. These treatments have a mean fire return interval ranging from every 6 to 19 years. The BECVOL method (Smit, 1996) was used to estimate aboveground components (tree height, leaf mass and canopy volume). In May 2015, the roots of twelve of the measured resprouts were excavated in fire blocks when the time since last burn was 2, 3, 15 and 25 years ago, respectively. Three discs were sawn from the top 50 cm of the main root and used for non-structural carbohydrate analysis and for approximate age determination. Material used for root total non-structural carbohydrate (TNC) analysis were oven dried, milled and sieved. For TNC analysis, oligosaccharides, polysaccharides and starch were extracted using various laboratory methods as described by Rohwer, E. A (2014). Age was determined for 33 of the samples by counting age rings using the LinTab apparatus.

Fire had a strong and positive effect ($p < 0.05$) on the growth rate of the aboveground components by causing a rapid growth increase within the first two years which then slows

down between 2 and 14 years after a fire. The recovery of *T. sericea* is rapid with a relative growth rate of 60 % for tree height, 140 % for canopy volume and 82 % for leaf mass, within a period of one year, between years one and two. In the third year after, there is the highest root TNC concentration. The rapid recovery of root TNC correlates well with aboveground growth. After a fire, mobilisation of root carbohydrates leads to the recovery of aboveground components that leads to an increase in leaves, photosynthesis then increases, which leads to the replenishment of root TNC, and this occurs within 2 to 3 years after a fire. In the study area *T. sericea* can be classified as a fire tolerant species because it coppices relatively fast and this leads to the rapid replenishment of root reserves. Controlled fire can be used to suppress the regrowth of encroaching *T. sericea* once the period of root TNC replenishment is determined. Based on the carbohydrate reserves subsequent to fire, the current fire regime on the plateau could not suppress the growth of *T. sericea*.

Key words: total non-structural carbohydrates, Waterberg Plateau Park, time since last burn, bush encroachment, coppice, BECVOL.

DEDICATION

I dedicate this thesis to my parents, Patricia and Norman Lutibezi. They have given me the drive and discipline to tackle any task with enthusiasm, dedication and determination. Thank you both for your encouragement, love and support.

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DECLARATION

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Date

ACRONYMS

ANOVA	Analysis of Variance
BECVOL	Biomass Estimates from Canopy VOLUME
GR	Growth Rate
MET	Ministry of Environment and Tourism
NUST	Namibia University of Science and Technology
SASSCAL	Southern African Science Service Centre for Climate Change and Adaptive Land Management
TSLB	Time Since Last Burn
TNC	Total Non-structural Carbohydrates
US	University of Stellenbosch
WPP	Waterberg Plateau Park

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CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

One-fifth of the world's surface is covered by savannas which are diverse ecosystems because of the existence of different vegetation types, such as: thorny trees with small leaves, grasses and forbs (Sankaran et al., 2005; Campbell & Reece, 2008). Most African savannas occur on deeply weathered and nutrient poor land surfaces and are characterized by the co-existence of trees and grasses (Bond, 2008). This ratio is determined by the interactions of nutrients, moisture, fire and herbivory (Scholes & Walker, 1993; Hipondoka & Versfeld, 2006; Bond, 2008) where water affects the growth period of a plant and nutrients affect the growth rate of a plant (Scholes & Walker, 1993).

The slow recovery of trees after a disturbance, such as a fire, would promote the existence of savannas with a continuous grass cover and a sporadic tree cover (Bond, 2008; February & Higgins, 2010). This co-existence in savannas can be explained either by the equilibrium model or the disequilibrium model (van Wilgen, 2009). The equilibrium model, exemplified by "Walter's (1971) two-layer model", which states that the co-existence of trees and grasses is due to the separation of rooting niches (Higgins et al., 2000; Ward, 2005; Ward et al., 2013). This model explains that grasses are the superior competitors for water in the topsoil, while woody species have exclusive access to and primarily rely on subsoil water below grass roots (Ward et al., 2013). On the other hand, the disequilibrium model states that there is no stable equilibrium and that a frequent disturbance such as fire may cause the loss of trees through competition with grass by biasing conditions in favour of the grasses or vice versa, where a disturbance such as herbivory may cause the loss of grasses through competition with trees (van Wilgen, 2009). With the disequilibrium model, there is coexistence through disturbances preventing the total domination of one form or the other and it is more significant in areas with higher rainfall. These theories are not mutually exclusive.

The interaction between life histories of trees (such as sprouting ability, fire survival at different life stages and tree mortality) and the occurrence of fire as a disturbance, often causes aboveground tree mortality resulting in a slower tree recovery rate than grass recovery rate and maintains the coexistence of trees and grasses in savannas (Higgins et al., 2000; Bond & Midgley, 2001; Joubert et al., 2008; Gandiwa & Kativu, 2009; van Wilgen, 2009; Gandiwa, 2011; Joubert et al., 2012). In cases where disturbances, such as fire, that maintain the co-existence of trees and grasses are absent, savannas may become dominated by woody vegetation. This is known as bush encroachment, which is described as the conversion of savannas to dense woody dominated thickets with little grass cover (Meik et al., 2002; de

Klerk, 2004). Savannas are economically important because they are home to most of the world's rangelands, livestock and wild herbivores which depend on the tree-grass co-existence (Sankaran et al., 2005). Rangelands in Namibia are faced with bush thickening of various encroaching species; this is partially due to a poor understanding of the vegetation dynamics in arid savannas (Joubert et al., 2008). Bush thickening has a negative impact on rangelands due to low productivity and the reduction of grazing land which negatively affects agricultural activities (Zimmerman & Mwazi, 2002; de Klerk, 2004). Bush thickening causes a decrease in animal production due to a decrease in the grazing carrying capacity of the land (Bester, 1998). In Namibia, an estimated N\$700 million in meat was lost annually due to bush thickening (de Klerk, 2004).

Terminalia sericea is an encroaching species in sandy soils and coppices vigorously when cut or burned in an uncontrolled manner (Bester, 1998). Fire may be used as a preventative management tool to manipulate the woody vegetation structure of savannas (Trollope, 1982; de Klerk, 2004; Smit et al., 2010), as it consumes dead and living material and acts as a top-down control on ecosystem structure (Bond, 2008), although in arid environments increased fire frequencies may negatively affect the grass component (Joubert et al., 2012; Trollope et al., 2014). In savannas where frequent burning occurs, sprouting is crucial for juvenile survival (Bond & Midgley, 2001). Resprouters survive after topkill by fire and recover relatively fast due to the presence of dormant buds protected by the bark or located just beneath the soil surface (Verdaguer & Ojeda, 2002). The ability of stems that are killed in a fire to resprout is a key life-history trait that promotes the persistence of trees in savannas (Higgins et al., 2000). Like environmentally induced changes, age and size related changes may enhance species fitness as trees face different challenges to survival at different life stages (Day et al., 2002). In order for a plant to sprout after a disturbance (complete removal of aboveground biomass) it needs stored reserves and meristems to support regrowth (Bond & Midgley, 2001). The ability of woody vegetation to recover relatively fast after a fire is due to the stored root reserves which include carbohydrates and nutrients (Wigley et al., 2009; Smit et al., 2010). One of the major carbohydrate storage components of woody plants is starch but sugars such as oligosaccharides and polysaccharides are also stored and used to facilitate growth (Bell & Ojeda, 1999; Kayofa, 2015).

Frequent burning has a significant negative effect on carbohydrate root reserves of the woody tree, *Acacia karroo* (Wigley et al., 2009), indicating that after a disturbance, stored reserves are depleted due to mobilization for regrowth (Bowen & Pate, 1993; Wigley et al., 2009). This suggests that it might be possible to reduce the regrowth of woody encroaching species through the more frequent use of fire and or other disturbances that may cause topkill of trees hence preventing replenishment of root carbohydrates to return to pre-fire concentrations.

1.2 Literature review

1.2.1 Bush encroachment and fire in savannas

The expansion of woody vegetation observed worldwide in savannas and grasslands has been due to changes in grazing intensity, climate and fire regimes (Bond & Midgley, 2000) but there is still not much agreement on the relative importance of each of these factors (Ward, 2005). The increase in grazing intensity causes the removal of grasses, which opens more areas for woody species to establish, and makes topsoil moisture available to trees allowing them to recruit rapidly. Increased rainfall years increases seed production of woody species (such as *Acacia mellifera*) and could thus lead to the increase of bush in an area (Joubert et al., 2012). Fire as a factor causes aboveground mortality of both grasses and trees. Despite fires favouring grasses, woody species are relatively well adapted to resprouting after fire (Bond & Midgley, 2001). Bush encroachment is a widespread problem in Namibia and *T. sericea* is a local encroacher species in the sandy soils of the Omaheke and Otjozondjupa regions (Bester, 1998; de Klerk, 2004), due to its tendency for deploying roots near the surface allowing it to compete for water and nutrients with shallow rooted plants such as grasses (Hipondoka & Versfeld, 2006). The shallow rooted trees explain why some encroaching bushes continue to persist even after the removal of grazers on rangelands (Hipondoka & Versfeld, 2006). If fire is appropriately managed and applied it can be used by farmers to combat bush encroachment, because controlled fire can potentially kill woody plants, and frequent fires reduce cover and maintain much of the woody vegetation within the flame zone by topkilling saplings and mature plants (Bond & Midgley, 2001; Sankaran et al., 2008; Gandiwa, 2011). Trees at the seedling and sapling stages can be easily removed by flames, thus fire can drastically reduce the tree population and prevent canopy closure favouring the formation of savannas, if it is properly managed (Accatino et al., 2010; Gandiwa, 2011). The study by Joubert et al. (2012) indicated that fire interrupts the transition from open grass bush thickets in arid savannas. The findings indicated that *Acacia mellifera* seedlings died in fires and fires affected regrowth.

Grazing management and prescribed burning after abundant rains are some of the methods used to combat bush encroachment (Zimmerman & Mwazi, 2002; Trollope, 2004). In some areas, dry seasonal hot fires are used to control bush encroachment, but these annual hot fires may cause loss of some fire sensitive species (Gandiwa, 2011). Fire frequency, which is a vital component of the fire regime, is defined as the average time interval between successive fires (Bond & Keeley, 2005) and it affects ecosystem functions such as, grass productivity, nutrient cycling and tree recruitment (Gandiwa & Kativu, 2009). A high fire

frequency and severity can reduce plant biomass and can also replace trees with shrub lands or grass lands (Bond et al., 2005). To control the density of trees with fire there needs to be an adequate mass of dry plant material to provide fuel load for fires to occur and spread. The fuel load is mostly provided by dead grass that accumulates sufficient biomass after years of adequate rainfall and low herbivory (Zimmerman & Mwazi, 2002; Govender et al., 2006; Accatino et al., 2010).

Without fire, large areas in savannas could potentially develop into closed woodlands, but this entirely depends on the total amount of rainfall and season of distribution (Govender et al., 2006). On the other hand, woody plants have developed several different strategies to survive frequent burning. These include resprouting from buds, development of thick barks that protect the tree from fire damage and the availability of carbohydrate reserves in the roots which assist with resprouting and are replenished between burns (Hoffman et al., 2000; Bond & Midgley, 2001; Cruz et al., 2002).

1.2.2 Below-ground carbohydrate storage and concentration

A lignotuber is a specialized swollen woody structure located at the base of some plants; these are reservoirs of carbohydrate and mineral reserves (Wigley et al., 2009; Paula et al., 2016). Lignotuber structures contain dormant buds from which resprouting occurs after a disturbance and evolve in ecosystems with highly frequent and severe disturbances i.e. where periodic fires are prevalent (Wigley et al., 2009; Paula et al., 2016). Multiple disturbances may have contributed to the formation of lignotubers and these lignotuber reserves are important in the continuous resprouting of some woody individuals such as the woody Mediterranean *Erica* species and *Acacia karroo* found in semi-arid ecosystems (Candell & Lopez-Soria, 1998; Wigley et al., 2009). The study by Cruz et al. (2002) on *Erica* species indicated that the smaller the storage organ the more vigorous the resprouting. The concentration of reserves in the lignotuber were not a pertinent driver of resprouting in the *Erica* species. The carbohydrates were mostly being used by the roots which seem to be the main carbohydrate sink (Cruz & Moreno, 2001). This could explain the transition of most plants for storing most reserves in the roots than in lignotuber structures if present.

Cruz & Moreno (2001) found that in central Spain, different seasons affected the concentration of root carbohydrates reserves found in the woody shrub, *Erica australis*. The study predicted that the concentration of carbohydrates in lignotubers of *E. australis* was expected to be high in summer when fires are most prevalent or in winter when cold conditions such as frost may cause topkill, but this was not the case. Instead, a depletion of carbohydrates from the roots

during summer and winter was observed, suggesting that the roots are the main carbohydrate sink for *E. australis* rather than the lignotubers (Cruz & Moreno, 2001).

The season in which fire occurs influences the resprouting ability of plants. For example, shoot regrowth is higher in the summer following spring burn than in autumn and winter after summer burn because photosynthesis and respiration both increase with an increase in temperature as in the Australian *Stirlingia latifolia* (Bowen & Pate, 1993). There is a greater decline in root starch of summer burned plants (near the end of the rainy season) than of spring burned plants (near the beginning of the rainy season), because resprouting in the summer plants occurs at a time when plants would normally experience a drop in carbohydrate reserves due to cold temperatures in autumn and winter (Bowen & Pate, 1993). The decrease in temperatures causes a decrease in the rate of photosynthesis, therefore when reserves are being mobilized, they are not being replenished rapidly as in warmer months where photosynthetic rates are faster (Bowen & Pate, 1993). Mobilization of reserves may be higher in colder seasons in order to help the plant during these harsh conditions. *Terminalia sericea* was found to be frost tolerant at the Waterberg Plateau Park (Amputu, 2016). This may be due to the sufficient storage of root reserves during the growing season which allows it to survive in cold conditions unlike the other trees in the area.

Cruz et al. (2002) indicated that the soil resource availability could influence the storage organ size of the woody shrub, *E. australis* found in central-western Spain. Findings indicated that areas with high soil nutrients had smaller storage organs and lower carbohydrate concentrations, due to nutrients and water found in the soils that assist in resprouting of *E. australis* (Cruz et al., 2002). On the other hand, areas with infertile soils unfavourable for plant growth had larger storage organs, to store all nutrients and carbohydrates necessary for resprouting (Cruz et al., 2002); thus, the percentage carbohydrate allocation is usually higher in dry and infertile soils. Resprouting was more vigorous in *E. australis* with smaller lignotubers which suggests that concentration of carbohydrate reserves in lignotubers is not the only driver of resprouting. The study concluded that moist and more fertile soils would favour vigorous resprouting due to the high amount of nutrients and water available in the soils. The resprouting vigour was unrelated to the concentration of reserves, and thus resprouting appears to be a function of root carbohydrate reserves and edaphic conditions (Cruz et al., 2002).

A few studies indicated that there is no correlation between plant height and the total non-structural carbohydrates (TNC) such as glucose, sucrose and starch, therefore no significant difference between size of belowground storage organ and plant height (Cruz et al., 2002; Wigley et al., 2009). In woody plants, it is a general phenomenon to have higher percentage

root biomass; this includes the entire belowground carbon and not only carbohydrates that can be mobilized for growth. The root: shoot ratio is a method used for estimating root biomass from the shoot biomass and it is essential for improving the accuracy of root biomass estimates (Mokany et al., 2006). The root biomass in woody systems ranges from 11 to 63 % (Mokany et al., 2006). At Stellenbosch, work done on Pines and Eucalyptus, the root: shoot ratio was between 10 to 30 % in wet areas (rainfall > 1000 mm) and between 25 to 55 % in areas with rainfall between 500 and 1000 mm. In semi-arid areas, roots made up as much as 70 % of the aboveground biomass (du Toit et al., 2016).

1.2.3 Atmospheric Carbon dioxide (CO₂) and its effect on TNC

Elevated atmospheric CO₂ may influence root carbohydrate concentrations. In Southern African savannas, generally the more atmospheric carbon available the more photosynthesis occurs and hence, more sugars are produced that may be used for growth and can be stored as root carbohydrates which will enable continuous resprouting of woody individuals (Buitenwerf et al., 2012). Plant species that therefore rely on stored carbon to support resprouting may do so more vigorously under elevated atmospheric CO₂ concentrations (Bond & Midgley, 2001). In *Kielmeyera coriacea*, a woody tree in south-central Brazil, less root carbohydrate reserves were mobilised under elevated CO₂, because elevated photosynthesis levels cause the recovering leaf area to act as a strong carbohydrate source and thus reduce the demand on stored root carbohydrates early during resprouting (Hoffman et al., 2000). The fast growth rates and increased ability of regeneration observed under elevated CO₂ may increase the ability of plants to withstand fire (Hoffman et al., 2000; Buitenwerf et al., 2012). Elevated levels of atmospheric CO₂ almost always stimulate the production of non-structural carbohydrates (Hoffman et al., 2000). C4 grasses can fix more carbon than C3 plants. Woody plants that have a C3 pathway have a photosynthetic rate that is 18% lower than grass (Scholes & Walker, 1993). Higher photosynthetic rate could lead to a high grass biomass which is able to suppress tree seedling growth as these two vegetation types compete for moisture in the top soil (Higgins et al., 2000).

1.2.4 Effects of fire as a disturbance on carbohydrate concentration

When a disturbance such as fire occurs, the concentration of carbohydrate reserves in the roots start to decrease due to the carbohydrates being used for shoot recovery during resprouting (Bowen & Pate, 1993). About 50-75% of the pre-fire carbohydrate reserves are consumed after burning as seen in the Australian shrub, *S. latifolia* (Bowen & Pate, 1993). The study by Wigley et al. (2009) indicated that the carbohydrate root reserves of the woody tree, *Acacia karroo* burned a year before the experiment were a third less than that of the

woody plants burned three years before the experiment. Multiple clippings of the shoots, which simulate continuous browsing as a disturbance, greatly reduced carbohydrate levels in plant roots and eventually led to plant mortality in *Erica* species (Candell & Lopez-Soria, 1998). These different studies indicate that frequent disturbances minimize the root reserves to levels that may eventually lead to plant mortality.

According to Bowen & Pate (1993), 1.5 to 2 years after a fire, the carbohydrate root reserves of *S. latifolia* returned to pre-fire concentrations and the plants by this time had successfully completed their reproduction. The rate of recovery of root carbohydrates to pre-fire concentrations is a major factor in the survival of the woody plants. In order to understand how woody species such as *T. sericea* become dominant, it is important to understand the dynamics of root carbohydrate recovery and plant growth after fire.

1.3 Background and Problem statement

The habitat type of the Waterberg Plateau Park (WPP), is the most south western edge of the more arid end of the woodland savanna in Namibia (Schneider, 1993; Eco Impact Consultants, 2011).

The park is divided into six fire zones which are divided into fire blocks, with roads acting as fire breaks, that have different histories (fire frequency and time since last burn (TSLB)). In the 1950's the farm owners burned every 4 years during dry cycles and every 3-4 years during wet cycles (Jankowitz, 1983). After a wet cycle in 1958, the whole plateau burned from a lightning induced fire. For nineteen years, no fires occurred and overgrazing and drought had a negative effect on the vegetation, causing a decrease in palatable grass species and an increase in woody species. At the end of the 1960s a controlled fire policy was implemented where no artificial fires were allowed to burn (Eco Impact Consultants, 2011). It is perceived that the park has become far more dominated by the woody vegetation since the termination of the regular burning programme by the farmers at the end of the 1950s. The reduction in anthropogenic fires and increase in woody species, such as *T. sericea*, is thought to have caused a reduction in the density of palatable climax perennial grass species such as *Anthephora pubescens*, *Brachiaria nigropedata* and *Digitaria seriata* (Jankowitz, 1983; Eco Impact Consultants, 2011). Fires at the plateau are accidental, planned or caused by lightning (Jankowitz, 1983). The mean fire return intervals at the plateau range from 6.2 years to 18.3 years (Joubert, unpublished data).

Bush encroachment, which is a form of land degradation, causes a decrease in biodiversity and in the carrying capacity of rangelands (Sweet, 1998; de Klerk, 2004). Bush encroachment thus causes severe economic loss for commercial and communal farming areas in Namibian

savannas (de Klerk, 2004). In areas where overgrazing is maintained for many years and the use of fire has been excluded from rangelands as a method to combat bush encroachment, thicket patches become the dominant matrix and the open grassy states are reduced to form patches (Joubert et al., 2008). Fires in arid Namibian savannas play a vital role in keeping areas in an open grassy state but only during a relatively small window period, which is at the time of potential seedling establishment (Joubert et al., 2008). In more mesic areas, fire frequency is viewed as being more important, because woody plant expansion is one of the greatest contemporary threats to mesic grasslands (Briggs et al., 2005), and the WPP being semi-arid, it is important to take into consideration different fire regimes.

Fire may be an important management tool in controlling bush encroachment as it can retard the growth of trees and suppress establishment of seedlings and saplings (de Klerk, 2004; Joubert et al., 2012), only if it is properly managed. The resilience of plants to fire is partially due to the presence of “fortuitous vegetative traits” such as resprouting that enable survival after fire (Mills & Fey, 2005). The ability of woody plants to resprout after topkill from fire is partially due to the stored root carbohydrate reserves (Cruz et al., 2002). It is therefore useful to determine how quickly root carbohydrates of resprouts return to pre-fire concentrations in order to implement suitable fire management strategies to assist in combating bush encroachment. It is important to know how fire affects root non-structural carbohydrate reserves, how these interact with aboveground components, and how they influence resprouting in woody species. Such information is essential in assessing the ecological impacts of disturbances which impact woody species and for designing management strategies accordingly.

1.4 Research rational /scientific contribution of research

The aim of the study was to investigate how time since last burn in the semi-arid savanna woodland of the Waterberg Plateau Park affects the growth and concentration of root carbohydrate reserves of encroaching *T. sericea*.

There is limited information about the relationships between the amounts of resources stored in roots and the resprouting ability when the total aboveground parts of trees are fully removed or destroyed, and on the role that non-structural root carbohydrate reserves play in resprouting of woody encroaching species after a fire. Most studies have focused on Mediterranean species (Bowen & Pate, 1993; Cruz et al., 2002), while the role of carbohydrates in savanna species has not been extensively researched among different species. The effect of fire on root carbohydrate reserves has not been extensively studied in Namibian savannas and it is therefore important to understand factors facilitating the regrowth of encroachers in order to

develop suitable management strategies, depending on the management objectives of the area. The purpose of the study is to contribute towards the lack of knowledge by supplying additional information on the impact of repeated fires on growth, root structure and stored carbohydrate reserves of *T. sericea*, which affect tree vigour and survival under intense disturbances. The results from this research may assist in the management of bush encroaching species through use of fire at the Waterberg Plateau Park and areas with similar biotic and abiotic conditions.

Key Questions:

- a) How rapidly do *T. sericea* resprouts grow after a fire?
- b) How rapidly do root TNC reserves recover after a fire?
- c) What is the interaction between aboveground growth and root TNC concentrations?

Research hypothesis

- a) The growth rate of *T. sericea* resprouts is more rapid after a fire in the first two seasons than later.
- b) Root TNC reserves recover within two seasons after a fire

CHAPTER 2: STUDY AREA AND SAMPLING DESIGN

The study was conducted at the Waterberg Plateau Park, found between 20° 37' S, 17° 08' E and 20°11' S, 17°26' E, in central Namibia about 280 km northeast of Windhoek and 64 km east of Otjiwarongo (Schneider, 1993). The Waterberg Plateau Park was established in 1965 as an Eland Game Reserve and declared a nature reserve in 1972 (Erb, 1993). The park is state property and is an important conservation area which aims to protect and breed rare, endangered and economically important large herbivores (Schneider, 1993; Eco Impacts Consultants, 2011; <http://www.met.gov.na>, 2016). The park has high value species and species whose status is endangered. Endangered species such as the black rhino (*Diceros bicornis*) and near threatened white rhino (*Ceratotherium simum*) are found in the park (Mukaru, 2009). These animals as well as the African buffalo (*Syncerus caffer*) are free from the foot and mouth disease virus (Eco Impacts Consultants, 2011). Other herbivores found in the park include roan (*Hippotragus equinus*), giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcelaphus caama*), eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*), sable antelope (*Hippotragus niger*), klipspringer (*Oreotragus oreotragus*), duiker (*Raphicerus campestris*), steenbok (*Raphicerus campestris*) and warthog (*Phacochoerus aethiopicus*) (Erb, 1993).

The semi-arid savanna woodland park is about 45 000 ha in size and is found at the southwestern tip of the Kalahari woodland. The sandstone plateau lies between 1550 m and 1850 m above sea level and between 100 m to 300 m above the surrounding plains (Schneider, 1993). The top of the plateau is made up of lithified dunes belonging to the Etjo formation, which forms part of the Karoo sequence (Erb, 1993). The sandstone is brown to light grey and medium-grained. Wind-blown Kalahari sand from the Kalahari basin in the east covers the sandstone (Schneider, 1993). Soils at the plateau are sandy with relatively low clay content of 3.4 % and dystrophic (Erb, 1993; Erckie, 2007; Nghalipo, 2016).

The annual average number of days with rainfall is about 40 to 50 days (Erb, 1993). The total annual rainfall on the plateau from years 2012 to 2015 (3 seasons) was 280 mm, 914 mm and 213 mm respectively, with rainfall concentrated in the summer months (November to March) (www.sasscalweathernet.org, 2015). The average daily maximum temperature in the hottest months range between 31 °C to 32 °C and from October to January temperatures rise up to 39.4 °C (Mukaru, 2009) and the average daily minimum temperature for the coldest months is between 4 °C and 5 °C, during June the temperatures can go as low as -5 °C (Erckie, 2007) and even as low as -14 °C (Amputu, 2016). The average maximum temperatures for years 2012 to 2015 were 32 °C, 33 °C, 30 °C and 37 °C respectively, and the minimum temperatures concentrated in May to September were -4 °C, -3 °C, -2 °C and -9 °C respectively

(www.sasscalweathernet.org, 2015). Frost occurs in winter months and is associated with the topography of the plateau, with a higher occurrence of low temperatures in the inter-dune valleys (Erckie, 2007). Weather readings from September 2011 to November 2015 are attached in APPENDIX I.

2.1 Sampling design

The park is divided into six fire zones, which were further divided into fire blocks by the road system. The study was carried out over period of two years from 2013 to 2015 in four fire blocks with well-established and varied fire histories, adjacent to each other.

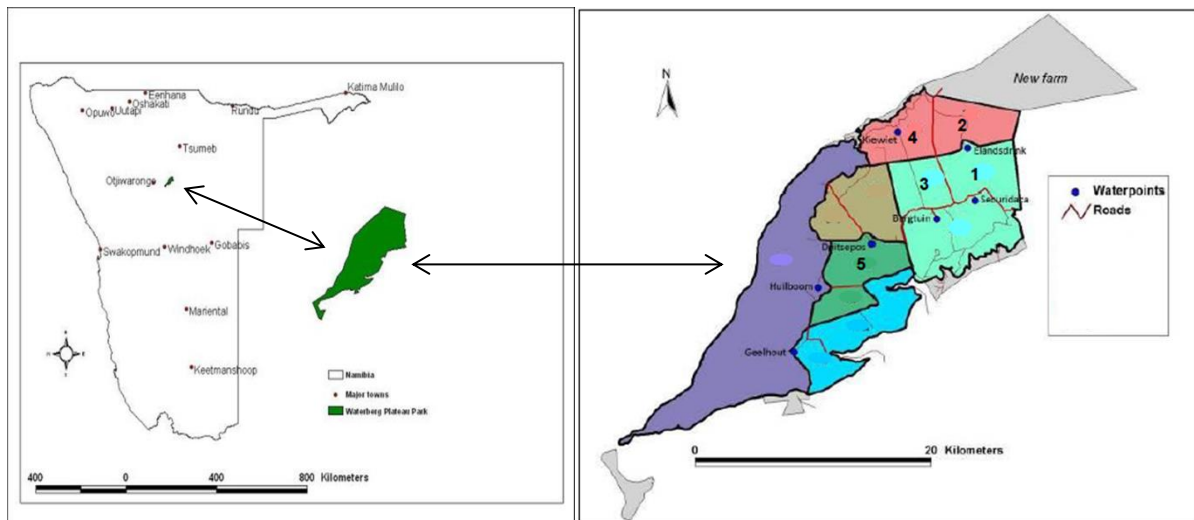


Figure 1: Location of the Waterberg Plateau Park (Source: Mukaru, 2009) and map of the park showing the four surveyed fire blocks. Roads and artificial water points in the park are included (Source: Eco Impact consultants, 2011).

Table 2.1: Fire histories of the surveyed fire blocks at the Waterberg Plateau Park by 2014 (Joubert, 2013: unpublished data). Each fire block is about 2500 ha in area.

Treatment block	Time since last burn (years)	Mean fire interval (years)
1	1	6.2
2	2	9.3
3	14	9.3
4	24	18.5

The time since last burn was at time of data collection (2014).

Table 2.2: Total woody cover in fire blocks with different time since last burn, Amputu (2016).

Treatment block	Time since last burn (years)	Total woody cover (%)
1	1	20
2	2	40
3	14	51
4	24	68

The soils in the four treatment fire blocks have a low clay content of 3,4 %, 0,6 % organic matter, 3,0 % silt and 94,7 % sand (Nghalipo, 2016). The soils on the plateau are classified as deep Kalahari sands. The vegetation is dominated by *T. sericea* and other common tree species in the park include *Acacia ataxacantha*, *Burkea africana*, *Combretum collinum*, *Combretum psidioides*, *Grewia flavescens*, *Grewia retinervis*, *Philenoptera nelsii*, *Ochna pulchra*, *Peltophorum africanum*, and *Ziziphus mucronata* (Jankowitz, 1983; Erb, 1993; Schneider, 1993; Amputu, 2016). Due to the combination of too cold and dry conditions on the plateau, some woody species, found in the woodland further north, such as *Pterocarpus angolensis* and *Baiea plurijuga*, are absent from this semi-arid savanna woodland.

Terminalia sericea, also known locally as the silver cluster leaf, is a common tree species in disturbance-prone and nutrient-poor savannas (Mannheimer & Curtis, 2009). *T. sericea* is a medium sized semi-deciduous tree species growing (when uncoppiced) as a single-stemmed tree reaching up to 8 m in height or a multi-stemmed shrub 4 – 6 m tall (Orwa et al., 2009). It grows in dense groups of various sizes forming thickets and producing a very large biomass (Amri, 2010). It is commonly used as fuelwood in many parts of southern Africa, and is also used for medicinal purposes such as curing diarrhoea, dysentery and diabetes, in rural communities (Orwa et al., 2009; Mannheimer & Curtis, 2009). *T. sericea* was chosen as the study species because it is considered as an encroaching species due to its high capacity for coppicing, its tendency to form thickets and is the dominant woody species in the study area (Jankowitz, 1983; Amputu, 2016). More knowledge of its regenerative capacity can contribute to suitable management strategies in different areas.

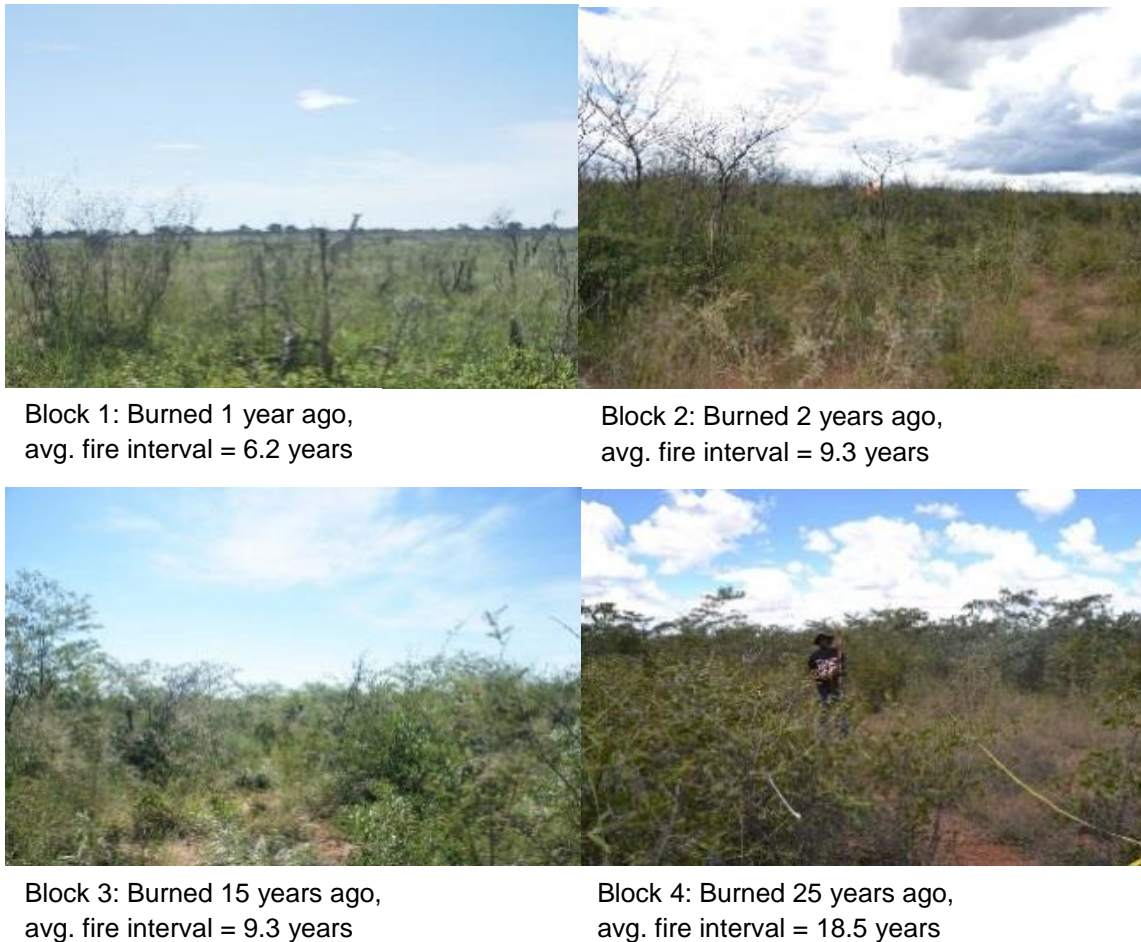


Figure 2: Images of blocks of different fire histories.

2.2 Sampling method

In each of the four fire blocks, six 200 m line transects were randomly laid out. These transects were part of a larger study under SASSCAL 148 and 73 which investigated the impacts of fire on biodiversity and bush encroachment in a semi-arid savanna woodland. The following SASSCAL research components were carried out along these transects: a vegetation survey (Amputu, 2016), soil nutrient dynamics (Nghalipo, 2016), animal resource utilisation (Uunona, 2014 & Aindongo, 2015) and buffalo movements (Joubert, unpublished data), and other current ongoing projects investigate insect, reptile and small mammal diversity.

Aboveground:

Data collection commenced in October 2014 with aboveground BECVOL 2.0 measurements (Smit, 1996) which were used to estimate growth. This study was conducted along a 200 m transect 20 m away from the vegetation survey transects. For this study, five points were

surveyed at 40 m intervals along the transect. At each point, BECVOL (Smit, 1996) measurements were done on the nearest *T. sericea* individual which was then marked with blue paste for identification purposes. The measurements included: tree height (A), height of maximum canopy diameter (B), height of first leaves or potential leaf bearing stems (C), maximum canopy diameter (D) and base diameter of foliage at height C (E) (Smit, 1996), see Figure 3. The parameters derived from the BECVOL measurements and calculations were tree height, canopy volume and leaf mass for each fire block. A total of 30 resprouts of *T. sericea* were sampled for the aboveground components in each treatment block. The skeleton height (burnt remains of stem), where present, were recorded and the mean skeleton height for each block was calculated (Appendix II). The data was processed using the BECVOL 2.0 (Smit, 1996) programme on a 32-bit computer.

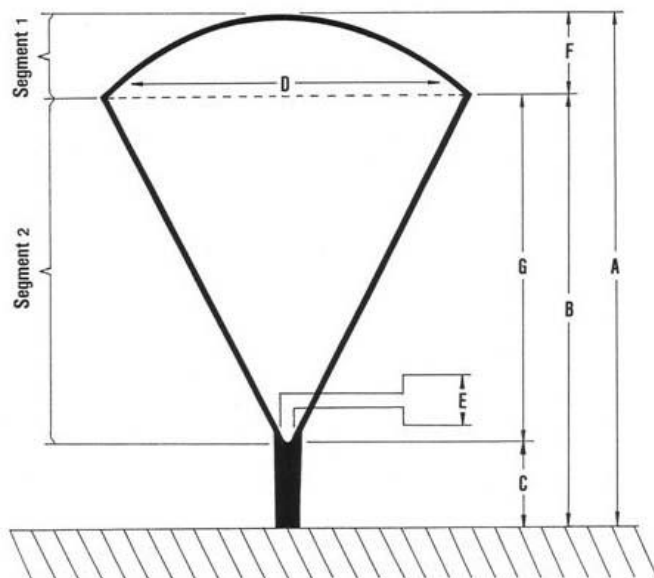


Figure 3: Schematic illustration of an ideal tree, its measurements and structure (Source: Smit, 1996).

Belowground:

Field methods

A total of forty-eight roots were excavated, 12 each from the four treatment blocks with different time since last burn at the end of the growing season in May 2015, because at this time the carbohydrates are not readily mobilised for growth as in other seasons. Along the 200 m transect, two of the already marked *T. sericea* resprouts were randomly selected for root excavation. Samples were collected when block 1, 2, 3 and 4 were burned 2, 3, 15 and 25 years ago respectively. All holes were covered after excavation. In some cases, an individual plant was defined as clumps of stems which are within 15 cm of each other. Most

individuals formed distinct clumps although some were connected underground and were identified as clones, especially in the recently burned area (Figure 5). The length, base diameter and number of roots were measured and recorded. Three discs sawn from the top 50 cm of the main root were used for TNC analysis in June 2015. The discs were labelled and stored in a freezer upon return from the field. The roots were dried, milled and TNC extracted.



Figure 4: Root measurements.



Clump of *T. sericea* in block burned 1 year ago. Exposed roots.

Figure 5: Images depicting a clump that seemed to be two individuals aboveground but were connected underground, revealing that it was one individual.

Laboratory methods

All laboratory procedures were conducted at the University of Stellenbosch due to a lack of equipment and expertise at the Namibia University of Science and Technology during the study period.

Milling in Forestry lab:

Root samples were oven dried at 65 °C. The root diameters were measured and roots were weighed. The dried roots were milled with the Condux milling machine and then finely milled in the Retsch ZM 200 mill through mesh sizes; 6.0, 2.0 and 0.5 mm at 800 revolutions per minute (rpm). The milled material was then sieved with the Retsch AS 200 shaker for 5 minutes through sieves of 850, 600, 425 and 250 microns at 60 amplitudes, in order to get a fine powder. The powder was placed in glass jars for storage purposes.



Figure 6: Condux machine, Retsch AS 200 shaker & Retsch ZM 200.

Horticulture lab:

Ethanol extraction (oligosaccharides):

4 ml of 80 % ethanol was placed into a test tube containing 100 mg of the root powder and tubes were put in a heating block for 30 minutes at 80 °C. The sugars are extracted at this temperature in order to get the molecules actively moving and to kill enzymes that may consume sugars, with the 80 % ethanol used to denature any active enzymes. Tubes were centrifuged for 5 minutes at 3000 relative centrifugal force (rcf), centrifugation separates the liquid from the residue. The centrifuged liquid was decanted into a different tube. 4 ml of 80 % ethanol was added to the residue and the above process was repeated three times. The liquid in the second test tube was used for further oligosaccharide analysis.

Water extraction (polysaccharides):

After decanting the last ethanol extract, 4 ml of distilled water was added to the remaining residue and test tubes were put in a heating block at 80 °C for 24 hours. The tubes were centrifuged and liquid was decanted into a different tube. This process was repeated three times. The decanted liquid was used for further polysaccharide analysis.

Starch extraction:

After decanting the third water extraction, in the remaining residue, 3 ml of a buffer solution at pH 4.7 was added and the tubes were placed in a heating block at 100 °C for 1 hour. The

buffer solution was added in preparation of amyloglucosidase (AMG) enzyme, which works best at this pH. The tubes were heated at 100 °C because this is the temperature (80-100 °C) where the starch molecules start opening up and the solution becomes gelatinous. The tubes were left to cool before adding 3 ml of the AMG solution. Tubes were then heated at 60 °C for 22 hours, this is the temperature most suitable for enzymes to work and break down glucose completely. After 22 hours, the temperature was increased to 100 °C for 30 mins. The tubes were then cooled and centrifuged. The decanted liquid was used for starch analysis.

Colorimetric test:

For the ethanol extraction, a x 10 dilution was done where 444 µl of ethanol extract and 4000 µl of distilled water were added into a test tube and vortexed to mix the solution. From the diluted solution, 200 µl was pipetted into 3 test tubes. One out of the three tubes served as a buffer solution; therefore 200 µl water was added to this tube and in the other test tubes 200 µl of 5 % phenol was added. The tubes were vortexed and 1 ml sulphuric acid was added to each tube. The solution was mixed and left to cool. Each glucose analysis was conducted in triplicate and calibrated against a glucose standard. A spectrophotometer was used to analyse the solution where blue light is absorbed by the yellow solution. The readings were done at an optical density of 490 nm. The above mentioned procedure was repeated for water and starch extractions.

Water extract: a x 4 dilution = 665 µl water extract and 2000 µl water

Starch extract: a x 21 dilution = 200 µl starch extract and 4000 µl water

Dilutions were made for each extraction because end results were too yellow and the spectrophotometer could not read them.

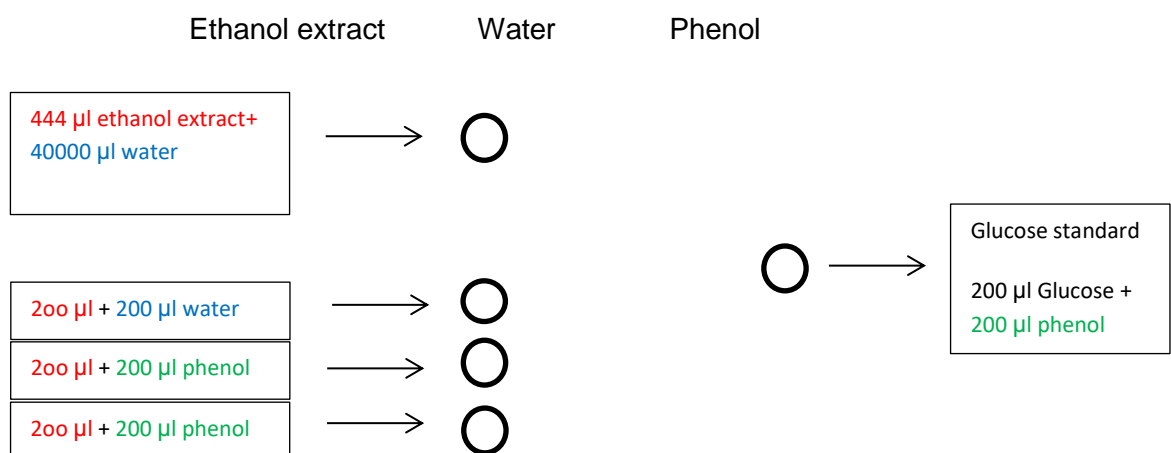




Figure 7: Example of triplicate dilutions.

Age determination

From the excavated roots, a disc was collected from the topmost part of each root for age determination. Most roots had a dead and hollow upper-most part due to fires or rotting therefore, a disc was taken from the biggest lateral root. The discs were sanded with sandpaper of increasing grades ranging from: 80 mm to 1200 mm. The age rings were counted, measured from bark to pith using the LinTab tree ring microscope at the Forestry lab in Stellenbosch.



Figure 8: LinTab tree ring microscope for measuring age rings.

2.3 Data analysis

All data was processed using STATISTICA 12 statistical software (Stat Soft Inc, 2002). The Kolmogorov-Smirnov test was used to test for normality of data. Where data was normally distributed, the main effects one-way of variance (ANOVA) was used to test for significant differences among treatments. The Fishers LSD *post hoc* test determined differences among treatments when ANOVA results were significant. For data that was not normally distributed, the Kruskal-Wallis non-parametric test was used followed by multiple regressions. The study

follows the space-for-time substitution because it analyses the temporal trend of different aged sites (Pickett, 1989). We therefore assumed that the space aspect did not vary significantly which is confirmed by the soil study conducted in the same time period which shows little variability in soil texture (Nghalipo, 2016).

Aboveground data: The data was not normally distributed therefore the Multiple comparisons (2-tailed) Kruskal-Wallis non-parametric test was used to test for significant differences. Differences in mean tree height, canopy volume, leaf mass and stem diameter with time since last burn were calculated in Statistica 12 (Stat Soft Inc., 2002).

The canopy density was calculated as Leaf mass/Canopy volume = density (g/m^3) for each block.

Absolute growth rate = change in tree height over a period / period of time i.e. (tree height year 2 – tree height year 1) / (year 2-year 1)

Relative growth rate = (change in tree height over a period / previous tree height) x 100

One of the transects that were laid out in Fire block 3, were in an area that was burned in 2014 (0 years ago). The transect was omitted for purposes of consistency, because it did not give a true representation of last burned 24 years ago, thus making the sample size of the fire block a total of 25 resprouts.

Belowground data: Kolmogorov-Smirnov test revealed normally distributed data for belowground components. A one-way ANOVA was used to test for significant differences in root TNC concentration among blocks with different time since last burn. Where data was significantly different, Fishers LSD post-hoc was used to test which blocks were significantly different (Stat Soft Inc., 2002).

CHAPTER 3: RESULTS

In this section, letters in figures are used to indicate significant differences, where letters shared among groups indicate no significant difference ($p < 0.05$). The bars indicate standard error, n = sample size and H = Kruskal Wallis test statistic. For the aboveground components, the sample size is as follows in different fire blocks: 1 year ago $n = 30$, 2 years ago $n = 29$ (one sample lost from data), 14 years ago $n = 25$ (transect in area burned 0 years ago was omitted), 25 years ago $n = 30$. For belowground components $n = 12$ in all fire blocks.

Aboveground

The tree height of *T. sericea* resprouts increased rapidly within the first two years after fire among the four fire blocks with different times since last burn, $H = 75.55$, $p < 0.05$ (Figure 3.1). Tree height growth follows the logarithmic curve and doubled in size from year 1 to 2 since last burn. A minimum height of 0.4 m, maximum 1.2 m in 1 year block, minimum of 0.5 m and maximum 1.8 m in block burned 2 years ago, and a minimum of 0.9 m and maximum 4.2 m in blocks burned 14 and 24 years ago.

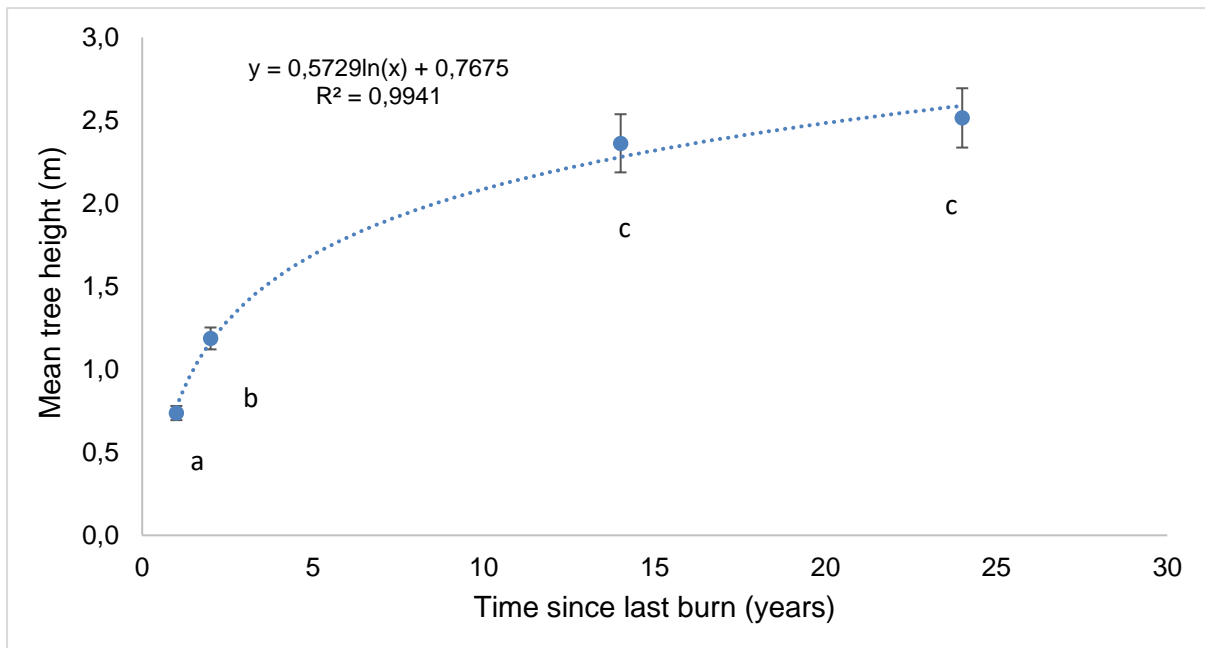


Figure 3.1: Comparison of mean tree height of *T. sericea* resprouts in fire blocks with different time since last burn.

Table 3.1: Height growth rate of *T. sericea* over different time periods. GR = growth rate.

Years	Absolute height GR/year (m)	Relative height GR (%)
1 to 2	0,45	61
2 to 14	0,10	8
14 to 24	0,01	1

Mean tree height rapidly increased by 61 % from year 1 to 2 relative to its previous height. From year 2 to 14 and 14 to 24, the rate declined by an order of magnitude.

The canopy volume of *T. sericea* resprouts differed significantly among the four fire blocks with different time since last burn, $H = 30.56$, $p < 0.05$ (Figure 3.2). In the first two years after a fire there was no significant change in the canopy volume of resprouts. The growth in canopy volume followed an exponential curve. Change in canopy volume occurred gradually between 1 and 24 years since last burn.

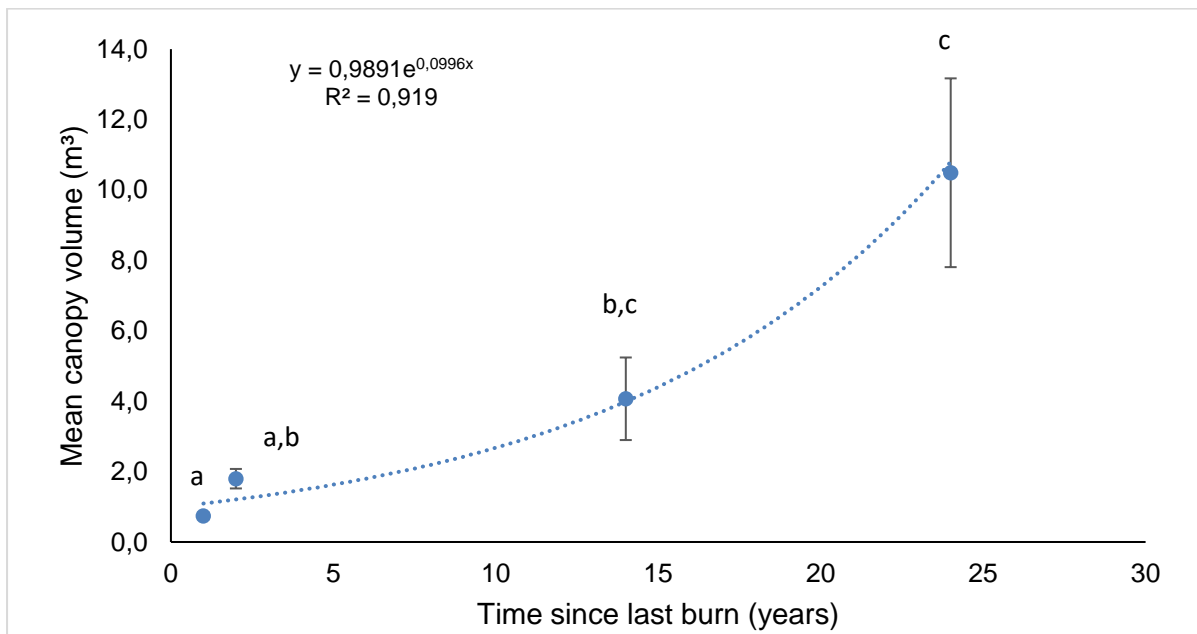


Figure 3.2: Mean canopy volume of *T. sericea* resprouts in fire blocks with different times since last burn.

Table 3.2: Canopy growth rate of *T. sericea* over different time periods.

Years	Absolute canopy GR/year (m ³)	Relative canopy GR (%)
1 to 2	1,06	143
2 to 14	0,19	11
14 to 24	0,58	14

Mean canopy volume rapidly increased by 143 % from year 1 to 2 relative to its previous canopy volume and slowed down thereafter.

The leaf mass of *T. sericea* resprouts differed significantly among the four fire blocks, $H = 31.30$, $p < 0.05$ (Figure 3.3). In the first two years after a fire there was no significant change in the leaf mass of resprouts. The exponential increase in leaf mass occurred between 1 to 14 years after a fire.

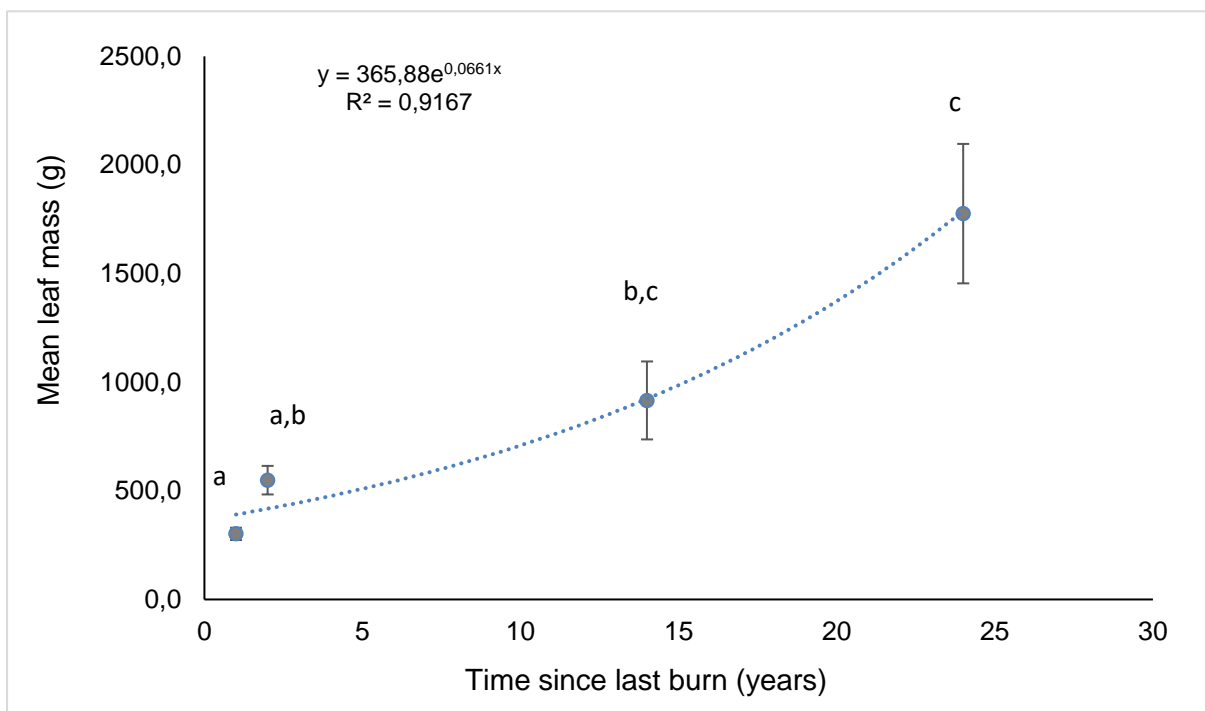


Figure 3.3: Mean leaf mass of *T. sericea* resprouts in fire blocks with different times since last burn.

Table 3.3: Leaf mass growth rate of *T. sericea* over a period of 25 years.

Years	Absolute leaf mass GR/year (g)	Relative leaf mass GR (%)
1 to 2	247,20	82
2 to 14	30,58	6
14 to 24	78,16	9

Mean leaf mass rapidly increased by 82 % from year 1 to 2 relative to its previous mass, which is about a 10-fold difference.

The aboveground canopy density differed significantly among fire blocks, $F = 45.9$, $p < 0.05$ (Figure 3.4), with density being two times higher in blocks burned 1 and 2 years ago than blocks burned 14 and 24 years ago.

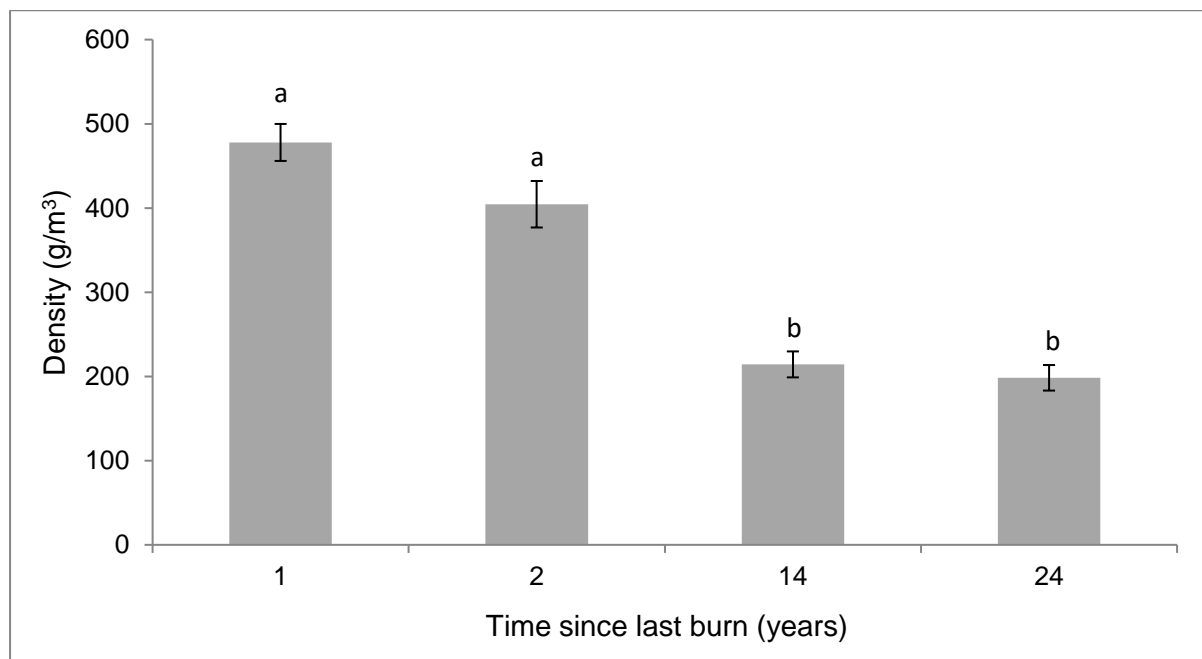


Figure 3.4: Mean canopy density of *T. sericea* in fire blocks with different time since last burn.

The number of stems of *T. sericea* resprouts differed significantly among the four fire blocks, $H = 64.08$, $p < 0.05$ (Figure 3.5). The graph follows the logarithmic decay curve, where the number of stems per individual declines with an increase in time since last burn. The highest mean number of stem per individual tree is 12 in the recently burned blocks and the lowest mean number of stems is 2 in the blocks burned many years ago.

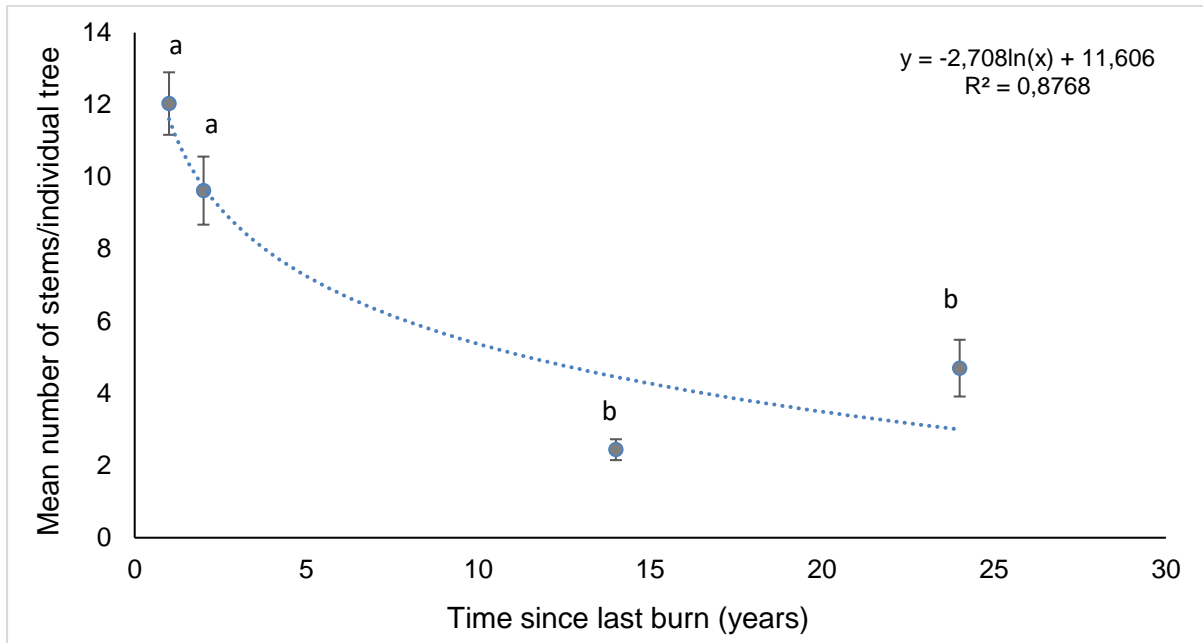


Figure 3.5: Mean number of stems per individual *T. sericea* woody tree in fire blocks with different time since last burn.

The stem diameter of *T. sericea* resprouts differed significantly among the four fire blocks, $H = 80.76$, $p < 0.05$ (Figure 3.6). There is no significant change in stem diameter within the first two years after fire. A logarithmic increase in diameter occurs between 1 to 14 years after a fire, with a threefold increase in diameter.

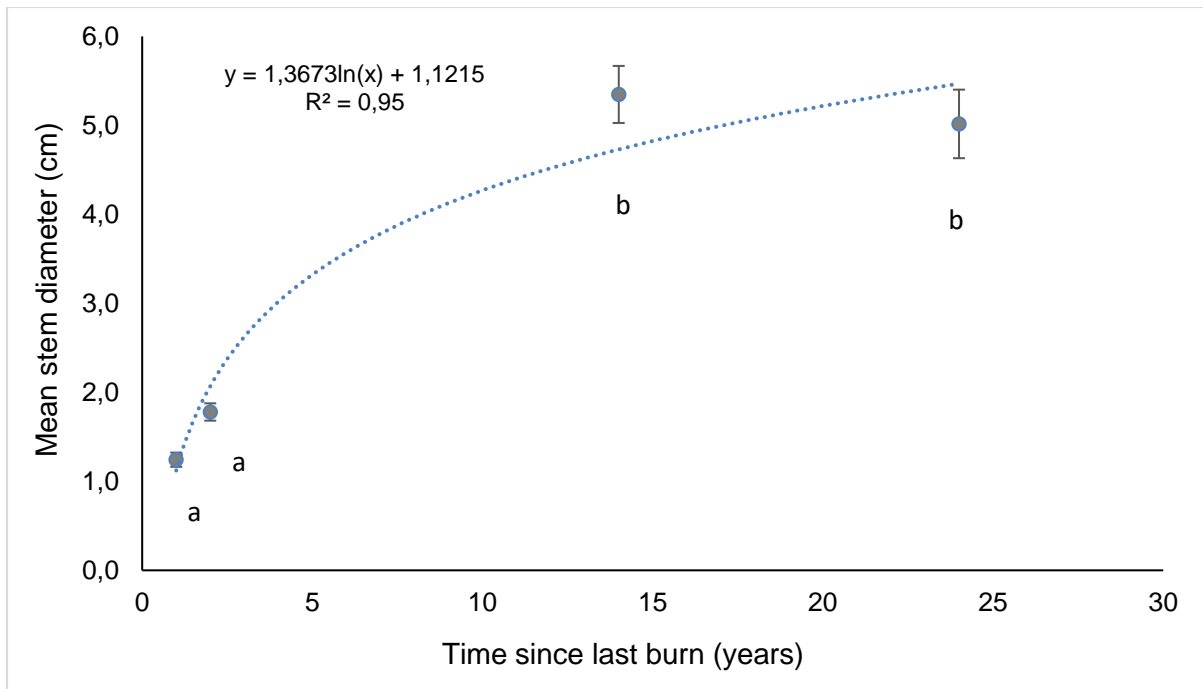


Figure 3.6: Mean stem diameter of *T. sericea* resprouts in fire blocks with different time since last burn.

Belowground

In early years of growth, *T. sericea* individuals have a tap root system but as the trees get older, the main root curves at a 90° angle and take on a lateral root system (Figure 3.7). In the present study, younger individuals with no skeletons had a tap root system while individuals with skeletons that resprouted after the fires had lateral root systems (Figure 3.8). See Appendix III for root measurements.

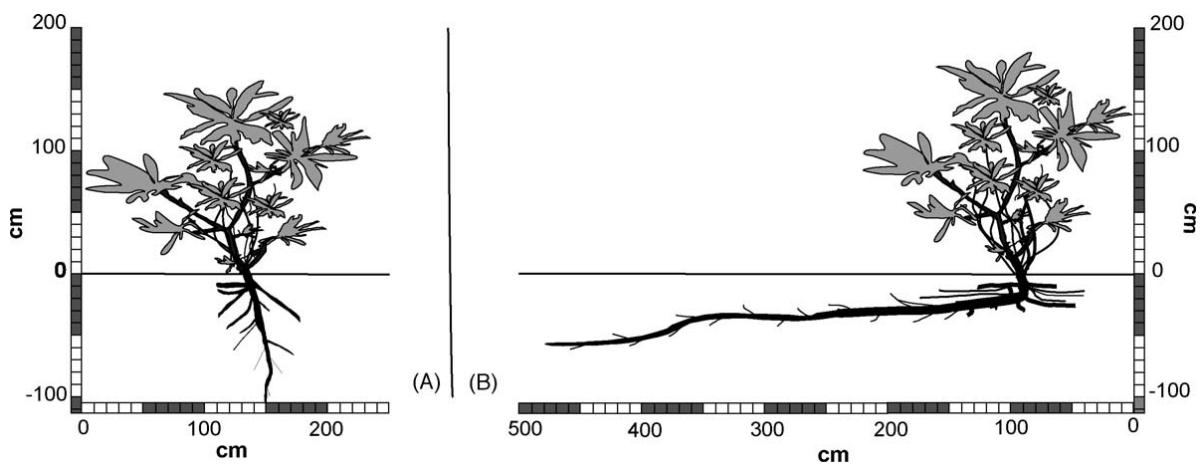


Figure 3.7: Rooting systems of *T. sericea* (Source: Hipondoka & Versfeld, 2006).



Individuals without skeletons have a taproot system



Individuals with skeletons have a lateral root system

Figure 3.8: Different root structures of *T. sericea* at the WPP.

Table 3.4: Total length and maximum depth of excavated roots in blocks with different time since last burn.

TSLB	Length of main root (cm)	Root Type	Max Depth (cm)	No. of lateral roots
2	360	lateral	87	3
	550	lateral	30	5
3	650	lateral	24	9
	610	lateral	24	2
15	380	lateral	41	5
	590	lateral	28	3
25	380	lateral	28	2
	410	lateral	30	6

The block burned 3 years ago had the longest excavated main roots, which were dug out at shallow depths of 24 cm.



Figure 3.9: Length of entire main root

From the excavated roots, each *T. sericea* individual has about 8 lateral roots on average, with 2 lateral roots on an individual being the minimum across all fire blocks and a maximum of 23 lateral roots on an individual in the block burned 25 years ago (Appendix III).

The effect of time since last burn on root TNC concentration was significantly different, $F = 3.58$, $p < 0.05$ (Figure 3.11). *Post hoc* analysis indicated that the block burned 3 years prior to the study had significantly higher root TNC than the other blocks burned 2, 15 and 25 years ago. There appears to be a rapid replenishment of reserves between 2 to 3 years after fire.

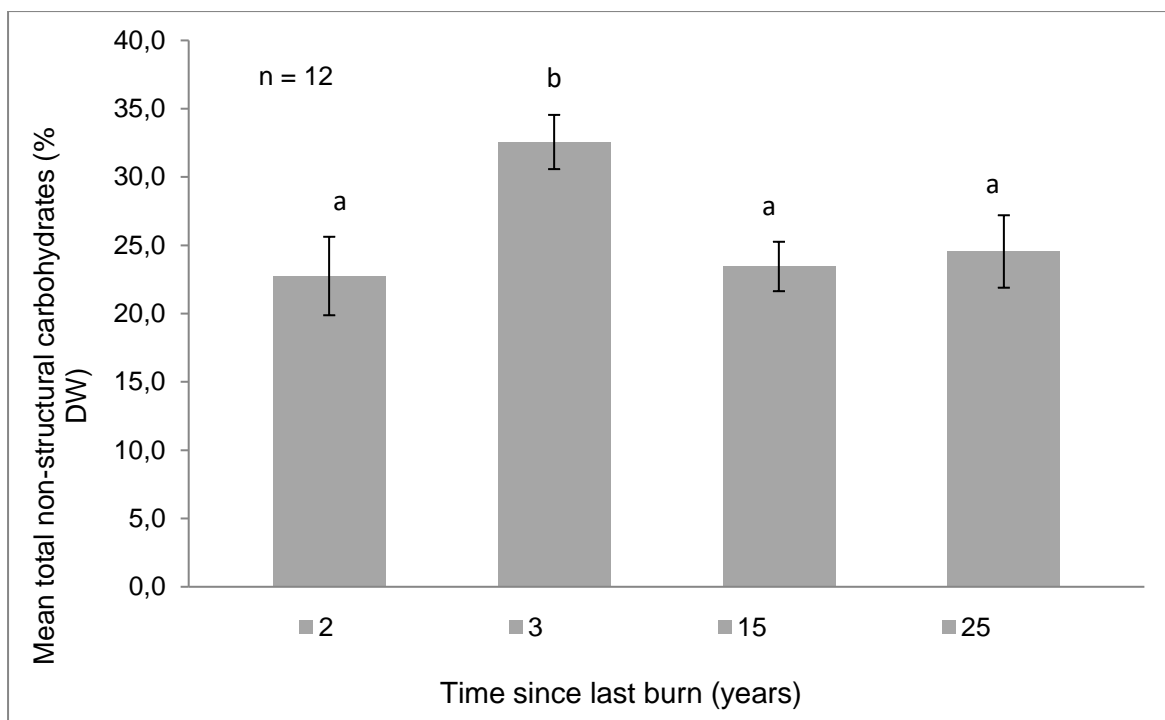


Figure 3.10: Mean root TNC concentration among fire blocks with different time since last burn.

Table 3.5: Mean concentration of oligosaccharides, polysaccharides and starch in different block with different time since last burn.

TSLB (years)	Oligosaccharides (mg/g)	Polysaccharides (mg/g)	Starch (mg/g)
2	5,3	4,4	13,1
3	6,0	5,6	21,0
15	7,6	4,5	11,3
25	5,9	4,6	14,1

Oligosaccharide and polysaccharide concentrations occurred in low quantities compared to starch (Table 3.5) and were not significantly different among the fire blocks. Starch concentrations were approximately 2 to 3 times higher than the other fractions and differed significantly. The block burned 3 years ago had significantly higher concentrations and this solely contributed to the overall greater TNC concentration found there.

An analysis of Variance showed that the effect of time since last burn on average age of roots was not statistically significantly different among blocks with different TSLB, $F = 1.83$, $p > 0.05$ (Figure 3.11), suggesting that the trees mostly established as a cohort around 20 years ago.

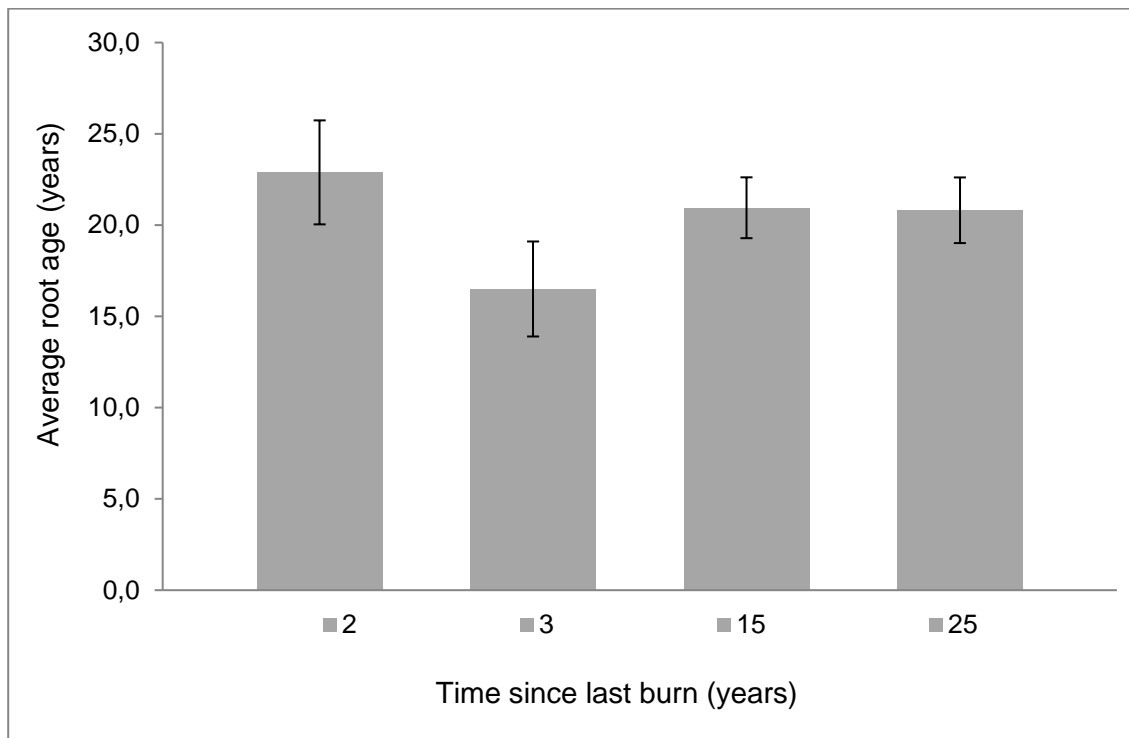


Figure 3.11: The average age of root sections in fire blocks of different time since last burn.

CHAPTER 4: DISCUSSION AND CONCLUSIONS

An increase in fire frequency, as described in Section 1.2.1, may cause an overall decrease in tree height even though individuals rarely suffer mortality (Smit et al., 2010; Higgins et al., 2000). The study on the influence of fire frequency on woodland structure and composition in Northern Gonarezhou National Park, Zimbabwe by Gandiwa & Kativu (2009), recorded a decrease in tree height of *Colophospermum mopane* and *Combretum apiculatum* with increasing fire frequency in the woodland area. This is due to fire limiting growth in terms of height of individuals (Figure 3.1). Fires that are more frequent would cause a firetrap that would lead to a decrease in the average height of individuals. The fire of 2013 caused topkill of trees that ranged from a height of 0 m to 3.6 m, as seen in the skeleton heights of the recently burned blocks (Appendix II). *Terminalia sericea* tree height follows a logarithmic growth curve, where a positive acceleration phase in height is observed over a period of one year after burn (Figure 3.1). After fire, the rapid increase in height, canopy volume and leaf mass growth rates over a period of one year (Table 3.1, 3.2 & 3.3), indicates the rapid resprouting ability of *T. sericea* immediately after a disturbance. The fast resprouting response is one of the attributes that make *T. sericea* a good encroacher. At exactly which stage both absolute and relative growth decline can be detected, but is not known.

Canopy expansion leads to plants intercepting more light thus causing them to be more productive by increasing the photosynthetic rate to some extent (Bond, 2000). The expansion of tree canopies may reduce grass photosynthesis and grass primary productivity due to shading and this may lead to trees outcompeting grasses, eventually leading to bush encroachment (Mordelet et al., 1997; Tanentzap et al., 2012). *T. sericea* has a wide canopy expansion and can thrive in nutrient poor soils thus making it an effective encroacher.

Savanna trees only reach the adult population once they escape fire zone, which is influenced by grass biomass (Higgins et al., 2000). When trees escape from this zone, ground fires rarely affect them, and therefore they continue to grow and establish. The rapid increase in tree height in a period of one year may be attributed to the woody trees growing to heights where they could possibly escape ground fires, thus allowing them to establish more efficiently. Between 2 to 14 years after a fire, the height, canopy volume and leaf mass growth of individuals is slow, with a maximum reached at about 14 years. This does not mean that growth stops but rather slows down as the plant does not allocate as much resources for growth because it managed to escape the fire zone.

The amount of leaf mass density is two times higher in the recently burned areas (Figure 3.4), which may lead to increased photosynthesis and thus lead to an increase in root

carbohydrates produced for growth and storage. The increase in leaf mass indicates higher available browse due to the new leaves, shoots, and stems that are more accessible, palatable and nutritious (Joubert et al., 2012; Scholes & Walker, 1993).

Terminalia sericea is a multi-stemmed sprouting tree, which according to Bond & Midgley (2001), is usually shorter than non-sprouters and risk being shaded by single stemmed individuals, and therefore they are usually limited to less productive or frequently disturbed sites as in the case of *T. sericea* on the plateau. The recently burned blocks have the highest number of stems per individual tree (Figure 3.5). The high number of stems per individual is usually associated with basal coppicing in response to burning (Gandiwa & Kativu 2009). Multiple stems are important because they increase the persistence of trees by providing a different life history strategy from seed regeneration and these contribute to maximizing the length of time individuals occupy a site (Bond & Midgley, 2001; Tanentzap et al., 2012). The high number of stems in recently burned blocks may be due to the fast resprouting ability of *T. sericea* and these are essential for the primary growth and survival of the woody trees. As the time since last burn increases the number of stems decrease will the stem diameter increases (Figure 3.5 & 3.6). This is due to secondary growth where stems begin to thicken and more reserves are allocated to structural growth towards the growth of a single stem. This may lead to trees escaping the fire zone, herbivory and understory shading. In the recently burned areas reserves are mobilized for growth to escape the fire zone and for storage in preparation for another disturbance (Wigley et al., 2009).

From the leaf mass density and the stem diameter, root reserves can be seen to be mobilized in the early years after a fire to leaf production to increase the amount of photosynthesis (which was not measured in this study) for replenishment and later into the woody structure to escape the fire zone.

Results from the vegetation survey data collected from Amputu (2016) during the study period, indicated a significant trend of increasing cover with an increase in years since last burn (Table 2.2). *Terminalia sericea* also had the highest cover and therefore was the most dominant of the species in the study area (Amputu, 2016). These results reveal how quickly *T. sericea* resprouts after a fire and its efficiency as a competitor due to it dominating the study area.

Terminalia sericea has an interesting root structure. Younger individuals have tap root systems and as the tree grows older the roots grow at a 90° angle, thus changing to a lateral root structure (Hipondoka & Versfeld, 2006). The change from taproot to lateral roots is an attribute that makes *T. sericea* an effective encroacher, because this enables trees to acquire water from the topsoil in low rainfall areas and thus compete with grasses for moisture (Hipondoka & Versfeld, 2006). Majority of trees with a skeleton height of >1 m had lateral roots and trees

without any skeletons had tap roots. This shows that as a tree increases in size, the root structure changes to support absorption of water in the topsoil which increases its competitive ability. The maximum depth dug in pursuit of roots ranged from 17 cm to 105 cm, these depths indicate how close to the surface the roots are in order to efficiently absorb moisture. At this stage, the trees are already established and are entering a phase of trying to outcompete competitors, such as grasses.

The resprouting ability of a plant is influenced by the size of the plant before the fire and by the TNC stored in belowground organs (Maguire & Meneges, 2011). The size of the trees before the fire, as seen in the skeleton heights (Appendix II), indicates that *T. sericea* trees were at an average height of 1.7 m, and from the root TNC concentrations in the block burned 3 years ago, these trees have sufficient root reserves to mobilize for regrowth after a disturbance.

Different fire regimes have a significant effect on the root TNC concentration of resprouts, with levels decreasing after a recent fire. A study done on *Stirlingia latifolia* indicated that root reserves fell by 50-75 % when plants resprouted after burn and took 2 years to return to pre-fire concentrations (Bowen & Pate, 1993). The repeated cutting (as a disturbance) of these trees caused further decrease in root carbohydrates and eventually death in some plants (Bowen & Pate, 1993). The topkill by fire caused the removal of aboveground components therefore resources need to be mobilized to regain the aboveground parts of the trees for photosynthesis. The mobilization leads to the depletion of stored root TNC concentrations of *T. sericea*, however, in this case a full recovery to pre-fire conditions is observed 2 to 3 years after a fire and an over compensation of reserves occurs 3 years after a fire. This rapid increase contributes to *T. sericea* successfully establishing and invading areas.

Soil moisture and nutrient availability may affect the amount of reserves stored by the plant in its below-ground organs prior to the disturbance and may also determine the relative size of the storage organ (Cruz & Moreno, 2001), which in turn, may affect the capacity of the plant to resprout (Cruz et al., 2002). The soils in the study area could be classified as nutrient poor (Nghalipo, 2016), therefore *T. sericea* trees rely more on their root stocks than on soil nutrients for resprouting purposes. After a fire, the residue left after burning of vegetation, known as ash, temporarily adds nutrients to the soil after one or two years since last burn. The ash nutrients may also have contributed to the rapid growth rate and replenishment of root TNC reserves of *T. sericea*.

The major carbohydrate contributing to growth of *T. sericea* in the present study is starch (Table 3.5). The oligosaccharides and polysaccharides contribute to the root TNC concentration but fire has more of an effect on starch concentrations, this was also found by

Kayofa (2015) in *Pterocarpus angolensis*. In *E. australis*, starch was found in greater amounts than other carbohydrates, with concentrations of 60–70% (Cruz & Moreno, 2001). Trees that are not in the understory have a higher photosynthetic capacity because they are more exposed to sunlight (Bond, 2000), therefore these may produce more carbohydrates for storage compared to other blocks. Trees in the block burned 3 years prior to collection were not found in the understory, therefore they could produce more leaf mass which leads to higher photosynthesis and thus produce and store more reserves compared to trees in blocks burned 15 and 25 years ago. This explains the high concentration of root TNC in the block. The root TNC concentrations accumulated up until 3 or more years after a fire, but by 15 years it stabilized to a lower level. The exact time when it stabilizes is unknown, but it is between 3 and 15 years.

The repeated disturbance of fire causes a reduction in root carbohydrates in woody species which limits the ability of the tree to resprout and thus increases mortality (Candell & Lopez-Soria, 1998), therefore more frequent fires can cause damage to trees by topkill and depleting stored reserves. The frequency of a disturbance has a significant role to play in the amount of stored reserves. The fires in this study were not as frequent, highest frequency being 6.2 years, which gave the trees sufficient time to build up root reserves during the fire free period. When the fires occurred, the trees had enough stored carbohydrates that were mobilized for growth and enabled the trees to rapidly resprout. Seedlings of resprouting plants allocate more resources to belowground storage while seedlings of non-resprouters allocate resources to aboveground parts (Bowen & Pate, 1993). The high concentration of root TNC compared to the aboveground components, three years after a fire, portrays that *T. sericea* as a resprouter allocates more of its easily mobilized carbohydrate resources to belowground storage. If the fires were more frequent, different results in the amounts of reserves might have been observed.

In younger or newly resprouting trees, it may be beneficial to make a trade-off between storage and growth, where photosynthesis in severe conditions may provide the growth potential needed for trees to establish but with greater risk of mortality (Bond, 2000). There is a cost associated with resprouting, where the plant stores resources in order to maintain a bud bank and support rapid regrowth after a disturbance, as depicted in the results where trees in blocks burned 2 to 3 years ago are in a height class of 1 – 2 m but have high replenishment, thus indicating a prioritization of photosynthesis for storage purposes over growth. Different studies have shown that resprouters have higher levels of carbohydrates than non-resprouting species (Verdaguer & Ojeda, 2002; Schwilk & Ackerly, 2005). As soon as a tree is able to photosynthesize, regardless of the aboveground biomass, it allocates majority of its resources to storage in preparation for another disturbance or for growth. Three years after a fire the root

carbohydrate concentrations in *T. sericea* are the highest thus indicating a rapid replenishment, therefore carbohydrate concentrations of *T. sericea* take 2-3 years to return to pre-fire concentrations. The fast replenishment of carbohydrates is another factor that makes *T. sericea* an effective encroacher.

Some studies have indicated that the diameter of the storage organ, i.e. lignotuber size of *Acacia karoo*, has an effect on the amount of TNC stored in the organ (Wigley et al., 2009). Smaller diameter storage organs have higher TNC concentrations, as it increases in size after a disturbance woody material accumulates, therefore diluting the TNC concentration (Wigley et al., 2009). Larger organs will store more TNC but at low concentrations (Wigley et al., 2009). Multiple regressions show that for *T. sericea* at the WPP, the lateral root base diameter does not significantly affect root TNC concentrations.

The success of seedling and saplings may be measured by their ability to produce and store belowground resources and maintain foliage above the shade of competitors, by maximizing allocation to growth (Day et al., 2002). An increase in tree age of the coniferous red spruce (*Picea rubens* Sarg.), in a light limited forest, showed a significant increase in leaf mass per unit area (Greenwood et al., 2008). In this study, the root age of the main lateral root was not significantly different among the fire blocks, but the different times since last burn which may give an indication of the age of trees (if the age of the uppermost part of the burned/hollow roots could be determined), may have the same effect on the leaf mass as in the case of the red spruce. If the uppermost burned part of the roots could be determined for age, most of the trees would be found to be older than 25 years and could all be classified as resprouts. As a tree gets older, the maximum leaf area decreases which causes a decline in the photosynthetic capacity of trees (Greenwood et al., 2008). The decrease in the photosynthetic capacity in older trees may have led to less carbohydrate reserves stored in fire blocks burned 15 to 25 years ago compared to the blocks burned 2 to 3 years because older trees cannot efficiently photosynthesize. As the relative growth rates decline, less photosynthetic products are allocated for storage.

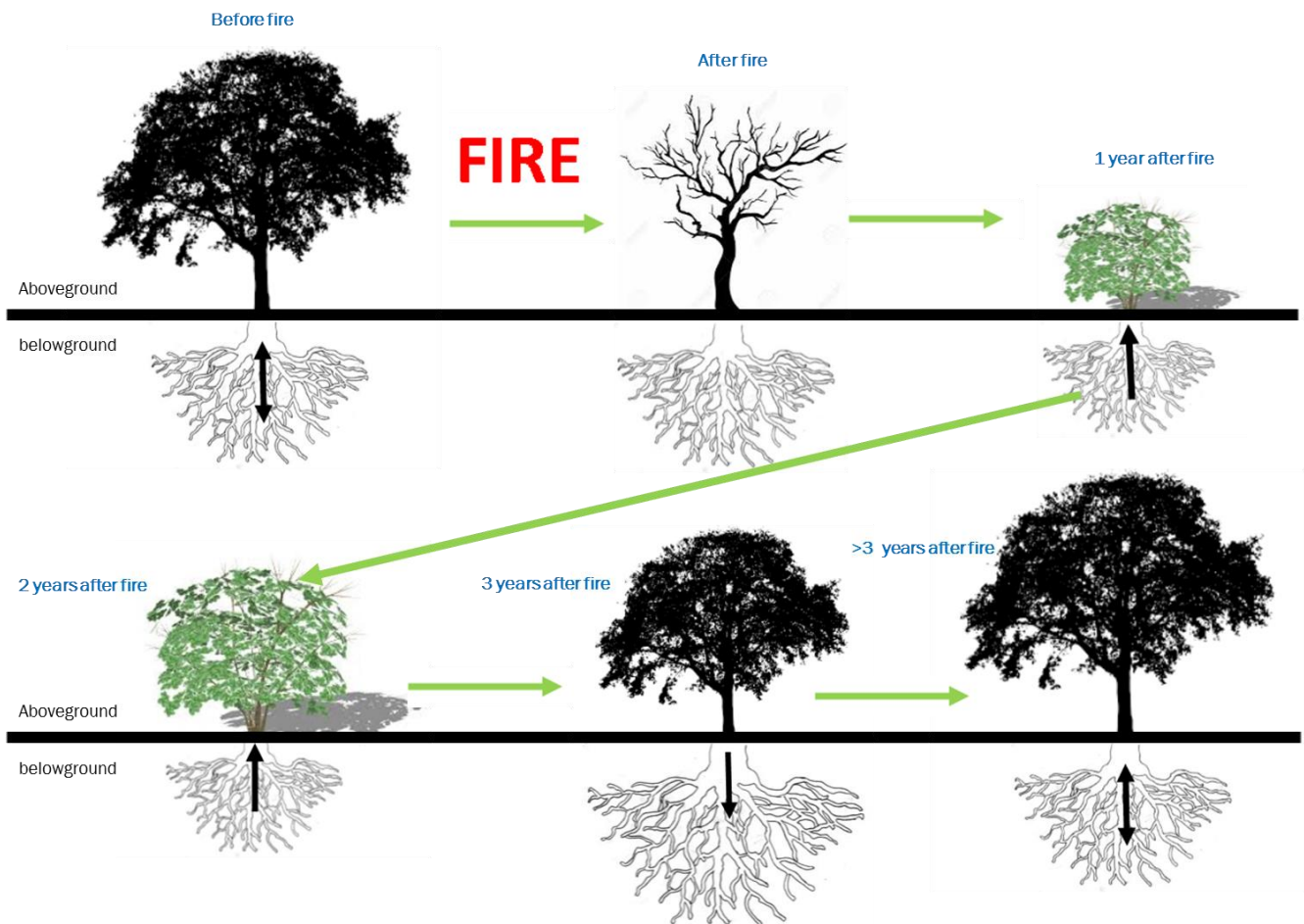
The absence of fire for 15 and 25 years, with a return interval of about 9 years, is not suitable to combat bush encroachment because by this time the trees have extended canopies which shade shorter vegetation such as grasses (Tanentzap et al., 2012). The roots at this stage are well extended to the surface which enables them to get access to surface water and may outcompete grasses which rely on the same water source (Hipondoka & Versfeld, 2006). This causes a low fuel load in these areas due to a lack of grass biomass.

CONCLUSIONS

The aim of this study was to better understand how fire affects the resprouting ability of *T. sericea* and how rapidly root TNC are replenished after a disturbance. The results indicated a rapid increase in aboveground components (tree height, canopy volume, leaf mass) over a period of one year. The results give an indication of the growth rate of *T. sericea* in the study area, with the rate being fairly rapid within a year of burning, this could be attributed to its fairly good resprouting and encroaching abilities. The aboveground components also give an indication of the available browse of *T. sericea* in the study area, with high available browse present in recently burned sites due to growth of new palatable shoots and leaves. The high browse in recently burned blocks may be due to the fast growth rate of aboveground components within a period of one year, relative to its previous size. The high cover of *T. sericea* in the study area is an indication of its tendency to coppice vigorously after a disturbance and successfully encroach the area. The relative height growth rate of this species rapidly increases and then declines between 2 and 14 years after a fire, this may be because of several reasons: a) trees channel carbohydrates into stem diameter growth, b) photosynthesis slows down due to age related decline and c) growth is allocated to other components such as wood.

Compared to other studies, a high root TNC concentrations of about 20% is observed in *T. sericea*, this amount of reserves is sufficient to allow for resprouting. Fire does cause a reduction in TNC concentration, but due to *T. sericea* being a resprouter and an effective encroacher, the concentrations are replenished fairly quickly, within 2-3 years after a fire to pre-fire concentrations. The TNC concentration does not show the same trend of gradual increase as in the aboveground components, due to *T. sericea* as a resprouter mobilizing most of its resources to storage. A trade off is seen to be made between growth and storage where in the first year priority is on leaf production for photosynthesis in order to produce more root TNC after a disturbance for storage which may be deployed for growth or as a reserve for another disturbance. The age of the roots did not have a significant effect on above and belowground components. Size and age cannot be separated from one another, because the bigger the tree, the older it is, in most species. *T. sericea* seems to be well adapted to relatively high fire frequencies. In the present study, based on the carbohydrate reserves after a fire, the current fire regime could not suppress the growth of *T. sericea*.

Conceptual framework



- Aboveground tree size represents the aboveground biomass and tree size at various stages
- Belowground root size represents the amount of root TNC reserves
- The black arrows represent the flow of reserve where:
 - ❖ Up-down arrow = reserves stored in roots from photosynthesis and some used for aboveground growth
 - ❖ Up arrow = reserves mobilized for aboveground growth
 - ❖ Down arrow = reserves are being stored in roots

Before the fire, carbohydrate reserves are being mobilized for growth of aboveground parts (if necessary) and there is sufficient aboveground biomass for trees to photosynthesize and store carbohydrates in the roots. A fire occurs and there is topkill. From year one and two after a fire, the root reserves are mobilized for aboveground growth. Three years after a fire, the tree has gained sufficient aboveground biomass to photosynthesize and reserves are being replenished and stored in the roots in preparation of another disturbance. After the third year, the root reserves are being mobilized for more aboveground growth and the root carbohydrate concentrations return to the amount before the fire.

CHAPTER 5: MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS BASED ON THIS STUDY

Results suggest that for this study species, *T. sericea*, an increase of the frequency in prescribed burning could lead to the maintenance of savannas through reduction in height of trees and in canopy expansion. It is important to take into consideration effects of fire frequency which were not a major part of this study. *Terminalia sericea* has a rapid root TNC replenishment, therefore to control its encroachment with fire, a few back to back fire years in very high rainfall cycles could suppress the growth but this depends on the soil conditions, amount of grass biomass and woody cover of other species.

Fire regime components such as fire intensity, frequency and season are important and need to be implemented into burning policies as these affect the woody vegetation cover. Rainfall is a major component to consider in policies as it determines the fuel load in an area. From the previous rainfall year, it may be possible to identify areas that need to be burned. The intensity of fires should be measured each time during burning, this is important to see what damage is caused at a certain fire intensity. High intensity fires are best for controlling undesired plants, but only when the grass fuel load is high. This study examined the effects of fire history in terms of time since last burn on only one woody species on the plateau. The effect of fire frequency on the root TNC of woody vegetation needs to be studied extensively on a larger scale looking at a larger sample size, taking into consideration different seasons, other vegetation types, comparing resprouters and non-resprouters and the additional effects of herbivory to determine if there are differences in root reserves among these factors. For age determination, the stem and the oldest part of the root which was burned or hollow in this study thus causing some difficulties in quantifying the age, needs to be analysed to determine if there is a correlation between the time since last burn and the age of the tree. The total grams of root TNC were not estimated which was a limit to this study because only concentrations were estimated. An up to date fire record is important for the park management in relation to fire and for understanding ecological processes such as the effect of fire on vegetation in a semi-arid savanna. For monitoring purposes, it is important to have maps showing the area and percentages burned, this can be provided by the Advanced Fire Information System.

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Appendix I: Weather readings

Table I. Weather readings of September 2011 to November 2015.

Station	Date	Air temp. (avg)	Air temp. (min)	Air temp. (max)	Precip. (total)
		[°C]	[°C]	[°C]	[mm]
Waterberg	Sep 2011				0,0
Waterberg	Oct 2011	21,5	5,0	34,9	0,0
Waterberg	Nov 2011	22,5	6,5	35,3	39,6
Waterberg	Dec 2011	21,7	5,5	33,3	110,1
Waterberg	Jan 2012	22,1	12,5	34,7	198,1
Waterberg	Feb 2012	20,4	11,5	30,2	305,5
Waterberg	Mar 2012	20,0	5,4	30,7	30,2
Waterberg	Apr 2012	18,3	5,6	29,9	22,6
Waterberg	May 2012	15,4	1,0	29,5	0,0
Waterberg	Jun 2012	12,7	-4,4	27,0	0,0
Waterberg	Jul 2012	12,4	-7,2	26,5	0,0
Waterberg	Aug 2012	17,1	-5,8	31,8	0,0
Waterberg	Sep 2012	18,6	-4,4	33,8	0,0
Waterberg	Oct 2012	23,7	2,1	35,4	6,2
Waterberg	Nov 2012	23,9	13,3	35,9	36,3
Waterberg	Dec 2012	22,8	8,1	33,3	65,2
Waterberg	Jan 2013	24,1	11,8	34,9	77,7
Waterberg	Feb 2013	24,2	10,6	37,7	42,2
Waterberg	Mar 2013	22,5	9,4	34,7	46,9
Waterberg	Apr 2013	17,8	2,1	32,2	0,2
Waterberg	May 2013	16,6	0,3	28,7	5,3
Waterberg	Jun 2013	14,2	-5,0	28,3	0,0

Waterberg	Jul 2013	13,9	-3,7	27,1	0,0
Waterberg	Aug 2013	14,9	-4,8	30,3	0,0
Waterberg	Sep 2013	19,9	-4,6	33,7	5,7
Waterberg	Oct 2013	23,7	3,3	35,8	3,4
Waterberg	Nov 2013	24,1	3,3	35,0	57,4
Waterberg	Dec 2013	21,9	10,6	34,3	156,9
Waterberg	Jan 2014	21,9	3,0	34,5	41,3
Waterberg	Feb 2014	20,5	12,4	30,0	315,7
Waterberg	Mar 2014	20,3	9,5	29,1	209,6
Waterberg	Apr 2014	17,3	5,6	26,5	118,3
Waterberg	May 2014	16,0	1,0	26,6	5,6
Waterberg	Jun 2014	13,2	-5,7	26,0	0,0
Waterberg	Jul 2014	13,3	-4,0	26,8	0,0
Waterberg	Aug 2014	16,6	-3,2	30,1	0,3
Waterberg	Sep 2014	19,9	1,6	33,3	0,0
Waterberg	Oct 2014	22,6	3,6	34,5	3,4
Waterberg	Nov 2014	22,3	8,4	33,1	72,4
Waterberg	Dec 2014	22,9	8,7	34,5	71,6
Waterberg	Jan 2015	24,4	10,0	35,0	14,4
Waterberg	Feb 2015	24,1	6,6	35,2	15,5
Waterberg	Mar 2015	21,5	9,0	32,9	33,2
Waterberg	Apr 2015	19,4	6,5	29,1	0,9
Waterberg	May 2015	17,1	4,0	28,9	0,0
Waterberg	Jun 2015	10,9	-9,1	25,9	0,0
Waterberg	Jul 2015	14,2	-8,8	28,0	1,0
Waterberg	Aug 2015	17,9	-0,4	32,6	0,0
Waterberg	Sep 2015	21,3	0,0	33,8	0,0

Waterberg	Oct 2015	24,8	4,0	36,1	14,3
Waterberg	Nov 2015	25,3	8,4	36,5	2,3

Appendix II: Skeleton height

Table I. Mean skeleton height of *T. sericea* resprouts in different fire blocks

Fire return interval	Time since last burn (years)	Mean skeleton height	Min & Max
6,2	1	1,6 ± 0,15	0 – 3,6 m
9,3	2	1,5 ± 0.23	0 – 3,5 m
9,3	14	0,8 ± 0,20	0 – 4,3 m
18,5	24	0,4 ± 0,12	0 – 1,8 m

Appendix III: Root type

Table I. Root type and depth of hole of *T. sericea* in blocks with different time since last burn.

Time since last burn (years)	Root Type	Max Depth (cm)	Number of lateral roots	Diameter at base (cm)
2	lateral	24	8	3,3
	tap	29	6	2,6
	lateral	37	22	5
	lateral	27	3	2,4
	lateral	28	15	3,6
	lateral	17	3	3,7
	lateral	32	7	5,1
	lateral	21	7	5,3
	lateral	25	11	4,6
	lateral	18	2	5,2
	lateral	87	3	3,4
	lateral	30	5	3
3	lateral	28	13	4,2
	tap	73	8	4,4
	tap	70	8	5
	lateral	30	13	2,5
	lateral	24	9	4,6
	tap	70	2	3,2
	lateral	30	4	3,1
	tap	49	6	4,7
	tap	90	6	3,2
	lateral	41	11	1,1
	lateral	24	2	2,1

	tap	67	14	5
15	lateral	32	16	2,9
	lateral	30	9	3,3
	tap	105	9	5,6
	tap	85	6	4,5
	lateral	18	5	4,3
	lateral	30	5	3
	lateral	23	7	3,5
	lateral	20	13	5,6
	tap	73	17	6,4
	lateral	41	5	3,8
	lateral	24	5	2,4
	lateral	28	3	2,7
	25	tap	18	11
lateral		23	8	5,8
lateral		28	2	2,4
lateral		60	23	2,4
lateral		39	12	3,7
lateral		36	11	2,5
lateral		29	3	3,6
lateral		30	6	3,1
tap		70	20	7,5
lateral		77	14	5,2
lateral		20	10	3,7
lateral		17	3	2,7