

The effect of fire damage on the growth and survival mechanisms of selected native  
and commercial trees in South Africa

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## Abstract

Surface fires are known to affect trees of different species differently, depending on the capacity of the bark to shield the cambium from heat. Tree bark characteristics differ among species and thus potentially influence the protective ability against cambium damage. The objectives of this study were to compare the protective role of bark against fire for selected indigenous and exotic species in the Western Cape, South Africa, and to investigate post-fire growth impacts following surface fire damage on *Pinus radiata*.

In the first part of the study, trees were felled and billets of 25 cm height harvested from different heights along the trunk. Bark thickness, compass direction, stem diameter at breast height, bark moisture content and relative height of the sample in the stem were tested for their effect on heat insulation capacity of bark. Heating experiments were conducted at 400°C on the fresh billets with intact bark. Time to heat the cambium to lethal 60°C was determined.

The second part of the study investigated the role of bark surface topology, bark density and bark chemical composition for its fire resistance. The same size billets were harvested from the lower trunk section of selected species. Surface topology was characterised by means of x-ray based computer tomography, density by moisture saturation method and bark chemical composition by thermo-gravimetric analyses (TGA).

The third part of the study investigated the impact of high intensity surface fires on growth of an 18 year old *Pinus radiata* plantation which was exposed to a ground fire 5 years prior to the analysis. Tree ring measurements were done on cores obtained by non-destructive coring method and various growth indices, based on yearly basal area increment (iBA) used to quantify growth response to the fire damage.

Statistical analysis based on correlation, multi-model inference and multiple regression revealed no significant influence of compass direction and diameter at breast height. Heat resistance was mainly determined by bark thickness and to a lesser degree by moisture content. In several species relative height at the stem modulated the bark thickness effect. Higher up the stem bark of the same bark thickness offered less protection against heat. The results also suggest that in particular bark topology plays a role, while the correlations with bark density and chemical composition could not be secured statistically. A main finding was

that fissures in the bark play a significant role. A regression model showed a significant influence of fissure width, fissure frequency and the minimum bark thickness to the cambium, which is a function of fissure depth. The results show that structural bark parameters are a necessary addition to explain heat resistance of bark. Statistical analysis employing one-way Anova and incorporating Tamhane's T2 Post Hoc test revealed significant growth reductions following high intensity surface fire damage on *Pinus radiata* in the fire year with the impact being passed on to the following year. The recovery phase extended a two year period. During this time the trees showed increased diameter growth probably due to increased water availability.

## Opsomming

Dit is bekend dat oppervlakkure in bos-ekostelsels verskillende boomspesies verskillend affekteer, afhange van die vermoë van bas om die kambium van hitte te beskerm. Baseienskappe verskil tussen spesies en het dus 'n potensiële invloed op die beskermende vermoë teen kambiumskade. Die doelwit van hierdie studie was om die beskermende rol van bas teen vuur te vergelyk tussen inheemse en uitheemse spesies in Wes-Kaapland, Suid Afrika asook om die na-vuur impak op groei te ondersoek met brandskade aan *Pinus radiata*.

In die eerste deel van die studie is bome geoes en stompe van 25 cm lengte van verskillende hoogtes verwyder. Basdikte, kompasrigting, stompdiameter by borshoogte, basvoggehalte en die relatiewe hoogte van die stomp in die stam is getoets vir hul invloed op hitte-isolasiekapasiteit van bas. Verhittingseksperimente is gedoen teen 400 °C op die vars stompe wat steeds bas opgehad het. Die tyd om die bas tot by 'n skadelike 60 °C te verhit is bepaal.

Die tweede deel van die studie het die rol van basoppervlaktopologie, basdigtheid, en die bas chemiese samestelling ondersoek in vuurweerstand. Dieselfde grootte stompe is geoes van die laer dele van die stam van uitgesoekte spesies. Oppervlaktopologie is bepaal deur middel van X-straal rekenaartomografie, digtheid deur die versadigingsvoggehaltemetode, en chemiese samestelling deur termo-gravimetriese analise (TGA). Die derde deel van die studie het die impak van hoë intensiteit oppervlakkure op groei van 18-jaar oue *Pinus radiata* ondersoek. Jaarringmetings is gedoen op inkrementboorsels wat nie-destrukties bekom is en verskeie groei-indekse, gebaseer op jaarlikse basale oppervlak aanwas, is gebruik om die groeireaksie op brandskade te kwantifiseer.

Statistiese analise gebaseer op korrelasie, multi-model inferensie, en veelvuldige regressie het gewys dat kompasrigting en deursnee op borshoogte nie 'n beduidende invloed gehad het nie. Hitteweerstand was hoofsaaklik bepaal deur basdikte, en in 'n mindere mate basvoggehalte. By verskeie spesies het die relatiewe hoogte die basdikte-effek gemoduleer. Hoër in die stam het dieselfde dikte bas minder beskerming gebied as bas van laer in die stam. Die resultate impliseer dat basoppervlaktopologie ook 'n rol speel in hitteweerstand terwyl basdigtheid en chemiese samestelling nie 'n statisties beduidende rol gespeel het nie. 'n Belangrike bevinding was dat gleuwe of openinge in die bas 'n beduidende rol speel. 'n

Regressiemodel wys dat 'n beduidende invloed deur gleufwydte, gleuffrekwensie en die minimum basdikte na die kambium. Die resultate wys dat strukturele basparameters 'n belangrike bykomende rol speel om hitteweerstand van bas te verduidelik. Die statistiese analise waar eenrigting ANOVA met Tamhane se T2 Post Hoc toets gebruik is toon dat 'n beduidende groeivermindering teweeg gebring is in die *Pinus radiata* as gevolg van skade veroorsaak deur hoë intensiteit oppervlakkige waarvan die impak eers in die jaar na die vuur sigbaar was. Die herstelfase het oor twee jaar gestrek. Gedurende hierdie tyd het die bome 'n toename in deursneegroei getoon, waarskynlik as gevolg van verhoogde waterbeskikbaarheid.

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## Chapter 1 Introduction

### Historical role of fires and their interaction with forests

Historically, fires have always been beneficial in maintaining ecological stability and biological diversity in forest ecosystems (e.g. O'Donnell et al. 2010; Stahlea et al. 1999; Abrahamson 1984; Harper 1977). Many man-made and natural forest ecosystems are shaped by fires. They are an integral part of these ecosystems and act as a catalyst to regeneration for certain species (Schoennagel et al. 2003; Chanyenga et al. 2012), while at the same time enhancing growth of the remnant crop by reducing competition for light, water and soil nutrients (e.g. Ford et al. 2010; Bond and Keeley 2005; Thonicke et al. 2001). Fire thus constitutes an important aspect from a population point of view.

### The current fire situation globally

There has, however, been a global increase in numbers and size of forest fires over the past decade. The result is a shift from stand-maintaining to stand-replacing fires (Westerling et al. 2006) that have caused enormous vegetation destruction and damage to forest ecosystems globally (e.g. van Mantgem et al. 2009; De Ronde 2008).

In many parts of the world, increased wildfires have been linked to global warming and climate change. For example western North America and south western British Columbia have experienced regional warming and water deficits that have directly affected trees in old forests, causing mortality to double up (Daniels et al. 2011). This phenomenon has also been observed in European forests where an increase in the number and size of wildfires has been linked to global warming (Rego 2005). In South Africa the effect of global warming and climate change has resulted in persistent drought conditions over the past decade (Calvin and Wettlaufer 2000), which contributed to increased fire weather conditions i.e. hot/dry conditions, warm temperatures and climatic water deficits within certain forestry regions (Goldammer 2007). These conditions increase mortality and fuel levels in forest ecosystems promoting chances of high fire risks (van Mantgem et al. 2009).

The warming effect also triggers insect pest outbreaks and pathogens that thrive in warm temperatures. These increase tree mortality (Allen et al. 2010; McCloskey et al. 2009; Kurz et al. 2008; Berg et al. 2006; Hickie et al. 2006; Safranyik et al. 1975). High degree of tree mortality results in significant changes to forest structure, including more open tree canopies

and increased fuel loads within forests (Axelson et al. 2009b), which indirectly contribute to fires.

Increased fire occurrences are also a result of intensified human activity within forest ecosystems, especially intervention in tropical and rain forests. Increased use of forests for tourism and recreational purposes, forest encroachment and fragmentation led to the depletion of these forests and created openings with dry plant material, which enhance the chances of forest fire events (Goldammer 2007; FAO 2003).

Apart from land use pressure, intensive forest management has in some instances contributed to severe wildfires in areas where selective logging and long term fire exclusion practices have led to accumulation of fuel. Prescribed burning has proven to be an effective method in controlling the fuel load, but improper implementation without consideration of the fire risks (e.g. burning in too dry or windy conditions) have in some instances been disastrous and destructive to plantations (Daniels et al. 2011; FAO 2003).

### **The current fire situation in South Africa**

As a result of the complex interaction of all the above mentioned contributing factors, South Africa has experienced an exponential increase in wildfire damage, particularly in the summer rainfall regions, which have been the most affected. Fire is by far the most important threat to forests and accounts for more than 80% (Figure 1) of losses within plantations (DAFF 2012).

Thousands of hectares of commercial timber plantations have been devastated by uncontrollable fires, especially between 2005 and 2009. Records show that South Africa has lost an average of 14 000 ha of forested areas to fires each year over the past 25 years (e.g. de Ronde 2008 and 2008c). This has seen local sawmilling and timber processing plants increasingly experiencing saw log shortages. In some regions the occurrence of wildfire damage has caused timber resources to diminish and manufacturing plants to close down, because of the negative effect on profitability (de Ronde 2008). With a likely increase in greenhouse gas concentration, and a projected increase in mean temperatures and more erratic rainfalls, drought conditions are likely to occur more frequently and will most likely be more severe (Christensen et al. 2007). This will further increase the number of fires and intensify forest destruction (Allen et al. 2010), further threatening the sustainability of the forestry industry in certain regions.

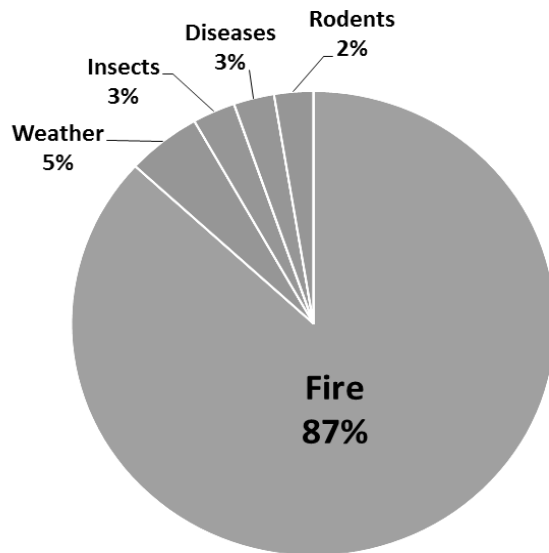


Figure 1.1: Plantation damage by fire and other causes in South Africa (according to DAFF 2012).

## 1.2 Forest fire research

The upsurge in fire frequency and intensity and the destruction caused to vegetation has raised alarm in the forestry sector in many parts of the world. In response there have been a range of fire-related research and development programs started to address the increased occurrence of wildfire damage (Goldammer 1999). Of the published research efforts, the vast majority of fire-related ecologic articles target the stand and landscape level. A search of published articles within the past three decades, between 1982 and 2013, specifically on the “effect of fires on forest trees” in the Scopus database returned 409 articles. 54 % of these studies have been conducted in North America, 19 % in Europe while South America, Asia, and Australia all had less than 10 % of published work. Notably, Africa had the lowest number of published work with 4 %. This calls for increased research efforts within the continent of Africa as a means of finding more informed solutions to tree protection in the wake of increased wild fire destruction.

Although wild fires impact both commercial and natural forests, there has however been minimal research effort investigating the impact of fires on natural forests. The search revealed that only 8 % of the studies had been conducted in natural forests as compared to 63 % in commercial plantation forests. There is need for enhanced research in both forest types to understand reaction and resilience patterns that can be used in plantation fire management decisions.

The resilience pattern of a plantation is determined by the ability of individual trees to withstand the impact of the fire damage. The impact of fires on individual trees has not been intensively investigated. Research on the impact of fire on individual trees was less than 2 %. 82 % of the literature was dominated by ecosystem level studies, which address the spatial impacts of fire on populations within stands and plant communities. The focus has extensively been on post-fire resprouting, recolonization, plant composition, stand structure, biodiversity, impacts on atmospheric carbon, impacts on soil nutrients and microbes among other ecosystem level effects (e.g. Murphy et al. 2010; Goldammer 2007; Werner et al. 2006; Werner 2005; Hoffmann & Solbrig 2003; Williams et al. 1999; Glitzenstein et al. 1995; Grace & Platt 1995; Lonsdale & Braithwaite 1991).

Limited attention was given to the impact of fire to individual trees within forests. This has led to a very poor level of understanding of the mechanisms of tree resistance to fire damage as pointed out by Gignoux et al. (1997) and Murphy et al. (2010), and a comprehensive quantification of the impact on post-fire growth is still outstanding. Knowledge of natural resistance of trees to fire damage and the fire-related implications on survival, growth and health is crucial for defining management standards and options in the wake of increased fire occurrence. Gignoux et al. (1997) thus advocate for more studies on the individual tree level to gain better insights. For this purpose a general characterisation of stress in trees may be applied, which defines stress by its intensity, duration, frequency and time of occurrence as suggested by Rötzer et al. (2012). In the case of fire regimes, Gill (1977) introduced the term “type of fire”, where he suggests a differentiation into subterranean ground fires and above-ground fires. The latter are further classified into surface and crown fires (e.g. Newton 2007; Brown 1995).

This study focuses on damage to the stem caused by surface fires resulting from the combustion of fuels accumulated on the forest floor, such as litter, leaves, twigs, branches, herbaceous woody plants and dead plant material. The temperature experienced by plant cells, as determined by the fire intensity (Eckmann et al. 2010), is an ultimate cause of tissue death. A study by Bova and Dickinson (2005) has however, reported that the most important determinant of tissue depth necrosis is flame residence time. This was found to explain 68% of tissue depth necrosis as compared to 27% explained by the flame intensity. Longer exposures to fires as determined by fuel levels and prevailing wind conditions can thus have a major influence on the extent of injury inflicted upon the tree. High temperatures can result in complete combustion which causes cell and tissue mortality. A brief and slight exposure to elevated temperatures may not result in mortality but cause temporary disruptions. These disruptions can either be indirect, following metabolic changes, or direct by protein denaturation, altered lipid mobility or chemical decomposition (Whelan 1995).

Surface fires are typified by intensities of less than approximately  $2500 \text{ kW m}^{-1}$  (Michaletz and Johnson 2007), although this varies with the amount of organic matter consumed (de Ronde 2008) as well as numerous physical and climatic factors e.g. vegetation structure, fuel condition, fuel moisture, fuel types, weather, slope and aspect (Eckmann et al. 2010; Pyne et al. 1996). Large amounts of fuel results in high heat, while the amount of moisture content in some places may lower the amount of heat release (Fischer and Binkely 2000). Fires are also likely to be more intense in hot months due to increased fuel load of high flammability. Slope and aspect influence the amount of fuel and moisture content at different elevations within the landscape thus indirectly influencing the fire intensity (Fischer and Binkely 2000).

Maximum temperatures in surface fires are typically about  $400^{\circ}\text{C}$  (VanderWeide and Hartnett 2011; Bauer *et al.* 2010) and are usually encountered near the base of a tree between 0 cm and 50 cm above the ground (Matthew and Johnson 2004; Miranda et al. 1993). Intense surface fires frequently inflict severe damage to individual trees. The above ground biomass of saplings and smaller trees is often destroyed (e.g. von Richter et al. 2005; Gignoux et al. 1997), whereas mature trees frequently survive (Hempson et al. 2014; Frazer and Davis, 1988; Donovan et al., 1993; Poorter and Hayashida-Oliver, 2000), but may experience fire as a major abiotic stress factor with various consequences for growth as well as susceptibility to other stressors (McHugh et al. 2003; Dickinson and Johnson 2001; Ducrey et al. 1996). Most of the work on tree stress resistance has been carried out with young plants, most often with seedlings (e.g., Walters and Reich, 1999). Given the changes in stress combinations and overall stress resistance with increasing tree size, the lack of stress studies on older plants forms an important knowledge gap.

Little research has been done to increase understanding of individual tree growth responses to surface fire damage. There is limited information specifying and or quantifying the insulative capacity of species under varying fire regimes. Although most surface fire impact studies have reported negligible impact on growth (Burrows et al. 1989; Woodman and Rawson 1982; Ducrey et al. 1996; Rozas et al. 2011), some studies have cited reduced growth over short periods of time (Elliott et al. 2002; Ford et al. 2010). Information on the extent of reduced growth over the recovery period as well as the duration taken before normal growth is restored among various species however, remains scarce. Therefore, it seems warranted to investigate structural properties of individual mature trees to compare species-specific adaptation strategies, recovery potential and possibly identify generic patterns that lead to improved surface fire resistance.



### 1.3 The objectives of the study

The study aims to determine differences in resistance to surface fire damage among different selected species and compare the differences in fire resistance among commercial and indigenous species in the Cape region of South Africa. Bark thickness has been identified as the main determinant to resistance against surface fire damage (e.g. Lawes et al. 2011; Bauer et al. 2010). The first part of the study aims to quantify the heat resistance capacity of the various species due to their bark thickness and in so doing rate them in order of their capacity to withstand surface fire damage. The second part investigates the contributing role of various bark properties to heat resistance capacity. Tree species differ in their bark density, topology and chemical constituents. The influence of these properties in heat conduction through the bark layer is unknown and is thus investigated in section two of the study. The last section of the study investigates the impact of surface fire damage on growth. The impact of surface damage on growth remains unclear and this section aims to clarify this by investigating the impact on *Pinus radiata* trees. Among all the studied species, the only species with suitable study sites, meaning ample sample size of same age trees comprising of burnt and unburnt trees for comparison was *Pinus radiata*.

### 1.4 Layout of the thesis

This thesis is structured as a cumulative work in three main chapters, each written as an article. Accordingly, three specific objectives have been laid down in chapters 2 to 4:

- In Chapter 2 the role of bark thickness, compass direction at the stem, tree size (dbh), relative stem height and available moisture content within the bark layer in insulation against cambial heat damage are determined.
- In Chapter 3 fire resistance properties of tree bark as a function of its surface topology, density and chemical composition are investigated.
- In Chapter 4 the impact of surface fire damage on post-fire growth is examined.

In Chapter 5 the findings presented in chapters 2, 3 and 4 are summarised and put into perspective of the objectives of this thesis and the current knowledge.

Chapter 2 has been published in the journal *Trees*, 28, 2014, 555-565

## 1.4 References

- Abrahamson, W.G. 1984. Species responses to fire on the Florida lake wales ridge. *American Journal of Botany* 71(1):35-43.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D. and McDowell, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Axelson, J.N., Alfaro, R.I. and Hawkes, B.C. 2009b. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. *Forestry Chronicle* 86:87–99.
- Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45:5950–5959.
- Berg, E.E., Henry, J.D., Fastie, C.L., De volder, A.D. and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219–232.
- Bond, W.J. and Keeley, J.E. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20(7).
- Bova, A.S. and Dickinson, M.B. 2005. Linking surface-fire behaviour, stem heating, and tissue necrosis. *Canadian Journal of Forestry Research* 35: 814–822.
- Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. In *Proceedings of the society of American forester’s, 1994 national convention* pp. 171-178.
- Burrows, N.D., Woods, Y.C., Ward, B.G. and Robinson, A.D. 1989. Prescribing low intensity fire to kill wildings in *Pinus radiata* plantations in Western Australia. *Australian Forestry* 52:45–52.
- Calvin, M. and Wettlaufer, D. 2000. *Fires in the Southern Cape Peninsula, Western Cape Province, South Africa*. IFFN No. 22:69-75.
- Chanyenga, T.F., Geldenhuys, C.J. and Sileshi, W.W. 2012. Germination response and viability of an endangered tropical conifer *Widdringtonia whytei* seeds to temperature and light. *South African Journal of Botany* 81:25–28.
- Christensen, J.H., Hewitson, B. and Busuioc, A. 2007. Regional Climate Projections. In Solomon S, Qin D, Manning M. (eds.), *Climate Change: The Physical Science Basis*.

*Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Daniels, L.D., Thomas, B.M., Amanda, B.S. and Shane, P.J.M. 2011. Direct and indirect impacts of climate change on forests: three case studies from British Columbia. *Canadian Journal of Plant Pathology* 33(2):108–116.

DAFF 2012. *Report on commercial timber resources and primary roundwood processing in South Africa 2010/2011.* Department of Agriculture, Forestry and Fisheries, Republic of South Africa.

de Ronde, C. 2008c. *Guide to assess wildfire damage in pine stands.* Deliverable D3.2-8 Unpublished paper for FIRE PARADOX WP 3.2: p 18.

de Ronde, C. 2008. *Knowledge base in damage assessment to forests and plantations.* Deliverable D3.2-7 of the Integrated project “Fire Paradox”, Project FP6-018505. European Commission p 20.

Donovan, L.A., Mausberg, J. and Ehleringer, J.R. 1993. Seedling size and survival for *Chrysothamnus nauseosus*. *Great Basin Nature* 53:237–245.

Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson, E.A., Miyanishi, K. (Eds.), *Forest Fires*. Academic Press, New York, 477-525.

Ducrey, M., Duhoux, F., Huc, R. and Rigolot, E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Canadian Journal of Forest Resources* 26:1366–1374.

Eckmann, T. C., Still, C. J., Roberts, D. A. and Joel C. M. 2010. Variations in Subpixel Fire Properties with Season and Land Covering Southern Africa. *EARTH Interactions* 6(14).

Elliott, K.J., Vose, J.M. and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. *South Journal of Applied Forestry* 26:18–25.

FAO 2003. *Fires are increasingly damaging the world's forests.* FAO news report, Rome.

Fischer, R.F. and Binkley, D. 2000. *Ecology and Management of Forest Soils* (3rd ed.). USA: John Wiley & sons.

Ford, C.R., Emily, S.M. and Gordon, A.F. 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleafpine (*Pinus palustris*). *Canadian Journal of Forest Research* 40:1410–1420.

- Frazer, J.M. and Davis, S.D. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76:215–221.
- Gignoux, J., Clobert, J. and Menaut, J. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110:576–583.
- Gill, A.M. 1977. Management of fire-prone vegetation for plant species conservation in Australia. *Search* 8:20–26.
- Glitzenstein, J.S., Platt, W.J. and Streng, D.R. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monograph* 65:441-476
- Goldammer, J.G. 2007. Wildland fires: Creeping and sudden disasters. *Crisis Response* 3:50-52, ISSN 1745-8633.
- Goldammer, J.G. 1999. Forests on fire. *Science*, available online, DOI: 10.1126/science.284.5421.1782a.
- Grace, S.L. and Platt, W.J. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology* 83:75–86.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, New York.
- Hempson, G.P., Midgley, J.J., Lawes, M.J., Vickers, K.J. and Kruger, L.M. 2014. Comparing bark thickness: testing methods with bark– stem data from two South African fire-prone biomes. *Journal of Vegetation Science*, available online, DOI: 10.1111/jvs.12171.
- Hickie, J.A., Logan, J.A., Powell, J. and Ojima, D.S. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research* 111(G2):12.
- Hoffmann, W.A. and Solbrig, O.T. 2003. The role of top kill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180:273–286.
- Kurz, W.A., Dymond, C.C., Stinson, G. and Rampley, G.J. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990.
- Lawes, M.J., Richards, A., Dathe, J. and Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212:2057–2069.
- Lonsdale, W.M. and Braithwaite, R.W. 1991. Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* 16:363–374.

- Matthew, B.D. and Johnson, E.A. 2004. Temperature-dependent rate models of vascular cambium cell mortality. *Canadian Journal of Forest Research* 34:546–559.
- McCloskey, S.P.J., Daniels, L.D. and McLean, J.A. 2009. Evaluation of the role of climate in driving western hemlock looper outbreaks. *Northwest Science* 83:225–238.
- McHugh, C.W., Kolb, T.E. and Wilson, J.L. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32:510–522.
- Michaletz, S.T. and Johnson, E.A. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22:500–515.
- Miranda, A.C., Fatima, O.D. and Ferreira, S.D. 1993. Soil and air temperatures during prescribed cerrado fires in central Brazil. *Journal of Tropical Ecology* 9:313–320.
- Murphy, B.P., Smith, J.R. and Priors, L.D. 2010. Frequent fires reduce tree growth in northern savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16:331–343.
- Newton, C.A. 2007. *Forest ecology and conservation*. A handbook of techniques. Oxford university press, Oxford.
- O'Donnell, A.J., Cullen, L.E., McCaw, W.L. and Boer, M.M. 2010. Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. *Dendrochronologia* 28:37–48.
- Poorter, L. and Hayashida-Oliver, Y. 2000. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology* 16:481–498.
- Pyne, S. J., Andrews, P. L. and Laven, R. D. 1996: Introduction to Wildland Fire. (2nd ed.). USA: John Wiley & sons.
- Rego, F. 2005. General introduction to forest fires in the Mediterranean environment. *Mediterranean Forests* 26(3):204-206.
- Rötzer, T., Seifert, T., Gayler, S. and Priesack, E. 2012. Effects of stress and defence allocation defence on tree growth: simulation results at the tree and stand level. In: Matyssek R, Schnyder H, Ernst D, Munch J-C, Pretzsch H (eds) *Growth and defence in plants: resource allocation at multiple scales*. Ecological studies 220. Springer, Heidelberg, pp 401–432.
- Rozas, V., Gonzalo, P.D.L., Ignacio, G.G. and Jose, R.A. 2011. Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25:895–905.

Safranyik, L., Shrimpton, D.M. and Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. In D.M. Baumgartner (Ed.) *Management of lodgepole pine ecosystems*. Pullman, WA, Washington State University Cooperative Extension, 406–428 pp.

Schoennagel, T., Turner, M.G. and Romme, W.H. 2003. The influence of fire interval and serotiny on post-fire lodgepole pine density in Yellowstone National Park. *Ecology* 84:2967–2978.

Stahlea, D.W., Mushoveb, P.T., Cleavelanda, M.K. and Roigc, F. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* 124:217-229.

Thonicke, K., Venevsky, S., Sitch, S. and Cramer, W. 2001. The role of fire disturbance for global vegetation dynamics: coupling Dynamic Global Vegetation Model. *Global Ecology and Biogeography* 10:661–667.

VanderWeide, B.L. and Hartnett, D.C. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261:1530–1538.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C. and Daniels, L.D. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.

von Richter, L., Little, D. and Benson, D.H. 2005. Effects of low intensity fire on the resprouting of the weed African Olive (*Olea europaea* subsp. *cuspidata*) in cumberland plain woodland, western Sydney. *Ecological Management and Restoration* 6:230–232.

Walters, M.B. and Reich, P.B. 1999. Research review. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist* 143:143–154.

Werner, P.A., Cowie, I.D. and Cusack, J.S. 2006. Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia. *Australian Journal of Botany* 54:283–296.

Werner, P.A. 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees: an experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30:625–647.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge university press, Cambridge.

Williams, R.J., Cook, G.D., Gil, A.M. and Moore, P.H.R. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 30:50–59.

Woodman, M. and Rawson, R. 1982. *Fuel Reduction Burning in Radiata Pine Plantations*. Res. Rep. No. 14. Victoria: Department of Conservation and Environment, Fire Management Branch.



## Chapter 2 **The protective role of bark against fire damage: a comparative study on selected introduced and indigenous tree species in the Western Cape, South Africa**

### **2.1 Abstract**

The objective of this first section of the study was to compare the protective role of bark against fire for three selected indigenous and five exotic species in the Western Cape, South Africa. Bark thickness, compass direction, stem diameter at breast height, bark moisture content and relative height of the sample in the stem were tested for their effect on heat insulation capacity of bark. Trees were felled and heating experiments were conducted at 400 °C on fresh billets with intact bark. Time to heat the cambium to lethal 60°C was determined. Statistical analysis based on correlation, multi-model inference and multiple regression revealed no significant influence of compass direction and diameter at breast height. Heat resistance was mainly determined by bark thickness, to a lesser degree by moisture content. In several species relative height at the stem modulated the bark thickness effect. Higher up the stem bark of the same thickness offered less protection against heat. Significant species-specific differences in heat resistance were apparent in the results, which could not be explained by bark thickness thus indicating further need for research in scrutinising these factors, which might help to explain the relative higher fire tolerance of certain species compared to others.

*Keywords: Bark insulation capacity, Fire resistance, Plantation trees, Indigenous trees, Heat transfer, Heat insulation, Multi-model inference*

## 2.2 Introduction

### Physical background of heat conduction

In surface fires, the tree bark acts as the main interface between the abiotic stressor and the cambium, but not all species are equally well protected. To understand the interaction of fire with a tree, some basic knowledge of the physical principles of heat conduction is helpful.

The thermal conductivity  $\lambda$  [W/mK] of a material depends on its cross-sectional area  $A$  [m<sup>2</sup>], the length  $l$  [m] the heat has to penetrate through it, the time  $t$  [s] for which the heat is applied, the heat  $Q$  [J] that is applied and the temperature difference  $\Delta T$  [K] between the two sides (Eq. 1):

$$\lambda = \frac{Ql}{At\Delta T} \quad (1)$$

The heat resistance of the bark is given by  $R_{th} = \Delta T / \Phi$  [KW], where  $\Phi$  is the heat flow  $\Phi = Q/t$  [W].

This leads to Eq. 2;

$$R_{th} = \frac{\Delta T}{Q} = \frac{tl}{A\lambda} \quad (2)$$

In the case of trees  $l$  is equivalent with bark thickness. The time is therefore a direct measure for the heat resistance of bark, if the thickness, cross-sectional area and thermal conductivity are known. The thermal conductivity  $\lambda$  depends largely on material properties, such as density, moisture content (MC), surface structure and chemical composition.

If the fire is hot enough and the duration long enough, the cambium behind the bark is damaged. Intense fires coupled with long exposure times cause deep and complete tissue necrosis (Hobbs et al. 1984) and are known to kill mature trees even if the wood itself is not burnt. When cambium necrosis occurs around the entire bole circumference (a process known as girdling), the translocation of photosynthates from the crown to the root system is interrupted and no new sapwood for water transport can be formed. This may ultimately result in the death of the tree due to water stress and depleted carbohydrates in the root system (Michaletz and Johnson 2007). The capacity of individual plant cells to withstand a constant exposure to heat does not significantly vary between plant species or between tissues within a plant. Generally, the lethal thermal point of mesophytic plants cells is

between 50 and 55°C (Gill 1995; Levitt 1980). The lethal temperature of the cambium is estimated to be at about 60°C (Bauer et al. 2010). Mortality can, however, occur at lower temperatures given sufficient exposure time (Bond and van Wilgen 1994; Alexandrov 1977).

Surface fires are often non-lethal and unlikely to kill the trees when girdling does not take place (Brown 1995). The efficiency of heat insulation of the bark determines the potential damage to the cambial region and ultimately also the probability of survival of a tree. The fact that there are known species-specific differences in the sensitivity to fire on the one hand and a general lethal cambial temperature threshold across all species on the other implies species-specific differences in bark insulation capacity due to morphological differences (de Bano et al. 1998; Agee 1993; Vines 1968, 1981).

Current literature points out bark thickness as the strongest contributor to insulative capacity (Lawes et al. 2011; Bauer et al. 2010) in accordance with physical theory. Thicker bark offers greater resistance against cambial death or extensive damage than thinner bark (Rigolot 2004; Stephens and Finney 2002; Mutch and Parsons 1998; Pausas 1997; Ryan and Reinhardt 1988). This is supported by the findings of Pinard and Huffman (1997), who found bark thickness to explain 63 % of the variation in time to lethal cambial temperature when exposed to heating, while Brando et al. (2012) report that bark thickness explained 82 % of heat transfer through the bark. It is also known that the bark thickness varies along the bole within the same tree. Typically, a linear correlation between the bark thickness and bole diameter is reported with the upper sections of the stem having thinner bark compared with the lower sections (Ryan and Reinhardt 1988). As the bole increases in size, so does bark thickness (Morrison 1995; Davis 1959). Consequently, big trees with thicker bark are better protected against cambial damage (Michaletz and Johnson 2007; Gignoux et al. 1997; Morrison 1995). High mortality thus occurs more often in smaller trees—even in low-intensity fires—while older trees are more resistant and have a higher probability to survive even severe fires (Catry et al. 2010; Morrison 1995).

However, there are contradicting opinions on the dominating role of bark thickness. Whelan (1995) argued that thick bark may increase the susceptibility to cambium necrosis in a less intense but slow-moving fire, by igniting and fuelling the fire and perhaps by retarding the rate of cooling once the cambium has been heated. Other studies have reported no significant differences in insulation of various species due to their varying bark thickness (Stephens and Finney 2002; Mutch and Parsons 1998; Swezy and Agee 1991).

Other bark properties, such as density, moisture content (MC) and thermal properties have been described to have a rather small contribution to heat insulation (Hengst and Dawson 1993; Reifsnyder et al. 1967; Martin 1963). A weak correlation was found between bark MC and the time required to reach the lethal cambial temperature: the MC accounted for about 4

% of the variations to peak cambial temperature and correlated negatively with insulation capacity (Pinard and Huffman 1997). This was attributed to the high thermal conductivity of water. Vines (1968) showed cambium temperature to be higher in trees with moist bark, while thick dry layers of outer bark resulted in a significant increase in heat resistance. Recent studies have, however, not found a significant effect of MC on insulation capacity (van Mantgem and Schwartz 2003; Uhl and Kauffman 1990). These controversial results suggest a strong species-specific role of MC.

While there is a considerable amount of knowledge on bark fire resistance, some information is still scarce. For example, it is recognised that fire resistance strongly depends on bark thickness, but additional work is required to further quantify the influence of compass direction, MC and assess the combined effect of bark thickness and MC along the stem. A very feasible way of doing this is by contrasting different species from fire prone environments.

Among the coniferous trees grown in Southern Africa, *Pinus radiata* is known to be very susceptible to heat-induced cambium damage because of its thin bark, even when exposed to light intensity fires such as fires in prescribed burns for fuel load management. *Pinus pinaster* and *Pinus taeda* with thicker bark are more resistant to low-intensity fires and *Pinus elliotii* is reported to be the most resistant pine species to fire damage (de Ronde 1982). In a pioneering work, de Ronde tested the insulation capacity of those pine species on pieces of bark, less than 12 mm in thickness, collected from fresh sawn timber sections at various heights, between 0.1 and 1.3 m. Unfortunately, the experimental conditions of this study only allowed a limited inference, since temperatures were modified between 200 and 300°C for specific species and the potential influence of varying bark thickness and MC was not investigated. The modification of temperature between species makes comparisons of insulation capacity at specific heating temperatures and understanding of the limit of their fire resistance difficult.

The objective of this part of the study was to test the insulation capacity of bark from plantation tree species, all exotic to South Africa, and compare them to the bark insulation of three indigenous species from the Western Cape region. All species, despite originating from different fire prone ecosystems around the world, have in common that they grow in the Mediterranean climate of the Western Cape of South Africa in natural or commercial forests and thus face similar fire risks. The natural vegetation is dominated by Fynbos, consisting of low growing heath and reeds interspersed by *Proteaceae*. The natural tree distribution is confined to ravines, riverine forests and other fire protected locations, while exotic species, grown in commercial plantations may invade the fire prone Fynbos region (Richardson 1998). This obvious difference in fire sensitivity warrants a contrasting analysis of bark

insulation between the species. As a key to analysing the function of bark as a heat insulator, the influence of varying bark thickness and MC along the stem was analysed. Additionally, the influence of the diameter at breast height (dbh) and compass direction of the sample at the stem were investigated. From these results mathematical models were developed to quantify heat insulation capacity when exposed to maximum surface fire intensity.

## 2.3 Materials and methods

### 2.3.1 Study area and sample Material

The trees used for the study were obtained from the Stellenbosch and Grabouw region in the Western Cape Province, South Africa. The province experiences a typical Mediterranean climate with warm, dry summers and wet, temperate winters. In summer the temperature averages 22°C, while it drops in winter to around 10°C (van Wilgen 1982; Wicht 1971), with low summer rainfall and an intermittent winter precipitation of approximately 884 mm per year, with substantial fluctuations, ranging from 464 mm in 2004 to 1586 mm annually in 1977 (Grab and Craparo 2011). The natural vegetation is dominated by Fynbos. The soil, which is often leached and infertile, is derived from sandstone and in some places granite and shale. Bordering the Fynbos vegetation in some areas are the industrial *Pine* and *Eucalyptus* plantations, established to supply timber to the local sawmills (van Wilgen 1982).

The selected tree species for this study were *Pinus pinaster*, *Pinus radiata*, *Pinus elliotii*, *Eucalyptus cladocalyx* and *Acacia mearnsii* as commercial species and *Ekebergia capensis*, *Rhus viminalis* and *Olea africana* as indigenous species. Five live and healthy trees of each species were harvested and 25 cm long billets were obtained from each tree at stem base (0.2 m), 15, 30 and 70 % of the total tree height to determine the bark-induced fire resistance along the trunk. Only billets with intact bark were considered to avoid artefacts.

The diameter at breast height, measured at 1.3 m, and the tree height were recorded for each tree, as well as the north direction. The fire resistance tests were performed on all four cardinal points.

### 2.3.2 Simulated fire exposure of the billets

To determine a species-specific heat resistance of the bark, the bark was heated through its thickness  $BT$  in a given area  $A$  (through a metal mask) at a temperature of 400°C and the time  $t$  that was required to heat the cambium to the lethal temperature of 60°C, was determined.

A fire was simulated with a standard 1,600 W electric heat gun (Black & Decker 1602/HID) with a temperature range of between 300 and 560°C. The billets were heated at a constant surface temperature of 400°C and at a constant distance of 1 cm. Previous tests had shown that the heat produced by the heat gun has the same effect as the fire of an open flame,

obtained by a blow torch. A portable temperature sensor (Testo, model 177 with a K type sensor) was used to monitor the temperature in the cambial region. A stop watch was used to determine the time from the start of the heating to the lethal temperature. A lapse period of 5 s after the heater was switched on was allowed before timing started to allow the bark temperature to reach a constant temperature of 400°C. An insulator plate made of aluminium and asbestos was used to shield the temperature probe from direct heat (Figure 2.1).

The bark thickness was measured with a vernier calliper at all four cardinal points and recorded. At each of the four cardinal points measurements were taken at the point of maximum bark thickness, avoiding fissures and intrusions where they existed. The heat was directed at the point of measurement. An intact section of the bark and the adjacent regions of cambium and sapwood were extracted for MC determination. The bark samples were weighed wet and oven dried (at 103°C) until constant weight. The MC was then calculated on the basis of the dry weight.

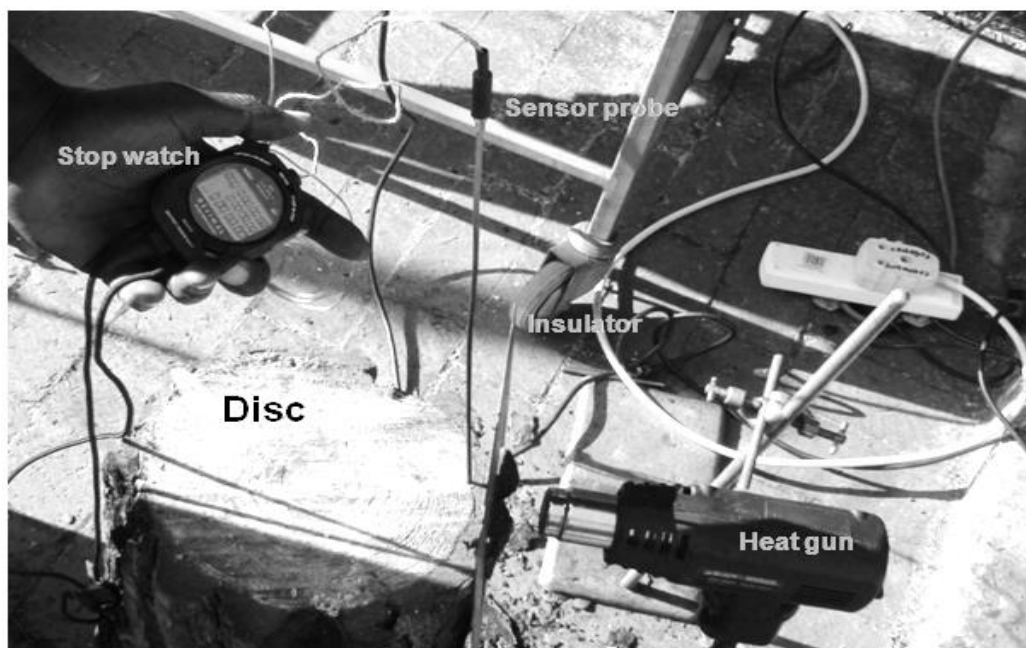


Figure 2.1: Experimental setup.

### 2.3.3 Statistical analysis

Statistical analysis of the data was based on traditional methods of data visualisation and preparatory correlation analysis, as well as testing before regression models were fit. The regression modelling itself followed two different avenues: (1) identification of the relevant variables and (2) the optimum combination of variables in a model for the prediction of

insulation capacity. The first avenue made use of a multi-model inference approach, while the second avenue of analysis was based on a classical selection of a best model approach.

### **2.3.3.1 Correlation analysis**

The first step of the data analysis was a correlation analysis of all variables. Pearson's correlation coefficients were calculated for all variables at the species level to obtain first information on the strength of the correlation between different variables and first indications of effects of co-linearity between independent variables.

### **2.3.3.2 Multi-model inference**

Burnham and Anderson (2002) emphasised that the influence of certain variables is more effectively revealed in a multi-model inference procedure, testing combinations of those variables in different models, as opposed to the classical model selection approach that fully relies on the fact that there is one best model. The latter could lead to the exclusion of variables with an explanation value, because of the model selection uncertainty, i.e. the probability to make inference on a wrongly selected model. Thus Burnham and Anderson (2002) suggested a procedure to determine the relative influence of variables across a selection of models, following the assumption that every model contains a certain information value and a variable that contributes highly across a set of models contains a high generic information value. The method is based on a model comparison by the Akaike information criterion (AIC), which has its theoretic foundations in information theory (Burnham and Anderson 2004). Another feature of the AIC is that the inclusion of additional variables is penalised, supporting the selection of parsimonious models. The multi-model inference according to Burnham and Anderson (2002) requires a full specification of a set of models that introduces the variables of interest in all possible combinations.

In this study, bark thickness, MC and relative height in the stem were used to specify the model set. First, all variables were entered alone, then with a second variable and finally all together so that all seven possible combinations were represented. Variable transformations and higher level variable interactions were excluded in this step to not complicate the interpretation of the results. All analyses were carried out separately for each tree species. Since several samples were taken from one tree along the stem, a typical clustered data structure was present within the data set (Schabenberger and Pierce 2002). Generalised least squares regression (gls), in the statistical package R (R Core Team 2012) was used to



fit multiple linear models that catered for autocorrelation of repeatedly measured components and also simultaneously solved the problem of heterogeneity and non-constant variance. The entire method is described in detail in Burnham and Anderson (2002), and will only be briefly explained here: An AIC value was obtained for each model as a result of the regression. Then the AIC difference  $-\Delta AIC$  for each model was obtained by subtracting the minimal (best) AIC value of all models from each single model AIC value. After an exponential transformation of the Akaike differences with  $e^{(-0.5\Delta AIC)}$  to  $\Delta AIC'$  the Akaike weights  $w_i$  were determined by dividing the  $\Delta AIC'$  values of each model by the sum of all  $\Delta AIC'$ . Based on the so obtained Akaike weights a relative contribution of each variable can be calculated by simply multiplying the obtained  $w_i$  values with the presence (1) or absence (0) code of a variable. Finally, the sum of the multiplication is calculated for each variable across models, which provides the relative information value.

### 2.3.3.3 Model selection

A best model had to be selected for prediction based on the information on variable importance gained in the multi-model inference. Additionally, a parsimony criterion was introduced via the choice of the AIC for model selection. Co-linearity between variables was investigated using the variance inflation factor (VIF), according to Wooldridge (2000). It indicates the magnitude of inflation in the standard errors associated with a particular coefficient of an independent variable. A maximum VIF value of 5, as proposed by Rogerson (2001), was used as a criterion to identify multi co-linearity. If two variables showed a higher VIF value, the one with the lower explanatory value was excluded from the regression modelling later on to avoid artificial boosting of  $R^2$  values without obtaining additional information. In the next step, the data was tested for the compliance with other assumptions of regression (homogeneity of variance, normality and independence of the residuals). To check for heteroscedasticity, a Levene test was applied and scatter plots of the residual over the predicted variable as well as quantile–quantile plots were used to assess the normality of the data.

A multiple linear model (Eq. 3), incorporating all the predictor variables and their quadratic transformations was used as a generic starting model to determine the factors influencing bark heat insulation capacity. Variables with minor or no explanation value were excluded by a stepwise procedure according to their explanation value in the model and the model AIC:

$$HT = a + b \cdot BT + c \cdot BT^2 + d \cdot DBH + e \cdot DBH^2 + f \cdot MC + g \cdot MC^2 + h \cdot H_{rel} + i \cdot H_{rel}^2 \quad (3)$$

Where HT is bark insulative capacity, i.e., time to heat the cambium (s) through the bark to a lethal temperature of 60°C, BT represents bark thickness (mm), DBH the diameter at breast height (cm), MC the moisture content (%) and  $H_{rel}$  is the relative height of the sample in the tree. In a next step bark heat insulation capacity, defined as heating time was plotted against the dominant variables to show the differences between species.

## 2.4 Results

### 2.4.1 Correlation analysis

The correlation analysis at species level revealed no significant influence of compass direction on the heat insulation capacity of bark. Thus the four measurements were pooled and averaged for the correlation analysis and all further analysis steps to decrease the influence of measurement outliers. The bark diameter values were also averaged accordingly. In the correlation analysis (Table 2.1) the DBH, taken as a measure of tree size, did not have a significant influence on heat insulation capacity (Kruskal Wallis;  $p = 0.000$ ) and was thus excluded from further analyses.

The results indicate a significant positive correlation between heating time and bark thickness for all species, except *R. viminalis*. In all other species bark thickness had the highest correlation of all independent variables to heating time. The correlation was positive, indicating an increase in heating time and thus insulative capacity with increasing bark thickness. MC correlated with heating time significantly only among the pines. The negative correlation suggests that increased moisture content in the bark of pines reduces resistance against heat damage. A significant correlation between MC and bark thickness was also only found amongst the pine species. Their MC increased with decreasing bark thickness up the tree. A significant correlation between MC and relative height was also only apparent in the pines. Relative height showed the second strongest correlation to heating time for all species. This negative correlation indicated decreased heating time with increasing height along the stem axis. This result is tied to the significant negative correlation between bark thickness and relative height (Table 2.1). Bark thickness decreased with increasing height, except for the thin barked broad-leaved species, such as *R. viminalis* and *O. africana*, where no correlations were found.

### 2.4.2 Multi-model inference

The information value of the tested variables determined in the multi-model inference procedure confirmed the dominant influence of the bark thickness across all species (Table 2). The dominance was more pronounced in the pines and decreased in the broad-leaved species where the information value of the relative height in the stem was almost equal to the one of bark thickness. At a second glance, a more differentiated picture emerges when the species-specific information values were considered (Table 2.2). For *P. radiata* the information value of  $H_{rel}$  was almost at the same level as bark thickness in contrast to the other pines. It is also interesting to note how strong the information value of the MC was in *P.*

*pinaster*, whereas it was substantially smaller in *P. radiata* and almost absent in *P. elliotii*. In all broad-leaved species the information value of MC was relatively small and in *A. mearsii* more or less absent.

Table 2.1: Bivariate Pearson's correlation coefficients for variables tested for their influence on bark insulation.

	<i>P. pinaster</i>		<i>P. radiata</i>		<i>P. elliotii</i>		<i>E. cladocalyx</i>		<i>E. capensis</i>		<i>R. viminalis</i>		<i>O. africana</i>		<i>A. mearsii</i>	
HT/BT	0.93	**	0.86	**	0.95	**	0.98	**	0.83	**	0.09	n.s.	0.58	**	0.99	**
HT/MC	-0.47	*	-0.40	•	-0.51	*	-0.23	n.s.	-0.25	n.s.	0.00	n.s.	-0.50	*	0.10	n.s.
HT/H <sub>rel</sub>	-0.80	**	-0.55	*	-0.80	**	-0.61	**	-0.70	**	-0.64	**	-0.48	*	-0.74	**
BT/MC	-0.43	•	-0.27	n.s.	-0.56	*	-0.25	n.s.	-0.15	n.s.	-0.41	•	-0.12	n.s.	0.12	n.s.
BT/H <sub>rel</sub>	-0.79	**	-0.51	*	-0.82	**	-0.56	*	-0.69	**	-0.35	n.s.	-0.13	n.s.	-0.76	**
MC/H <sub>rel</sub>	0.64	*	0.45	*	0.63	*	0.33	n.s.	0.02	n.s.	0.33	n.s.	0.07	n.s.	-0.31	n.s.

*HT* heating time to cambium damage, *BT* bark thickness, *MC* moisture content, *H<sub>rel</sub>* relative height at the tree—with 0 denoting the bottom and 1 the top

Significant correlations are shown in grey with a single ( $p < 0.05$ ) or double ( $p < 0.01$ ) asterisk Significance levels of  $p < 0.1$  are marked with a dot

### 2.4.3 Selection of best regression model

The collinearity was accounted for in the model selection approach. Collinearity diagnostics revealed that *H<sub>rel</sub>* was only providing additional information for *P. pinaster*, *E. cladocalyx* and *E. capensis*. It was thus consequently excluded from regression for all other tree species as well as moisture content.

Table 2.3 shows the coefficients for estimating heat resistance for the various species according to the best models. The resulting models revealed a linear relationship between heating time and bark thickness at varying heights. Heating time increased with increasing bark thickness.

Table 2.2: Results of the multi-model inference on the variable information value: (a) the calculated absolute values, b) the absolute values for selected subgroups.

a) Variable information value			
Species (species group)	BT	H <sub>rel</sub>	MC
<i>P. radiata</i> (conifer)	1.00	0.99	0.23
<i>P. pinaster</i> (conifer)	1.00	0.41	0.68
<i>P. elliotii</i> (conifer)	1.00	0.47	0.07
<i>E. cladocalyx</i> (thick-barked, broad-leaved)	1.00	0.92	0.19
<i>E. capensis</i> (thick-barked, broad-leaved)	1.00	1.00	0.28
<i>R. viminalis</i> (thin-barked, broad-leaved)	0.65	1.00	0.18
<i>O. africana</i> (thin-barked, broad-leaved)	1.00	0.50	0.20
<i>A. mearnsii</i> (thick-barked, broad-leaved)	1.00	0.72	0.05

b) Aggregate variable information value			
Groups	BT	HR	MC
Across all species	7.65	6.00	1.88
Pines	3.00	1.86	0.98
Thick-barked, broad-leaved	3.00	2.63	0.52
Thin-barked, broad-leaved	1.65	1.50	0.38

*BT* bark thickness, *H<sub>rel</sub>* relative height at the stem, *MC* moisture content in %

If bark thickness was considered as the only factor, the specific heat insulation capacity per mm bark is shown in Table 2.3. The difference in  $R^2$  obtained between the best model (Table 2.3) compared with the model with bark as the only predictor (Table 2.4) provides an indication for the effect size of  $H_{rel}$ .

Table 2.3: Model coefficients for estimating heat resistance for the various species.

Variable	<i>P. pinaster</i>	<i>P. radiata</i>	<i>P. elliotii</i>	<i>E. cladocalyx</i>	<i>E. capensis</i>	<i>R. viminalis</i>	<i>O. africana</i>	<i>A. mearnsii</i>
Model fit R <sup>2</sup>	0.82	0.99	0.97	0.99	0.96	0.99	0.99	0.95
Intercept	77.9419	23.8649	0	0	51.7834	0	14.4389	0
BT	5.5107	8.8545	18.1672	14.7820	17.3385	13.8440	8.6897	16.7497
<i>H</i> <sub>rel</sub>	-3.3626			-0.7480	-12.7362			

Table 2.4: Percentage contribution of bark thickness to heat insulation.

Variable	<i>P. pinaster</i>	<i>P. radiata</i>	<i>P. elliotii</i>	<i>E. cladocalyx</i>	<i>E. capensis</i>	<i>R. viminalis</i>	<i>O. africana</i>	<i>A. mearnsii</i>
Model fit R <sup>2</sup>	0.41	0.41	0.67	0.81	0.23	n.s.	26	0.49
Intercept	26.09	23.86	-3.39	-4.75	-0.86	16.71	14.44	-27.39
BT	8.18	8.85	15.99	14.83	22.46	8.78	8.69	18.88

In the overview, three groups of heat resistance patterns are distinguishable: (1) the pines, (2) the thick-barked broad-leaved species (*E. cladocalyx*, *E. capensis* and *A. mearnsii*) and (3) the thin-barked broad-leaved species (*R. viminalis* and *O. africana*). The influence of relative height is illustrated in Figures 2.2 and 2.3, in which the effect of bark thickness and heating time are visualised in scatter plots. The fitted regression line supports the visualisation of species-specific differences. From the intercept the modelled bark thickness at ground level can be read while the slope shows the changes along the stem from the bottom to the top.

Interpreting the information in Figures 2.2 and 2.3 in combination, it becomes obvious that *E. capensis* has a higher insulation capacity in relation to the expected bark thickness effect. This trend can also be observed to a lesser extent in *P. elliotii*, *A. mearnsii*, *R. viminalis* and *O. africana*. Some species with thin bark also possess greater fire resistance than those with thick bark. For instance among the pines, *P. pinaster* had the thickest bark, but the most fire resistant species was *P. elliotii*. Likewise, among the thick-barked broad leaved species, *A. mearnsii*, *E. cladocalyx* and *E. capensis* had similar thick bark at the base of the trunk while clearly the most fire resistant species was *E. capensis*.

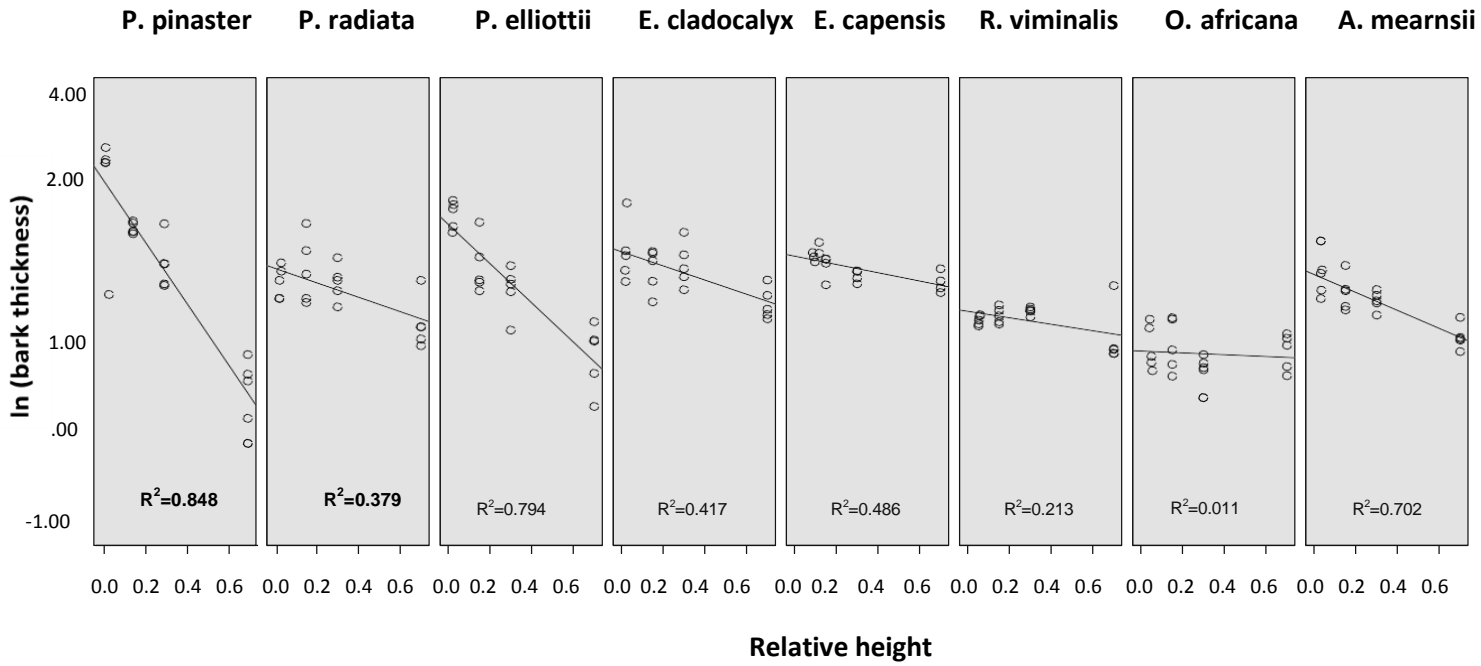


Figure 2.2: ln-transformed bark thickness (mm) as a function of relative height in the stem.

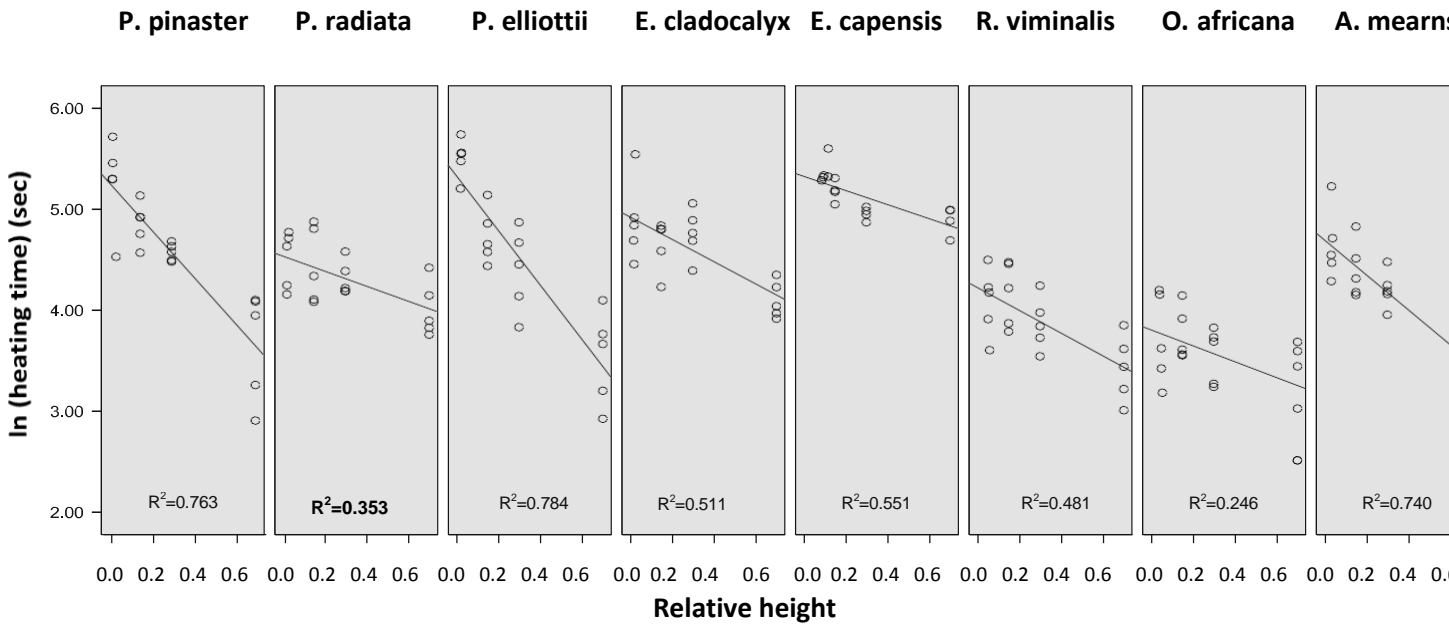


Figure 2.3: ln-transformed bark insulation capacity, expressed as heating time (s) as a function of relative height in the stem.

## 2.5 Discussion

The results obtained in this study showed that bark thickness explained more of the fire resistance than any other of the tested variables, which was to be expected, considering the prominent effect of bark thickness in the physically derived calculation of insulation capacity (Eqs. 1, 2). The outcomes of the species comparison were interesting. Among the pines, *P. radiata* with the thinnest bark had the lowest heat resistance capacity to cambial damage at any given bark thickness, while *P. elliotii* was the most resistant. The results are in line to those of de Ronde (1982), who studied the same species within the Cape forest region. The outcome of this experiment, like the findings of de Ronde (1982) attribute the vulnerability of *P. radiata* to its thin bark, unlike both *P. pinaster* and *P. elliotii*, which are both thick barked. Among the indigenous species *E. capensis* had the highest heat resistance capacity due to its thick bark, while *R. viminalis* and *O. africana* had lower heat resistance capacity. For thick-barked species in the study, namely *P. pinaster*, *P. elliotii*, *E. cladocalyx*, *E. capensis* and *A. mearnsii* the bark thickness contributed more to heat resistance than in thin-barked species (Table 2.4). The findings were similar to those of Brando et al. (2012) and Pinard and Huffman (1997), who reported bark thickness to contribute 63 and 82 %, respectively, to heat resistance against cambial damage. Harmon (1984) also found a linear relationship between heating time to lethal cambium temperature and bark thickness. He did, however, not consider possible influences of relative height in his study. Bark thickness was thus confirmed as the main factor influencing heat resistance as reported by several studies (e.g. Lawes et al. 2011; Catry et al. 2010; Rigolot 2004; Peterson and Ryan 1986).

A novel result of this study is that relative stem height was a good substitute for bark thickness for all species where bark thickness did not change too much along the stem. The majority of broad-leaved species are known to maintain a more or less constant bark thickness along the entire stem and have been reported to be more heat resistant along the bole (Fernandes et al. 2008). The pines, on the other hand, have a greater bark taper with greater proportion of outer bark at the bottom than at the top (Figure 2.2). It might be a genetic trait of pines from fire-prone environments to form thicker bark at the bottom of the trunk to acquire additional resistance against ground fires. The less attenuated effect of bark taper in *P. radiata* explains its inferior heat tolerance to ground fires compared with the other two pine species in the study.

The fact that bark MC was negatively correlated with heating time for all species can be attributed to the physical properties of water, namely its high heat conductivity. The findings of this study support those of VanderWeide and Hartnett (2011), Agee (1993) and Vines (1968) in concluding that a high bark MC is correlated to a lower heat resistance. Pinard and



Huffman (1997) reported contradictory results, by presenting evidence that a higher bark MC increased the heat resistance. A possible explanation might be that due to its higher heat conductivity, the presence of water within the bark layer could result in higher initial heat absorption, resulting in evaporation before the heat is conducted to the cambium. However, this might only be a short lived effect because once the water has evaporated, the heat will conduct faster through the moist bark layers to the cambium than in the absence of moisture. The presence of moisture, therefore, results in an increase in heat conduction through the bark layers. Due to its high heat capacity, moisture retains heat for a longer period of time, thereby exposing the cambium to an extended period of heat.

There were also clear differences in bark MC between species. Because of the rather constant bark thickness along the trunk, broad-leaved species are likely to maintain the same level of moisture within the bark layer at different trunk heights. It is thus not surprising that MC did not correlate significantly with heating time along the trunk. A significant correlation between MC and relative height was only observed in the pines, where MC increased with increasing tree height. This concurs with the findings of Harmon and Sexton (1995) who found MC to decrease from the tip to the ground. A significant correlation between MC and bark thickness was also only observed in the pines. Moisture content increased with decreasing bark thickness up the tree, which is most likely a consequence of the bark structure of pines. Pines, as opposed to the other species in the study, have a strongly structured, deep fissured bark, and a small phloem proportion, which contains the majority of moisture in the bark. Consequently, more moisture would be present at the top of the tree where higher proportions of phloem occur (van Mantgem and Schwartz 2004). The spaces within the dead outer bark layers are filled with air, which adds to the heat resistance observed in the pines at the bottom of the stem.

The quantitative results of the heat insulation capacity suggest a substantially lower insulation compared with values obtained by van Mantgem and Schwartz (2003), who estimated the time required for the cambial cells of incense cedar, ponderosa pine and white fir to be killed in trees of 1 cm bark thickness to be approximately 10 min (600 s) when exposed to temperatures of 400°C. Van Mantgem and Schwartz (2003) heated living trees based on an electrical copper heating pad in the conifer forests of California. At the same temperature, the results of this study show the average insulation capacity of a tree with 1 cm bark thickness to be around 2.12 min (127.46 s) for the commercial species and 2.45 min (147.04 s) for indigenous species. Comparisons of the individual values show no clear differences in heat resistance between indigenous and commercial species. A key result is that the over proportionally high heat resistance performance of some species in relation to bark thickness, which can probably be attributed to chemical or structural properties of the bark that have not been accounted for in this section of the study. Bark density, which was

reported to have an influence on heat resistance capacity (Vines 1968; Reifsnyder et al. 1967) was also not considered in this section. These factors are potentially responsible for the observed pattern and the percentage of insulation not accounted for by bark thickness. Although bark thickness is the main factor influencing heat resistance capacity in surface fires, it does not entirely explain the heat resistance capacity of trees.

In this study a temperature of 60°C was defined as lethal threshold to obtain comparable results between the studied species. It is, however, well known that extent of damage is dependent on fire temperature as well as flame residence time (Hengst and Dawson 1993; Uhl and Kauffman 1990). Therefore, brief exposures to elevated temperatures may not result in cell or tissue death, but only in a temporary disruption of physiological and biochemical activities (Whelan 1995). Cambium cells can die at lower temperatures, if the exposure time is long enough. Increased heat exposure time is known to result in an exponential increase in cell death rates (Dickinson and Johnson 2004), which means at a constant temperature the time required to kill plant tissue decreases exponentially (Bond and van Wilgen 1994).

In this study bark thickness along the stem was taken as a substitute for tree age, to reduce the impact on the ecosystem and limit the amount of felled trees, especially the protected indigenous species. It could be argued that trees of the same diameter but different age may differ in terms of bark structures. However, that factor was taken into consideration in the regression models. The overall heat resistance of a tree is mainly a result of the bark thickness and the specific heat resistance of the bark (Table 2.4). The specific heat resistance was significantly reduced by relative height in *P. pinaster*, *E. cladocalyx* and *E. capensis* (Table 2.3). That means for trees of the same bark thickness, bark structure or chemical properties change with increasing height and induce a decreasing heat tolerance. This is a further indication showing that some tree species are mainly adapted to withstand ground fires.

The high fire resistance of some species can be linked to the bark structure of these species. The bark of *P. ellioti* is furrowed and cross-checked into irregularly rectangular, papery-scaly plates, while that of *A. mearnsii* and *E. capensis* is similarly fissured with hard protective plates. The thickened bark rising above the furrows in *P. ellioti* and the hard protective plates of the other species possibly offer more protection to the inner bark and the cambium against heat from the outside. Interestingly, the thin-barked species *R. viminalis* and *O. africana* showed a clear reduction of specific heat resistance with increasing  $H_{rel}$  beyond what could be expected from only the bark thickness (Figures. 2.2, 2.3). That means these two species are able to resprout after fires (von Richter et al. 2005) and have adapted to ground fires to protect particularly the lower stem sections.

This study suggests that the effect of bark structure and composition seems to be a further influencing factor that is responsible for the inter-specific differences of heat resistance of bark. This is supported by further evidence that the physical bark structure, i.e. density, texture, anatomy, fissuring and scaling, plays a significant role in thermal insulation (Harmon 1984). For example the air trapped in void spaces of structured bark increases heat insulation due to low heat conductivity (e.g. Pinard and Huffman 1997). Highly structured barks were thus associated with higher heat insulation (Bauer et al. 2010; Fahnestock and Hare 1964). This study gives some indication that it is not necessarily the bark fissures alone that have an effect. This can be seen by the very comparable specific heat insulation capacity of *P. radiata* and *E. cladocalyx*; the first with a structured and the second one with a smooth bark. Thus further research is warranted on the effects of topological bark structure, bark density and chemical composition and their influence on heat resistance of bark.

## 2.6 Conclusion

Surface fires penetrating through the bark can damage trees at their lower trunk sections when the cambium is destroyed or kill the tree when necrosis around the entire bole circumference occurs. The dominant factor influencing heat resistance capacity was found to be bark thickness, confirming other studies. Furthermore, investigated variables such as compass direction, tree size and moisture content were found to be less relevant, while the relative height at the stem contributed additionally in three thick-barked species. There were no clear differences between indigenous and exotic species. However, the differences were more species-specific and seem to be not only an effect of bark thickness but also of the specific heat insulation capacity of bark, which can be attributed to structural, physical and chemical properties and will be researched in the next chapter to fully understand the role of bark as the interface between fire and the tree.

## 2.7 References

- Agee, J.K. 1993. *Fire ecology of pacific north west forests*. Island Press, Washington.
- Alexandrov, V.Y. 1977. *Cells, molecules and temperature*. Springer, Berlin, p 330.
- Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45:5950–5959.
- Bond, W.J. and van Wilgen, B.W. 1994. *Fire and plants*. Chapman and Hall, London.
- Brando, P.M., Nepstad, D.C. and Balch, J.K. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behaviour. *Global Change Biology* 18:630–641.
- Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. In *Proceedings of the society of American forester's, 1994 national convention*, pp. 171-178.
- Burnham, K.P. and Anderson, D.R. 2002. *Model selection and multimodel Inference. A practical information—theoretical approach*, 2nd edn. Springer science Business Media LLC, New York, pp 71, 75, 167-169.
- Burnham, K.P. and Anderson, D.R. 2004. Multimodel Inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Catry, F.X., Rego, F., Moreira, F. and Fernandes, P.M. 2010. Post-fire mortality in mixed forests of central Portugal. *Forest Ecology and Management* 260:1184–1192.
- Chanyenga, T.F., Geldenhuys, C.J. and Sileshi, W.W. 2012. Germination response and viability of an endangered tropical conifer *Widdringtonia whytei* seeds to temperature and light. *South African Journal of Botany* 81:25–28.
- Davis, K.P. 1959. *Forest fire: control and use*. McGraw-Hill Book, Michigan, pp 31–47.
- de Bano, L.F., Neary, D.G. and Folliott, P.F. 1998. *Fire's effects on ecosystems*. John Wiley and Sons, New York.
- de Ronde, C. 1982. The resistance of Pinus species to fire damage. *South African Forestry Journal* 122:22–25.
- Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson EA, Miyanishi K (eds). *Forest fires*. Academic, New York, pp 477–525.

- Dickinson, M.B. and Johnson, E.A. 2004. Temperature-dependent rate models of vascular cambium necrosis. *Canadian Journal of Forest Research* 34:546–559.
- Ducrey, M., Duhoux, F., Huc, R. and Rigolot, E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Canadian Journal of Forest Research* 26:1366–1374.
- Fahnesock, G. and Hare, R.C. 1964. Heating of tree trunks in surface fires. *Journal of Forestry* 62:799–805.
- Fernandes, P.M., Vega, J.A., Enrique, J. and Rigolot, E. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256:246–255.
- Gignoux, J., Clobert, J. and Menaut, J. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110:576–583.
- Gill, A.M. 1977. Management of fire-prone vegetation for plant species conservation in Australia. *Search* 8:20–26.
- Gill, A.M. 1995. *Plant stems: physiology and functional morphology*. Academic, New York.
- Grab, S. and Craparo, A. 2011. Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973–2009. *Agricultural and Forest Meteorology* 151:406–413.
- Harmon, M. 1984. Survival of trees after low-intensity surface fires in the Great Smoky Mountains National Park. *Ecology* 65:796–802.
- Harmon, M.E. and Sexton, J. 1995. Water balance of conifer logs in early stages of decomposition. *Plant Soil* 172:141–152.
- Hengst, G.E. and Dawson, J.O. 1993. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24:688–696.
- Hobbs, R.J., Currall, J.E.P. and Gimingham, C.H. 1984. The use of “thermo-color” pyrometers in the study of heath fire behaviour. *Journal of Ecology* 72:241–250.
- Lawes, M.J., Richards, A., Dathe, J. and Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212:2057–2069.
- Levitt, J. 1980. *Responses of plants to environmental stresses*. Vol. I: chilling, freezing, and high temperature stresses, 2nd edn. Academic, New York.

- Martin, R.E. 1963. Thermal properties of bark. *Forest Products Journal* 3:419–426.
- Matthew, B.D. and Johnson, E.A. 2004. Temperature-dependent rate models of vascular cambium cell mortality. *Canadian Journal of Forest Research* 34:546–559.
- McHugh, C.W., Kolb, T.E. and Wilson, J.L. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32:510–522.
- Michaletz, S.T. and Johnson, E.A. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22:500–515.
- Miranda, A.C., Fatima, O.D. and Ferreira, S.D. 1993. Soil and air temperatures during prescribed cerrado fires in central Brazil. *Journal of Tropical Ecology* 9:313–320.
- Morrison, D.A. 1995. Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of NSW* 115:109–119.
- Mutch, L.S. and Parsons, D.J. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. *Forest Science* 44:341–355.
- Newton, C.A. 2007. *Forest ecology and conservation*. A handbook of techniques. Oxford university press, Oxford.
- Pausas, J. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science* 8:703–706.
- Peterson, D.L. and Ryan, K.C. 1986. Modeling post-fire conifer mortality for long-range planning. *Journal of Environmental Management* 10:797–808.
- Pinard, M.A. and Huffman, J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* 13:727–740.
- Reifsnyder, W.E., Herrington, L.P. and Spalt, K.W. 1967. *Thermophysical properties of bark of shortleaf, longleaf, and red pine*. Bulletin no. 70. School of Forestry, Yale University, Yale.
- Richardson, D.M. 1998. Forestry trees as invasive aliens. *Conservation Biology* 12:18–26.
- Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* mill. and *Pinus pinea* L. *Plant Ecology* 171:139–151.
- Rogerson, P.A. 2001. *Statistical methods for geography*. Sage, London.
- Rötzer, T., Seifert, T., Gayler, S. and Priesack, E. 2012. Effects of stress and defence allocation defence on tree growth: simulation results at the tree and stand level. In: Matyssek, R., Schnyder, H., Ernst, D., Munch, J-C, and Pretzsch, H. (eds) Growth and

defence in plants: resource allocation at multiple scales. *Ecological studies* 220. Springer, Heidelberg, pp 401–432.

Ryan, K.C. and Reinhardt, E.D. 1988. Predicting post-fire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:291–1297.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, version 2.15.1. Vienna, Austria. <http://www.R-project.org>

Schabenberger, O. and Pierce, F.J. 2002. *Contemporary statistical models for the land and soil sciences*. Taylor and Francis, New York.

Schoennagel, T., Turner, M.G. and Romme, W.H. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology* 84:2967–2978.

Stephens, S.L. and Finney, M.A. 2002. Prescribed fire mortality of sierra nevada mixed conifer tree species: effects of crown damage and forest floor consumption. *Forest Ecology and Management* 162:261–271.

Swezy, M.D. and Agee, J.K. 1991. Prescribed-fire effects on fineroot and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21:626–634.

Uhl, C. and Kauffman, J.B. 1990. Deforestation, fire susceptibility and potential tree responses to fire in the eastern Amazon. *Ecology* 71:437–449.

VanderWeide, B.L. and Hartnett, D.C. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261:1530–1538.

van Mantgem, P.J. and Schwartz, M. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *Forest Ecology and Management* 178:341–352.

van Mantgem, P.J. and Schwartz, M. 2004. An experimental demonstration of stem damage as a predictor of fire-caused mortality for ponderosa pine. *Canadian Journal of Forest Research* 34:1343–1347.

van Wilgen, B.W. 1982. Some effects of Post-Fire Age on the Above- Ground Plant Biomass of Fynbos (macchia). *Journal of Ecology* 70:217–225.

Vines, R.G. 1968. Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16:499–514.

Vines, R.G. 1981. Physics and chemistry of rural fires. In: Gill AM, Groves RH, Noble IR (eds). *Fire and the Australian biota*. Australian Academy of Sciences, Canberra, pp 129–150.

von Richter, L., Little, D. and Benson, D.H. 2005. Effects of low intensity fire on the resprouting of the wild African Olive (*Olea europaea* subsp. *cuspidata*) in Cumberland plain woodland, western Sydney. *Ecological Management and Restoration* 6:230–232.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge university press, Cambridge.

Wicht, C.L. 1971. The Task of Forestry in the Mountains of the Western and Southern Cape Province. *Proceedings of the Annual Congress of the Grassland Society of South Africa* 6:20–27.

Wooldridge, J.M. 2000. *Introductory econometrics: a modern approach*. South Western College, p 824.



## Chapter 3 Fire resistance properties of tree bark as a function of its surface topology, density and chemical composition

### 3.1 Abstract

Ground fires are known to affect trees of different species differently, depending on the capacity of the bark to shield the cambium from heat. Bark thickness has been identified to be decisive a variable in fire resistance. This second part of the study further focuses on the role of bark surface topology, bark density and bark chemical composition for its fire resistance. For a set of tree species growing in the Western Cape of South Africa, additional samples have been analysed by means of x-ray based computer tomography for their spatial surface macro-structure. Bark density measurements and bark chemical constituents analysed by thermo-gravimetric analyses (TGA) were tested to see how the specific heat resistance capacity of bark of those species was influenced, when bark thickness was kept constant. The results suggest that in particular bark topology plays a role, while the correlations with bark density and chemical composition could not be secured statistically. A main finding was that fissures in the bark play a significant role. A regression model showed a significant influence of fissure width, fissure frequency and the minimum bark thickness to the cambium, which is a function of fissure depth. The results show that structural bark parameters are a necessary addition to explain heat resistance of bark.

*Key words: Bark insulation capacity, specific heat resistance, bark surface structure, thermo-gravimetric analysis, computer tomography*

### 3.2 Introduction

Tree bark offers the main protection against surface fire damage (de Bano et al. 1998; Agee 1993; Vines 1981). Bark thickness has been reported to be the main protection factor against fire damage, with thick barked trees showing greater resistance to heat damage than thin barked trees (Bauer et al. 2010; Lawes et al. 2011; Rigolot 2004; Stephens and Finney 2002; Mutch and Parsons 1998; Ryan and Reinhardt 1988; Pausas 1997).

Some studies have gone further and quantified the role of bark thickness in heat insulation and found bark thickness to explain 63 % (Pinard and Huffman 1997), 82 % (Brando et al. 2012) and about 85% (Odhiambo et al. 2014) of insulation against heat damage to the cambium in thick barked tree species. Wesolowski et al. (2014) reported a similar number for three eucalypt species with different bark characteristics, ranging from 61 to 94 %. Hempson

et al. (2014) studied the effect of bark thickness and stem diameter on fire response for several fynbos and savannah plant groups prevalent in South Africa and found that bark thickness combined with stem diameter accounted for 95% of fire resistance. However, these findings show that bark thickness, despite having a major role in heat insulation, does not account completely for insulation against cambial heat damage during surface fires.

Several studies have investigated other bark properties that potentially affect the heat insulation capacity. The effect of moisture content on heat insulation was shown to be insignificant in some studies (e.g. Odhiambo et al. 2014; Hengst and Dawson 1993), while it was reported to have some impact in others (Wesolowski et al. 2014). The latter authors have conclusively demonstrated with sequential placement of temperature sensors in the bark that moisture in the periderm is positive due to the evaporative cooling effect while higher moisture contents near the cambium reduces the insulation capacity of bark.

Bark density has been reported to have a weak positive correlation with heat resistance capacity (Lawes et al. 2011; Agee 1993; Reifsnyder et al. 1967). These studies show that as bark density increases, thermal conductivity through the bark layer decreases thus increasing the heat resistance. In contrast, however, a study by Bauer (2010) suggests that less dense bark with more internal air spaces may be advantageous for an increased fire resistance due to the additional insulation effects afforded by the air pockets. Dense bark could be expected to conduct heat better, because of fewer air spaces disrupting the heat flow. Several studies have reported negligible influence of bark density on heat insulation capacity (van Mantgem and Schwartz 2003; Hengst and Dawson 1993; Vines 1968). The exact influence of bark density to its heat insulation is thus not clear and is investigated further in this section.

Trees of different species have varying bark structures (e.g. Nicolai 1986), which affect thermal properties; for example highly structured bark with deep fissures provides better resistance against heat damage compared to smooth bark (Bauer et al. 2010; Nicolai 1986; Harmon 1984; Fahnestock and Hare 1964). Fissures in the outer bark trap air, which disrupts the heat passage to the cambium due to the poor heat conductivity of air and as a result increases the insulative capacity of the bark (Pinard and Huffman 1997). The role of bark structure has, however, been largely neglected when studying bark heat resistance. The exact contribution of bark structure to heat resistance is unknown. The mechanism by which bark structure contributes to heat insulation is not clearly understood and is investigated in this section.

The role of chemical components in bark with regards to fire insulation is also not well understood. Bark consists of cellulose, hemicelluloses, lignin and a high content of extractives and inorganic material referred to as ash (Pereira et al. 2003; Fengel and

Wegener 1984). In this study it was hypothesised that the heat resistance of the bark layer is related to the degradation temperatures of the major chemical components and that the ability to resist heat damage is therefore affected by the thermal stability of these chemical components. The degradation temperature of bark specific chemical components, as well as ash content was determined with Thermogravimetric Analysis (TGA) and correlated to the species specific heat resistance capacity.

Odhiambo et al. (2014) determined the heat resistance for various bark thicknesses for different species and derived a bark thickness independent heat resistance factor. A major finding of Odhiambo et al. (2014) was that bark thickness and moisture content are insufficient to explain the variation of heat resistance between species, which is the grounding for looking into further factors that could explain the species specific differences. Thus the main objectives of this paper are to determine the degree to which bark density, the chemical components of the bark and bark topology affect the species-specific heat resistance (HRC).

### 3.3 Materials and methods

#### 3.3.1 Study area and sample selection

Samples were obtained from trees growing in the Stellenbosch and Grabouw region in the Western Cape, South Africa. The natural vegetation is dominated by Fynbos. Bordering the Fynbos vegetation in some areas are commercial Pine and Eucalyptus plantations, established to supply timber to the local sawmills (van Wilgen 1982). Forest fires commonly occur in summer and have become a recurrent phenomenon over the past decade (Calvin and Wettlaufer 2000).

Billets of 25 cm height (Figure 3.1) were obtained from the lower trunk section, which is mostly affected by surface fires, of mature healthy trees growing in forest patches and plantations within the region. The tree species selected for the study comprise of commercially relevant species, i.e. *Pinus pinaster*, *P. radiata*, *P. elliotii*, *Eucalyptus cladocalyx* and *Acacia mearnsii*, as well as indigenous species common to the area, i.e. *Rhus viminalis* and *Olea africana*.



Figure 3.1: Sample billets.

### 3.3.2 Surface topology

From each species, a single healthy tree with no signs of defects or diseases was selected and a billet was cut off between the ground level and 50 cm height. The billets were scanned with a microfocus CT (Computer Tomography) system from General Electric Phoenix (V|Tome|X L240) with a NF180 high resolution tube. CT scanning is a proven method to measure macro structure of wood and bark (zu Castell et al. 2005, Nikolova et al. 2009; Seifert et al. 2010).

The scan acquisition time was 500 ms per image at an average of between 2000 - 3000 images per CT scan depending on the magnification. The scan settings range was between 120 – 200 kV, 100 – 150  $\mu$ A and at a scan resolution of 111 – 142  $\mu$ m.

The scan produced several cross-sectional images of each species, distinctly displaying the bark features. 15 images of a scan stack were randomly selected for detailed surface analysis study to provide a representative sample of the scan slice for a billet. Further image analysis was conducted in the imaging software Image J. Fissures were the dominant features characterising the outer bark of those species with structured bark. Any natural intrusion into the bark from the surface in both vertical and horizontal direction was regarded as a fissure; spaces resulting from broken bark were not considered as fissures. The amount and size of fissures were determined. The size was established by measuring the depth and width of fissures. The depth was measured from the perceived outer surface to the valley bottom of the fissure, while the width was measured as the distance across the edges of the top most section of the fissure boundaries.

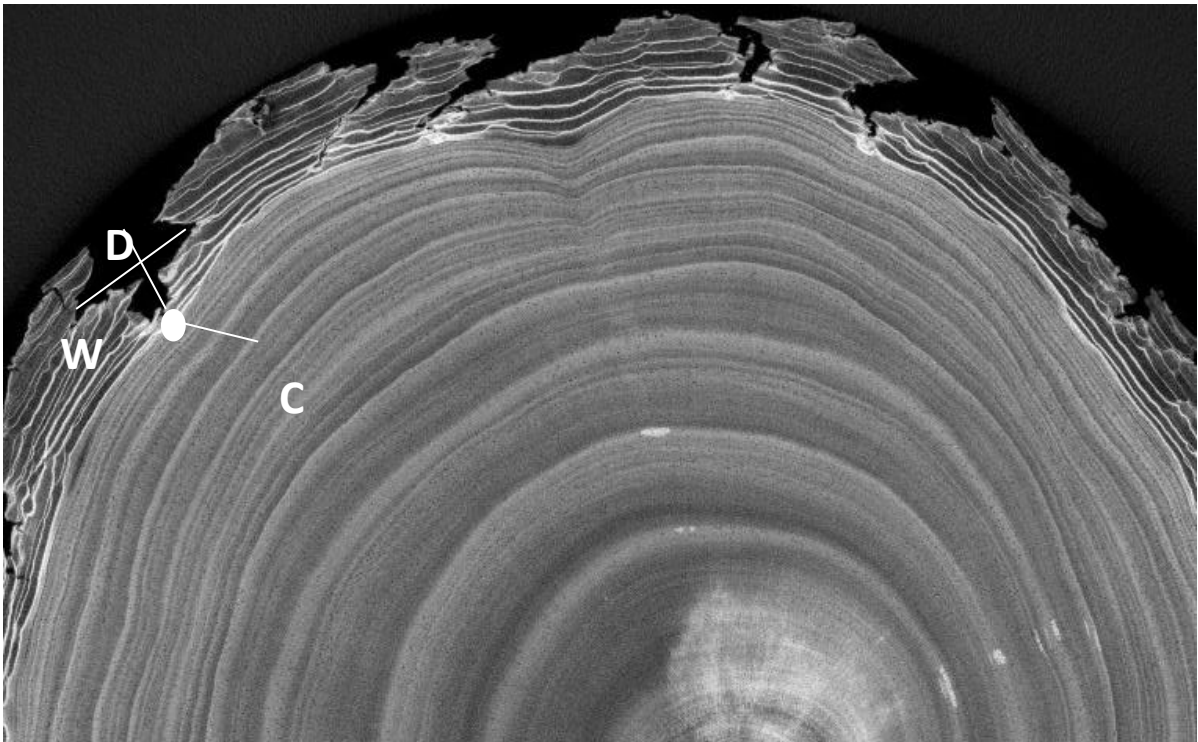


Figure 3.2: Computer tomography image of a scanned *Pinus radiata* stem. The measurements of fissure properties (W: width and D: depth) are indicated as well as the cambial region (C).

A set of topological descriptors was calculated and tested for their influence on HRC of the bark (Table 3.1). The minimum bark thickness is the reduced bark thickness at the point of the fissure and surface extension ratio refers to the increased surface length of the outer bark due to the fissure opening. The 'total' value represents the cumulative value of all the fissures present in the entire circumference of the image slice.

Table 3.1: Topological descriptors of bark tested for their influence on heat resistance capacity.

Variable	Formula for calculation	Further information
Width of fissures $W$ (mm)		see Figure 3.2
Depth of fissures $D$ (mm)		see Figure 3.2
Standardised number of fissures $N_{Fiss}$	$N_{Fiss} = \frac{\sum_{i=1}^n i}{c}$	Where $i$ is the each individual fissure on cross-section, $n$ the total number of fissures and $c$ the circumference of the cross-section inside bark.
Width/depth relation $WDR$	$WDR = \frac{W}{D}$	
Depth/width relation $DWR$	$DWR = \frac{D}{W}$	
Surface length proportion $pSL$	$pSL = \frac{SLB}{SFS}$	Where $SLB$ is the surface length of bark with fissures and $SFS$ , the surface lengths assuming a smooth surface.
Surface length of bark with fissures $SLB$ (mm)	$SLB = W_{mean} \cdot D_{mean} \cdot N_{Fiss} \cdot \frac{1}{2}$	Where $W_{mean}$ and $D_{mean}$ are the average width and depth of fissures, assuming an equilateral triangle as a fissure form
Minimum bark thickness $MBT$ (mm)		Minimum bark thickness at bottom of fissures
Cumulative min. bark thickness $cMBT$ (mm)	$cMBT = \sum_i^n MBT_i$	

### 3.3.3 Bark density

The bark density of the different species was determined with the Diana Smith method (Smith 1954). Pieces of bark from five billets of each species were exposed to alternating over- and under-pressure in a water tank for a period of five days to completely saturate them with water. The basic density can then be calculated according to Equation 4:

$$\rho [g / cm^3] = \frac{1}{\frac{m_{sat} - m_{dry}}{m_{dry}}} + \frac{1}{1.53} \quad (4)$$

Where  $m_{sat}$  is the fully saturated mass and  $m_{dry}$  the oven-dry mass.

The density of each species was then correlated to the HRC.

### 3.3.4 TGA Analysis

The chemical components contained in the bark of each species were analysed by TGA with a universal TGA instrument model TGA/500/2000. Two samples, each weighing approximately 10 mg and obtained from two trees per species were heated in an inert nitrogen atmosphere with a purge gas flow of 500 mm/min at a rate of 20°C/min from 25°C to 600°C. The average degradation temperatures of the two duplicate samples obtained from derivative thermo-gravimetric (DTG) graphs and the remaining ash content were recorded for each species and correlated to HRC.

### 3.3.5 Heat resistance capacity

Various fissure properties were correlated to the HT of the selected species, which were derived from Odhiambo et al. (2014) and are listed in Table 3.2. The heat resistance was determined by measuring the time until the cambial area reached 60°C after applying heat at 400°C to the outside bark. The regression models presented in Table 2.3 in the previous chapter were used to estimate the heat resistance as a function of bark thickness. Some pine species showed an additional influence of relative height at the stem. To eliminate the bark



thickness and height effect and to derive the species-specific heat resistance capacity from HT, the models of Odhiambo et al. (2014) were applied to estimate the heat resistance with 0.1 cm bark thickness and at 0.02 relative height. This way a comparison of different tree species was possible regardless of the bark thickness.

Table 3.2: Species specific and thickness-independent heat resistance capacity.

	<i>Pinus pinaster</i>	<i>Pinus radiata</i>	<i>Pinus elliottii</i>	<i>Eucalyptus cladocalyx</i>	<i>Acacia mearnsii</i>	<i>Rhus viminalis</i>	<i>Olea africana</i>
HRC	132.98	112.39	181.42	147.82	167.49	138.44	101.34

### 3.3.6 Statistical analysis

The correlation of HRC and fissure properties was statistically determined by stepwise regression in SPSS. In addition to the stepwise selection procedure, variance inflation factors were tested to avoid multi co-linearity effects. The properties tested against HRC included: number of fissures; depth and width of fissures; proportions of depth/width and width/depth; fissure area; total area of fissures; minimum bark thickness; total minimum bark thickness; surface extension ratio; total surface extension ratio.

A high multi co-linearity among the tested parameters was found and a multi-model inference approach was thus used to test various parameter combinations and highly correlated parameters with minimal contribution to the model were eliminated. The selected best model comprised of non-collinear parameters with significant contribution to the model.

### 3.4 Results

#### 3.4.1 Density and chemical composition

Density, ash content and degradation peaks of the bark specific components for all species are listed in Table 3.3.

Table 3.3: Bark density, ash content and thermal degradation temperatures.

	Density (g/cm <sup>3</sup> )	Ash content (%)	Peak 3 (°C)	Peak 4 (°C)
<i>P. pinaster</i>	0.35	7	410	493
<i>P. radiata</i>	0.46	5	412	500
<i>P. elliotii</i>	0.59	9	402	487
<i>E. cladocalyx</i>	0.45	5.5	414	494
<i>A. mearnsii</i>	0.59	8	409	495
<i>O. africana</i>	0.50	9.5	-	483
<i>R. viminalis</i>	0.39	11	-	471

Figure 3.3 shows a typical DTG curve from *E. cladocalyx* samples and illustrates the reproducibility of the two individual measurements. TGA/DTG curves look similar for all species and the only difference is the peak position.

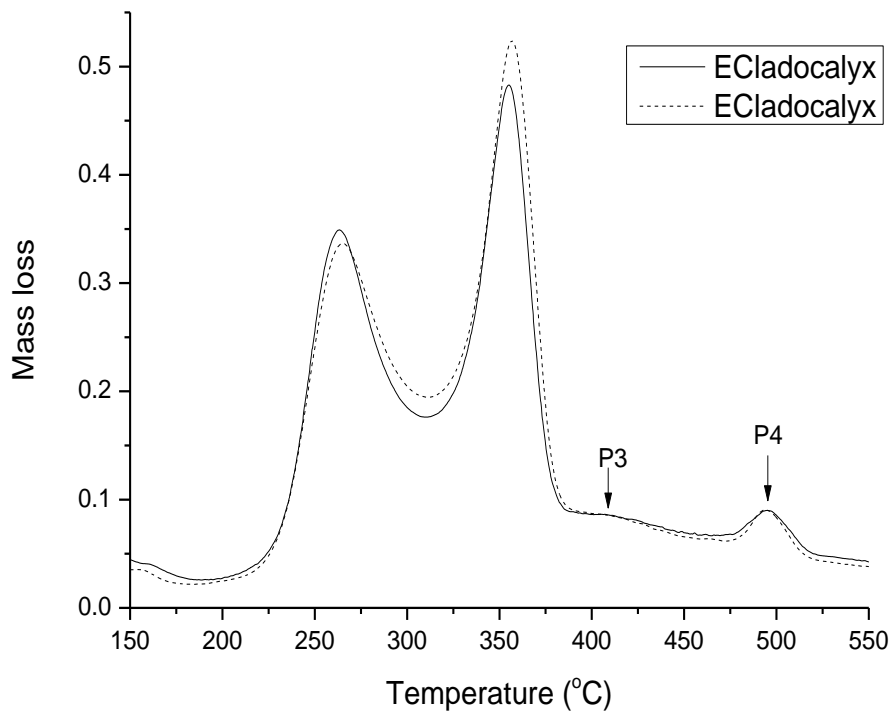


Figure 3.3: DTG curves of *E. cladocalyx*.

The first degradation peak at approximately 250°C can be assigned to the degradation of hemicelluloses and lignin and the second peak around 330°C to the degradation of cellulose (e.g. Sancez-Silva et al. 2012; Huang et al. 2011). Both peaks also appear in clear wood. Peak 3 and 4 (marked with an arrow) represent the degradation of components that are bark specific and do not typically occur in clear wood. These components degrade at higher temperatures and were considered to have an effect on the species specific heat resistance capacity. Peak 3 was not present in the bark of *O. africana* and *R. viminalis* (Table 3.3).

However, no correlation between chemical components and HRC could be found and the exact identification of these components was therefore not deemed necessary. Table 3.4 shows the proposed model fit curves for these properties when plotted against HRC, the  $R^2$  and p values. The degradation temperature of peak 3 (around 400°C) showed no correlation with HRC.

Table 3.4: fitting parameters for HT correlation with density, degradation temperatures and ash content.

HRC as function of	Model fit curve	R <sup>2</sup>	p value
Density	Exponential	0.333	0.102
P3	-	-	-
P4	Exponential	0.323	0.106
Ash content	Power	0.05	0.303

The bark density showed also no significant effect on HRC.

### 3.4.2 Bark topology

The model that was finally selected to explain the HRC contained the following independent variables: minimum bark thickness MBT, the exponentially transformed standardised number of fissures  $N_{Fiss}$ , the cumulative minimum bark thickness  $cMBT$  and the width of fissures  $W$ .

The model explained 81% ( $R^2 = 0.81$ ) of HRC. Each of the included factors had a significant impact on heat resistance capacity and the addition of each of them to the model increased the adjusted  $R^2$  value, thus minimising the model's estimation error. The biggest explanatory contribution, as indicated by the Beta value in Table 3.5, was  $N_{Fiss}$ , which means a lower HRC as fissure frequency increases per bark surface. The explanatory contributions of the other factors were found to be in the same range. However, the fissure width correlated negatively while the minimum bark thickness and the cumulative minimum bark thickness showed a positive correlation. The latter result signifies that the minimum protective bark thickness at the bottom (cambial) side of the fissure is a decisive variable, and this holds for the average minimum thickness as well as for the sum of all minimum thick bark pieces. The Beta values of the regression are confirmed by the partial correlations, which rank the variables for their contribution to the explanation of HRC accordingly. Of significance to the study is the bivariate correlation between HRC and single variables depicted by the partial correlation in Table 3.5. Partial correlation controls or removes the influence of other factors such that it reflects only the influence of a single factor.

Table 3.5: Model coefficients.

Model	Unstandardized Coefficients		standardized Coefficients	t	Sig.	Partial Correl.	Collinearity Statistics	
	B	Std. Error	Beta				Tolerance	VIF
Constant	149.881	1.490		100.603	0.000			
Minimum bark thickness	17.273	1.168	0.304	14.784	0.000	0.386	0.365	2.740
Exp. number of fissures	-11.589	0.433	-0.407	-26.760	0.000	-0.604	0.670	1.493
cumulative min. bark thickness	0.694	0.032	0.333	21.428	0.000	0.518	0.640	1.562
Width of fissures	-20.910	1.101	-0.320	-19.000	0.000	-0.473	0.545	1.833

### 3.4.3 Bark topology and heat resistance of studied species

*E. cladocalyx* and *A. mearnsii* are smooth barked, broad leaved species whose heat resistance capacity is not affected by the presence of fissures. The other species can be classified into thick barked pines and thin barked, broad leaved species i.e. *R. viminalis* and *O. africana*. Their topological features are shown in Figures 3.4 and 3.5 below:

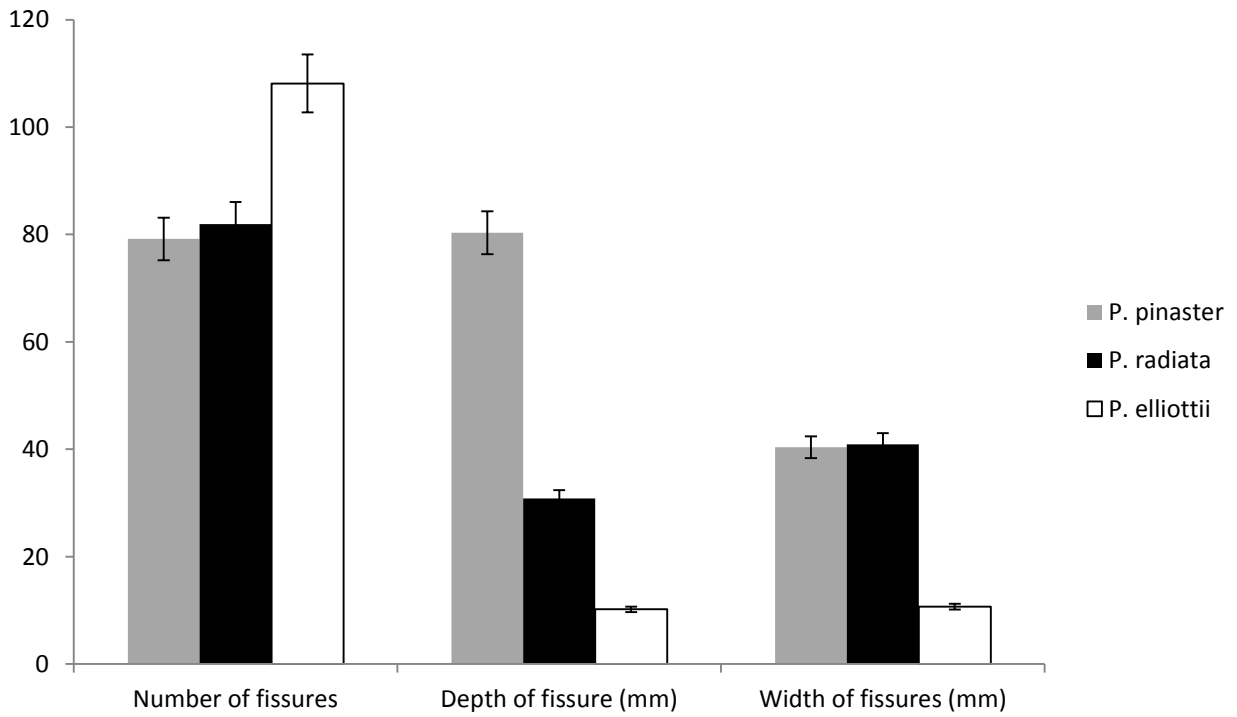


Figure 3.4: Fissure frequency and dimensions in pines.

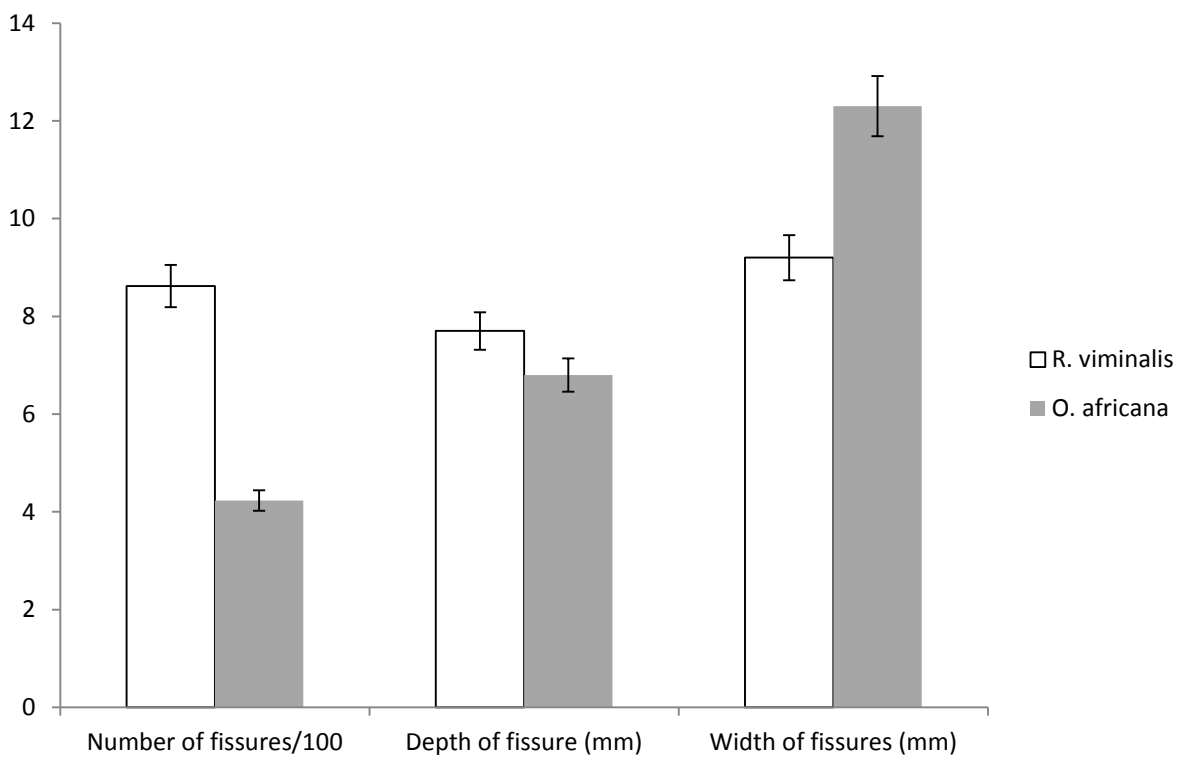


Figure 3.5: Fissure frequency and dimensions in thin barked broad leaved species.

### 3.5 Discussion

Although bark density differed greatly between species, no impact on HRC was found and the correlation proved to be insignificant ( $p = 0.102$ ), which might be due to small sample numbers since an  $R^2$  of 0.333 suggested a certain contribution of bark density to HRC. The result are however, supported by studies of van Mantgem and Schwartz (2003), Hengst and Dawson (1993), Vines (1968) and Reifsnyder et al. (1967), which have also reported a weak influence of bark density on heat resistance capacity.

A study by Bauer et al. (2010) has associated high bark density with increased heat conductance due to internal “air spaces” which may provide additional insulation effect. Dense bark will thus be expected to conduct more heat because of its lesser number of air spaces. The findings of this study however contradict this theory. If *E. cladocalyx* and *A. mearnsii* are compared, Odhiambo et al. (2014) has shown both species of the same size to have approximately the same bark thickness. *A. mearnsii* has a higher density compared to *E. cladocalyx* as shown in Table 3.3 and would therefore be expected to have a lower HRC due to higher heat transmission. The findings of Odhiambo et al. (2014) though, show no significant differences in HRC between the two species disapproving the findings of Baer et al. and confirming density to have minimal influence on HRC as has been previously reported.

The main thermal property of bark associated with its heat insulation is thermal diffusivity (Vines 1968). Thermal diffusivity is the ease with which a temperature pulse moves through a piece of bark and is mainly determined by the bark thickness (Peterson and Ryan 1986; Hare 1965; Martin 1963). The possible contribution of bark density to heat insulation is thus overshadowed by the dominant influence of bark thickness. The study established the chemical components within the bark layer of trees. Tree bark comprises of hemicellulose, lignin and cellulose which are also present in wood and two additional bark chemical components, represented by P3 and P4 (Figure 3.3), which are bark specific. Despite the component P3 not being identified in *O. africana* and *R. viminalis*, it can be considered to be a component part of the bark layer, since it was present in the bark of the rest of the five studied species.

The unique characteristic about the components P3 and P4 is that they degrade at higher temperatures and thus formed the focus in the investigation, since the tests were done based on HT estimated at 400°C. At this temperature hemicellulose, lignin and cellulose are expected to have degraded as they degrade at approximately 250°C and 330°C respectively. Lignin degrades over a wide range of temperatures from 250°C to 700°C (Sanchez-silva et al. 2012) and could not be independently identified. While P3 could not be correlated with

HT, P4 showed no correlation with HT ( $R^2 = 0.323$  and  $p = 0.106$ ). The degradation temperatures of the two chemical components show that they differed very little among all the species (Table 3.3; except for P3 in *O. africana* and *R. viminalis* which could not be identified) and no significant effect on HT could be found. It was initially hypothesised that the chemical components vary in their thermal stability and could affect the HT either by retarding or enhancing the degradation of bark which was not the case.

Bark differs from wood by a high content of extractives, including organic solvents, water solubles and polyphenolics, as well as by a high amount of inorganic material referred to as ash (Pereira et al. 2003; Fengel and Wegener 1984). The ash content is an approximate measure of the mineral salts and other inorganic matters content in the bark layer. Its composition within the bark layer has not been previously verified but normally varies between 0.2% and 0.5% in wood (Klyosov 2007; Rowell 2005). The results show ash content in the bark layer to vary from 5 to 11% (Table 3.3) thus indicating a higher amount of inorganic material in bark as compared to wood. This amount could have potentially been increased by sand or dirt lodged in bark fissures. Nevertheless, the correlation of ash content and HT was not significant. Bark chemical components do not therefore have an impact on HT. There might however, be scope for further research with large sample numbers here as well.

Tree bark can either be smooth or structured, and the topology of structured tree bark is dominated by fissures. The fissures vary in frequency and sizes. The number of fissures was found to have the highest partial correlation (-0.604) with HRC (Table 3.5). Increased number of fissures will therefore have a negative effect on the heat insulation ability of bark. This shows that when bark thickness, the main factor influencing heat resistance capacity, is constant, species with higher number of fissures are more likely to experience heat damage than those with fewer number of fissures.

The effect of heat insulation is further lowered by reduced bark thickness due to fissure intrusion into the bark layer. This is directly linked to the fact that thin bark is more vulnerable to heat damage than thick bark (e.g. Rigolot 2004; Stephens and Finney 2002; Mutch and Parsons 1998; Pausas 1997; Ryan and Reinhardt 1988). The correlation between heat resistance and minimum bark thickness is positive indicating an increase in heat resistance as minimum bark thickness increases (at constant total bark diameters). The fissures thus reduce the insulative ability of the bark layer at the points where they exist through reduction of the bark thickness. The presence of a single deep fissure results in significant heat damage at the fissure point (partial correlation = 0.386;  $p = 0.0001$ ). The extent of the damage is intensified when there are several deep fissures (cumulative minimum bark



thickness partial correlation = 0.518;  $p = 0.0001$ ). The heat resistance capacity of the bark layer is thus significantly reduced as the number of deep fissures increases.

Heat resistance capacity is further lowered when the fissures are wider. The effect of wide fissures has a lower partial correlation to heat resistance ( $-0.473$ ,  $p = 0.0001$ ) compared to minimum bark thickness. The fact that average fissure width was significant in addition to cumulative minimum bark thickness, which would already cover an exposure of the cambium, is interesting. It could be due to the fact that insulating air is trapped in narrow fissures, forming a laminar zone, while the heat draft removes the additional insulation 'bubbles' from wider fissures.

The study shows that bark topology significantly impacts on the heat resistance capacity of a tree. Fissures create openings in the bark layer that increase cambial exposure to heat damage. This refines findings of Bauer et al. (2010), Nicolai (1986) and Harmon (1984) who reported that highly structured bark with deep fissures or scaly bark provides more resistance against heat damage compared to smooth barks, because of the air pockets. The fissure width might play a decisive role in this context. However, in contrast to the findings of the before mentioned authors, more recent results suggest that species with smooth, thick bark seem to offer greater resistance to heat damage, as for example *E. cladocalyx* and *A. mearnsii*, (Odhiambo et al. 2014) when considering trees of equal bark thickness.

### **Bark topology and heat resistance of studied species**

The barks of *E. cladocalyx* and *A. mearnsii* are smooth and topology has therefore no or a minimal influence on heat insulation. The two species are thick barked with no significant differences in bark thickness and do not differ in their heat insulation capacities considering trees of the same diameter. They are more resistant to heat damage, relying mostly on their thick bark, which contributes about 85% to heat insulation (Odhiambo et al. 2014).

Among the three pine species, *P. radiata* had the lowest heat resistance (Table 3.2) as has also been reported by de Ronde (1982). This is mainly due to its thin bark compared to *P. pinaster* and *P. elliotii*. The bark of *P. radiata* contains a large number of fissures, on average 0.75 fissures per cm circumference (outside bark). The fissures are shallow but wide in nature allowing direct contact with flames, as was also noted by de Ronde (1982). The effectiveness of the bark in insulating against heat damage is therefore reduced. Since the results have shown fissures to have a significant influence on heat resistance capacity, there is a likelihood that part of the low heat resistance experienced by *P. radiata* is as a result of the high number of wide fissures within the thin bark, which increase cambial exposure and enhance vulnerability to heat damage.

*P. elliotii* is the most heat resistant among the three pine species mainly due to its thick bark (e.g. de Ronde 1982). *P. pinaster* also has a thick bark, which has been shown to exceed that of *P. elliotii* (Odhiambo et al. 2014). However, the two species showed inconsistent heat resistance capacities in relation to their bark thickness effect that could be attributed their bark structure. *P. elliotii* had a significantly higher number of fissures than *P. pinaster*. It also had the smallest size of fissures, which are significantly shallower and narrower compared to those in *P. pinaster* (Figure 3.4). *P. pinaster* bark has a high number of fissures averaging 0.75 fissures per cm circumference (outside bark) and the fissures are deep and wide with increasing size as the tree diameter increases. The wide fissures allow direct heat contact as also stated by de Ronde (1982). The minimum bark thickness is also significantly reduced by the deep fissures thus exposing the cambium to greater risk of thermal damage. The results have shown that the reduced minimum bark thickness due to the presence of deep, wide fissures and their increased number significantly lowers the bark's heat resistance capacity. The unexpectedly low heat resistance capacity of *P. pinaster* bark compared to *P. elliotii* can thus be attributed to its bark topology.

On the contrary the small fissures in the bark of *P. elliotii* expose a smaller cambial area to heat damage. Because of their narrow shape, they inhibit direct contact of flames and heat penetration through the bark and might trap bubbles of air as additional insulation. The fissure valley is also protected by the thick bark surrounding it. This phenomenon was reported by both de Ronde (1982) and Fahnstock and Hare (1964) who found the fissures of *P. elliotii* to be less exposed to intense heating due to the protection accorded them by outer bark layers rising over the fissure valley.

*R. viminalis* and *O. africana* have low resistance against heat damage due to their thin bark. The bark of these species contains a large number of fissures, with the number of fissures of *R. viminalis* significantly exceeding that of *O. africana*. Both species have shallow fissures with no significant differences in the depths (Figure 3.5). Fissure depth does not therefore result in differences in minimum bark thickness of the two species. The species have wide fissures, which expose a larger cambial area to heat damage, thus increasing the vulnerability to heat damage.

The topology of *R. viminalis* makes its bark much less effective in insulation against cambial heat damage compared to *O. africana*. *R. viminalis* has been reported to have no significantly different bark resistance to heat damage compared to *O. africana* (Odhiambo et al. 2014). This is likely due to the differences in bark thickness in which the thickness of *R. viminalis* exceeds that of *O. africana*. Such small differences in bark thickness have been reported to have significant contribution to heat insulation capacity (Schoonerberg et al. 2003). Bark thickness therefore has the most influence on heat resistance capacity

overriding the influence of surface topology, which was to be expected. The impact of bark topology on heat resistance must thus always be considered in conjunction with the bark thickness of a species.

### **3.6 Conclusion**

Bark density, chemical components of bark and ash content had no significant effect on heat resistance capacity but this might change with increasing sample size.

Bark topology, on the other hand, had a significant impact on the heat resistance capacity of different tree species. Although the contribution of fissures to heat insulation is secondary to bark thickness and depends on the size and number of fissures, there is a significant contribution. Deep, wide fissures significantly lower the heat resistance capacity of bark. The latter is further weakened as the number of these fissures increases.

### 3.7 References

- Agee, J.K. 1993. *Fire ecology of pacific north west forests*. Island Press, Washington.
- Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45:5950–5959.
- Brando, P.M., Nepstad, D.C. and Balch, J.K. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behaviour. *Global Change Biology* 18:630–641.
- Calvin, M. and Wettlaufer, D. 2000. *Fires in the Southern Cape Peninsula, Western Cape Province, South Africa*. IFFN No. 22:69-75.
- de Bano, L.F., Neary, D.G. and Folliott, P.F. 1998. *Fire's effects on ecosystems*. John Wiley and Sons, New York.
- de Ronde, C. 1982. The resistance of Pinus species to fire damage. *South African Forestry Journal* 122:22–25.
- Fahnesock, G. and Hare, R.C. 1964. Heating of tree trunks in surface fires. *Journal of Forestry* 62:799–805.
- Fengel, D. and Wegener, G. 1984. *Wood: Chemistry, Ultrastructure, Reactions*. Walterde Gruyter, Berlin.
- Hare, R.C. 1965. Contribution of bark to fire resistance of Southern trees. *Journal of Forestry* 63(4): 248-251.
- Harmon, M. 1984. Survival of trees after low-intensity surface fires in the Great Smoky Mountains National Park. *Ecology* 65:796–802.
- Hempson, G.P., Midgley, J.J., Lawes, M.J., Vickers, K.J. and Kruger, L.M. 2014. Comparing bark thickness: testing methods with bark– stem data from two South African fire-prone biomes. *Journal of Vegetation Science*, available online, DOI: 10.1111/jvs.12171.
- Hengst, G.E. and Dawson, J.O. 1993. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24:688–696.
- Huang, Y.F., Kuan, W.H., Chiueh, P.T. and Lo, S.L. 2011. Pyrolysis of biomass by thermal analysis–mass spectrometry (TA–MS). *Bioresource Technology* 102:3527–3534.

- Klyosov, A.A. 2007. *Wood-Plastic Composites*. John Wiley & Sons, Inc., New Jersey.
- Lawes, M.J., Richards, A., Dathe, J. and Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212:2057–2069.
- Martin, R.E. 1963. Thermal properties of bark. *Forest Products Journal* 3:419–426.
- Mutch, L.S. and Parsons, D.J. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. *Forest Science* 44:341–355.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148-160.
- Nikolova, P., Blaschke, H., Matyssek, R., Pretzsch, H. and Seifert, T. 2009. Combined application of computer tomography and light microscopy for analysis of conductive xylem area of beech and spruce coarse roots. *European Journal of Forest Research* 128(2):145 – 153.
- Odhiambo, B.O., Meincken, M. and Seifert, T. 2014. The protective role of bark against fire damage: a comparative study on selected introduced and indigenous tree species in the Western Cape, South Africa. *Trees* 28(2):555-565.
- Pausas, J. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science* 8:703–706.
- Pereira, H., Graca, J. and Rodrigues, J.C. 2003. Wood chemistry in relation to quality. In: Barnett, J.R., Jeronimidis, G. (Eds.). *Wood Quality and its Biological Basis*. Blackwell Publishing, Oxford pp 53–83.
- Peterson, D.L. and Ryan, K.C. 1986. Modeling postfire conifer mortality for long-range planning. *Environmental Management* 10(6): 797–808.
- Pinard, M.A. and Huffman, J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* 13:727–740.
- Reifsnyder, W.E., Herrington, L.P. and Spalt, K.W. 1967. *Thermophysical properties of bark of shortleaf, longleaf, and red pine*. Bulletin no. 70. School of Forestry, Yale University, Yale.
- Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* mill. and *Pinus pinea* L. *Plant Ecology* 171:139–151.
- Rowell, R.M. 2005. *Handbook of Wood Chemistry and Wood Composites*. CRC Press, Madison, USA.

- Ryan, K.C. and Reinhardt, E.D. 1988. Predicting post-fire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:291–1297.
- Sanchez-Silva, L., López-González, D., Villaseñor, J., Sánchez, P, and Valverde, J.L. 2012. Thermogravimetric–mass spectrometric analysis of lignocellulosic and marinebiomass pyrolysis. *Bioresource Technology* 109: 163–172.
- Schoonenberg, T., Pinard, M. and Woodward, S. 2003. Responses to mechanical wounding and fire in tree species characteristic of seasonally dry tropical forest of Bolivia. *Canadian Journal of Forest Research* 33:330–338.
- Seifert, T., Nickel, M. and Pretzsch, H. 2010. Analysing the long-term effects of artificial pruning of wild cherry by computer tomography. *Trees* 24(5):797-808.
- Smith, D.M. 1954. *Maximum moisture content method for determining specific gravity of small wood samples*. Forest Products Laboratory, Forest Service, U. S. Department of Agriculture.
- Stephens, S.L. and Finney, M.A. 2002. Prescribed fire mortality of sierra nevada mixed conifer tree species: effects of crown damage and forest floor consumption. *Forest Ecology and Management* 162:261–271.
- van Mantgem, P.J. and Schwartz, M. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *Forest Ecology and Management* 178:341–352.
- van Wilgen, B.W. 1982. Some effects of Post-Fire Age on the Above- Ground Plant Biomass of Fynbos (macchia). *Journal of Ecology* 70:217–225.
- Vines, R.G. 1968. Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16:499–514.
- Vines, R.G. 1981. Physics and chemistry of rural fires. In: Gill AM, Groves RH, Noble IR (eds). *Fire and the Australian biota*. Australian Academy of Sciences, Canberra, pp 129–150.
- Wesolowski, A., Adams, M.A. and Pfautsch, S. 2014. Insulation capacity of three bark types of temperate Eucalyptus species. *Forest Ecology and Management* 313: 224–232.
- zu Castell, W., Schrödl, S. and Seifert, T. 2005. Volume Interpolation of CT Images from Tree Trunks. *Plant Biology* 7:737 – 744.

## Chapter 4 **The effect of surface fire damage on tree ring growth of individual *Pinus radiata* trees -**

### **4.1 Abstract**

Severe fires, with intensities exceeding 400°C can penetrate beyond the bark layer and damage or completely kill a tree's cambium. Short-term growth reductions following surface fires have been reported for some species. The last section of the study investigated the impact of surface fires on growth of *Pinus radiata* by measuring growth response on the tree rings in the years following the fire damage. The tree ring measurements were done on cores obtained at stem base and breast height. Various growth and stress indices, based on yearly basal area increment (iBA) values, were calculated to quantify pre- and post-fire growth differences. An unburnt control site was used to detect growth changes resulting from the fire in the experimental plot. Statistical analysis employing one-way ANOVA and incorporating Tamhane's T2 Post-Hoc test revealed significant growth reductions following high intensity surface fire damage on *Pinus radiata* in the fire year with the impact being passed on to the following year. The recovery phase extended a two year period. During this time the trees show increased diameter growth due to probable increased water availability.

*Key words: high intensity surface fire damage, Pinus radiata, growth rings, earlywood, latewood, growth reduction*

## 4.2 Introduction

Fire is a very prominent abiotic stress factor in many ecosystems. The impact of fire stress on tree growth can be differentiated based on its intensity, duration, frequency and time of occurrence (Rötzer et al. 2012). Additionally, it can be expected that the affected tree parts govern the effects on tree growth. In this context fire resistance mechanisms of trees are highly species-specific (Odhiambo et al. 2014; Wesolowski et al. 2014). Different fire types, such as surface fires and crown fires as defined by Gill (1977), Brown (1995) and Newton (2007), might also lead to different reaction patterns. However, based on the existing body of literature it is difficult to differentiate cambium char and needle scorch effects since often the compound effects are reported. This study is dedicated to cambium damage inflicted by surface fires.

Historically, surface fires do benefit forest ecosystems by enhancing vegetation growth (e.g. O'Donnell et al. 2010; Bond and Keeley 2005; Thonicke et al. 2001). Increased frequency of fire weather environment due to climate change has led to more destructive fires that cause tree mortality or negative growth consequences on surviving trees (van Mantgem et al. 2009; de Ronde 2008; Westerling et al. 2006). This has prompted the need for increased awareness on the negative growth impacts of such fires on trees.

The trunks of most trees possess traits that enable cambial protection in low- to moderate-intensity fires, ranging between 200 and 220°C (Bauer et al. 2010). Thus mature trees typically resist such fires (Fernandes et al. 2008). Severe fires, with temperatures exceeding 400°C (Bauer et al. 2010; Wesolowski et al. 2014) can penetrate beyond the bark layer and damage or completely kill even a mature tree's cambium (Michaletz and Johnson 2007; Dickinson and Johnson 2001). Evidence of surface fire damage can be seen on the bark of trees as char marks for several growth seasons. Where the cambium is killed, scars in the wood are often formed as permanent marks of the fire event (Newton 2007; Michaletz and Johnson 2007; Dickinson and Johnson 2001).

However, in order to predict the growth response after fire events it is important to understand the reaction of the tree to stress but also to judge economic damage. Reports highlight short term growth reductions following surface fire damage, e.g. the ones by Elliott et al. (2002) on *Pinus strobus* and by Ford et al. (2010) on long leaf pines (*Pinus palustris*). A study on *Pinus ponderosa* provided conflicting findings with both growth reductions and increases after surface fires of varying frequency (Peterson et al. 1994). Hempson et al. (2014), Bauer et al. (2010) and Ducrey et al. (1996) reported low intensity surface fires not to have a negative impact on growth. Given the conflicting nature of past studies, despite a



body of literature on the subject, it can be stated that there is no clear understanding of the impact of surface fires on tree growth.

The exact processes through which surface fires may impact tree growth are unknown. It has been reported that cambial death around the entire bole circumference cuts water and nutrient supply to the leaves, while at the same time restricting translocation of photosynthates to the roots due to damaged phloem and xylem tissues. This results, eventually, in death of the tree (Rozas et al. 2011; Ducrey et al. 1996). The potential impact of reduced water and nutrient supply, as well as photosynthate translocation due to partially damaged cambium is largely unknown and could potentially impact growth.

It is also known that higher temperatures can inflict damages to plant cells either indirectly, following metabolic changes, or directly by protein denaturation, altered lipid mobility or chemical decomposition (Whelan 1995). Fire may also cause mechanical stress resulting in deformed tracheids. The temperature seems to be mainly affecting tracheid enlargement and fire damaged trees are prone to forming cell walls consisting only of the middle lamella and primary walls (Vaganov et al. 2004; Larson 1994). These changes could potentially slow future tree growth.

The investigation of surface fires impact based on growth response on the tree rings provides a useful and reliable quantitative technique for evaluating the impact of fires on trees (Brown and Wu 2005; Brown et al. 1999; Baisan and Swetnam 1990). Growth conditions and stresses are typically reflected in the width of tree rings. The width of the ring is the average growth process throughout the entire growing season and thus represents the overall effect of the disturbance within the entire season (Fritts 1976). Trees affected by temporary disturbance factors, such as fire, experience changes in growth not correlated with variations in the long term factors i.e., the climate, soil, topography, and biota (Fritts 1976). Short term reduction in ring width is frequently associated with stress, such as foliar damage, which causes reduced leaf area and loss of photosynthetic capacity (Filion and Cournoyer 1995; Vega et al. 2010; Wallin et al. 2003). It can be expected that biophysical or biochemical disruptions at the trunk that affect optimal photosynthetic functions would also be reflected in the tree ring widths.

Diameter growth is typically mostly affected in the year following a fire event (Ford et al. 2010). The reduction is short term, lasting only 1–3 years, after which growth rates return to approximately pre-fire levels (e.g. Murphy et al. 2010; Goldammer 2007; Werner 2005; Hoffmann and Solbrig 2003; Werner et al. 2006; Williams et al. 1999). This assumption is mainly based on the impact of crown fires. Growth reduction can be seen as abrupt narrowing of growth rings for several years after the fire (Stahle et al. 1999; Schweingruber

1993). However, it is not entirely clear if surface fires would also cause a similar damage if needle scorch is absent.

This study seeks to investigate possible growth reduction trends following high intensity surface fire damage on *Pinus radiata* in South Africa. Various studies have been conducted to evaluate wildfire damage in commercial pine plantations in Southern Africa (e.g. de Ronde 2008b; de Ronde et al. 2004a; de Ronde and du Plessis 2002; de Ronde et al. 1986) but no attempt has been made to summarize species-specific guidelines for wildfire damage assessment in even-aged stands. Such knowledge is important for improved understanding of the short and longer-term effects of fire on the species. Thus *Pinus radiata* was sampled as a major commercial plantation species worldwide.

*P. radiata* is grown mainly for sawlog production in South Africa (SA 2011). It occupies a total area of 58,999 hectares and is confined to the Cape region (SA 2011). *P. radiata* grows among a Fynbos shrubland vegetation base where it thrives on the high winter precipitation experienced in the region (de Ronde 2008a). Plantations in the Cape region often experience fires during the hot summer months between December and March. These have become a recurrent phenomenon over the past decade due to enhanced drought conditions and increasing temperatures (Calvin and Wettlaufer 2000).

In this study ring width measurements on *Pinus radiata* were used to determine the impact of surface fires on growth by employing various indices for quantifying the extent of the damage and the pattern of radial stem increment reaction of cambium charred trees compared to unaffected trees in the same stand. To focus on the effect of surface fires only, trees were selected that showed stem char but no indication of additional crown damage. The tree ring widths after the fire incident were compared with those of unburnt trees of the same compartment to assess possible growth effects with the null-hypothesis that unburnt and stem charred trees grow in the same way.

## 4.3 Methodology

### 4.3.1 Study site

The study was conducted on a *Pinus radiata* plantation, compartment M35a, located next to the Jonkershoek Nature reserve (33° 57'S, 18° 55'E) in the Western Cape Province, South Africa. The area experiences a typical Mediterranean climate with warm, dry summers and wet, temperate winters. In the summer temperature averages 22°C and drops to around 10°C in winter (van Wilgen et al. 1990; van Wilgen 1982). The low summer rainfall and intermittent winter precipitation average approximately 884 mm per year, with substantial fluctuations, ranging from 464 mm in 2004 to 1586 mm annually in 1977 (Grab and Craparo 2011). The rainfall figures for the period of the study are shown in Table 4.1.

Table 4.1: Rainfall data for the study period

Year	Rainfall (mm)
2006	1000.8
2007	1191.8
2008	1284.3
2009	1138.9
2010	875
2011	768
2012	1009.4

The sampled compartment was fairly small covering an area of 2.42 ha. The trees were 18 years old and had uniform growth conditions. The compartment area had gently sloping terrain with a sparsely distributed understory comprising of grass and low growing shrubs.

The plantation experienced a high intensity surface fire in February 2009. The lower trunk sections of the trees were burnt to an average height of about 1.0 m with char marks still evident at the time of the study i.e. January 2014. Anecdotal evidence gathered from the compartment history records at the local forestry office show that the crowns were not affected. There was no mortality among the charred trees that could be associated with crown fire (e.g Wade and Ward 1975; Cooper and Altobellis 1969), which is especially relevant in *P. radiata* whose crown is more susceptible to crown scorch due to its fine needles (de Ronde et al. 2004a). There was also no evidence of defoliation found that could

be associated with burnt twigs or epicormic shoots in the sampled compartment as opposed to other compartments in the burnt area. With evidence of crown damage being non-existent, surface fire was assumed to be the cause of possible negative growth among the affected trees. Part of the compartment was not burnt because the fire was stopped at a fire break (Figure 4.1b), which prevented it from crossing over to the unburnt section that was subsequently sampled for control.

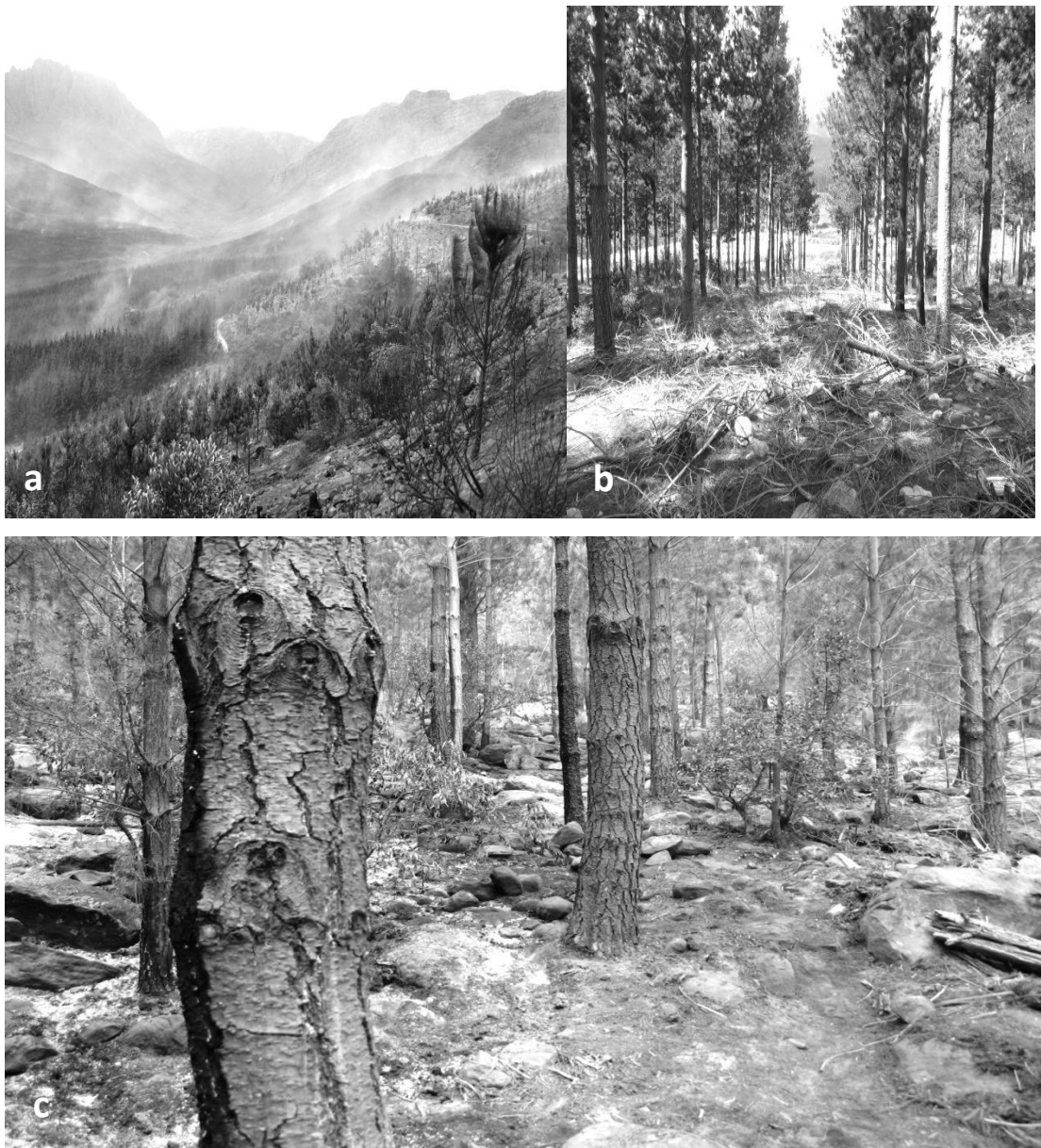


Figure 4.1: a) The Jonkershoek fire in 2009, b) a fire break separating the burnt and unburnt compartment section and c) a charred lower trunk section and ash residue (Photos: Simon Ackerman).

### 4.3.2 Data collection

The compartment was consequently divided into two study sections, the burnt site and the unburnt site which was used as a control site. The burnt site covered an area of 0.89 ha while the control site had an area of 0.28 ha. 30 trees from each site were selected for the study. The trees on the control site were randomly selected while those on the burnt site were selected based on the presence of a visible char mark covering more than half of the bole diameter. The entire burnt site was represented in the selection with trees at the boundary rows being excluded to avoid boundary effect. Tree sizes were determined from DBH measurements at 1.3 m above ground. Fixed area square plots measuring 30 x 30 and 25 x 25 square meters were used for stem density determination in the burnt and control sites respectively. Six plots within the burnt site and three in control site were selected to represent entire areas of the respective sites. The trees in each sample plot were counted and the density determined by averaging the number of trees in the sample plots from each site. The result was then extrapolated to stand density per hectare. At the time of the data collection, the burnt site had a stem density of 344 stems per hectare while the control site had 464 stems per hectare.

Tree rings were measured from samples obtained by coring with an increment borer. The fire came from the North-Eastern direction in the burnt site. Four cores were obtained per tree; two cores were extracted at the DBH (1.3 m), one each from the Northern and Eastern facing sides of the trunk, while the other two were each extracted at 50 cm above ground (later referred to as the stem base) on the burnt and opposite unburnt (South West) sides of the charred stem base. From the control site, with no burnt trees, cores were taken at DBH point on the North and East locations of the trunk.

### 4.3.3 Core preparation and tree ring measurements

The cores were labelled with site, tree number and the trunk location from which they were extracted. In the laboratory the cores were permanently glued to the wooden trays and then sanded using an 80 and then 400 grit sand paper to clearly reveal the growth rings.

Each growth ring width was determined from the addition of early and late wood for both pre- and post-fire periods from 2006 to 2013. The measurements were done on a LINTAB TM 6 Tree-Ring Station, in which the rings were observed under a microscope connected to a PC installed with the RINNTECH TSAP-Win software. The measurements were done with a resolution of 1/100mm.

The impact of the fire on growth was determined from annual basal area increments (iBA) of the growth rings. iBA values were calculated from the ring width values of both sites. Annual changes in early and late wood widths were analysed to gain a better understanding of the role of the fire induced stress on wood formation, which are not evident in tree-ring width series (Fonti et al. 2009b, 2010; Matisons and Dauškane 2009).

#### 4.3.4 Statistical analysis

The difference in tree size between the burnt and control sites, basal area increments and early and late wood dimensions within each site were analysed using one-way ANOVA in SPSS. Tamhane's T2 post hoc test was used to test basal area increments and anatomical width differences between the years. Graphical interpretations of the results are presented using error bar graphs.

The impact of the fire and tree response to fire stress was analysed using growth indices proposed by Lloret et al. (2011). These indices include resistance, recovery, resilience and relative resilience. The indices employed in this study for determining the impact of fire damage on growth of the trees were: resistance, recovery and resilience. Resistance (Rt) quantifies the decrease from the pre-fire period to the fire year, Resilience (Rs) represents the ratio between post-fire and pre-fire growth increment and Recovery (Rc) describes the growth reaction after the fire year. The indices were calculated individually on the basis of iBA. iBA of three years before the fire year, the fire year, and three years after the fire year were used in the calculations according to Pretzsch et al. (2012):

$$\text{Resistance (Rt)} = \text{Fr}/\text{PreFr}$$

$$\text{Recovery (Rc)} = \text{PostFr}/\text{Fr}$$

$$\text{Resilience (Rs)} = \text{PostFr}/\text{PreFr}$$

$$\text{Relative resilience (Rr)} = ((\text{PostFr}-\text{Fr})/(\text{PreFr}-\text{Fr})) (1-(\text{Fr}/\text{PreFr}))$$

Where: Fr is the basal area increment during the fire year

PreFr is the mean basal area increment of the three years  
before the fire

PostFr is the mean basal area increment of the three years  
after the fire

#### 4.4 Results

Both the burnt and control trees grew in the same compartment with similar growth conditions. There were no significant differences in tree size (DBH) between trees sampled on the two sites based on Mann-Whitney U-Test ( $p = 0.94$ ,  $F(1.58)$ ). The general growth pattern on both sites conforms to the rainfall figures (Figure 4.2). The observed decline in growth on both sites between 2010 and 2011 is thus mainly attributed to moisture deficiency due to declining rainfall in those years. However, the decline in 2009 and recovery in 2011 do not follow the precipitation curve.

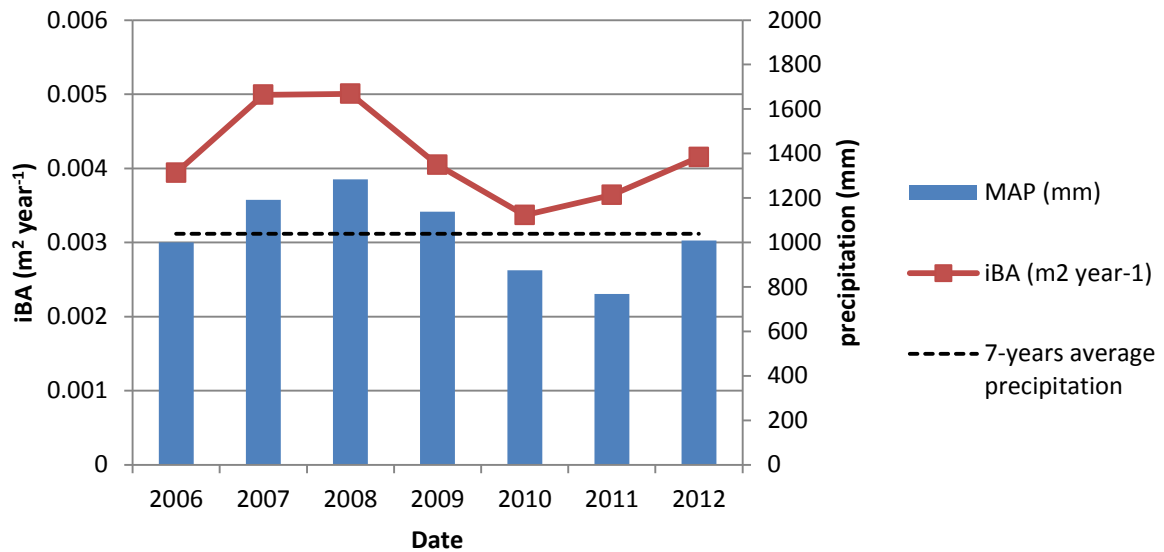


Figure 4.2: Relationship between mean annual precipitation (MAP) and basal area increment (iBA)

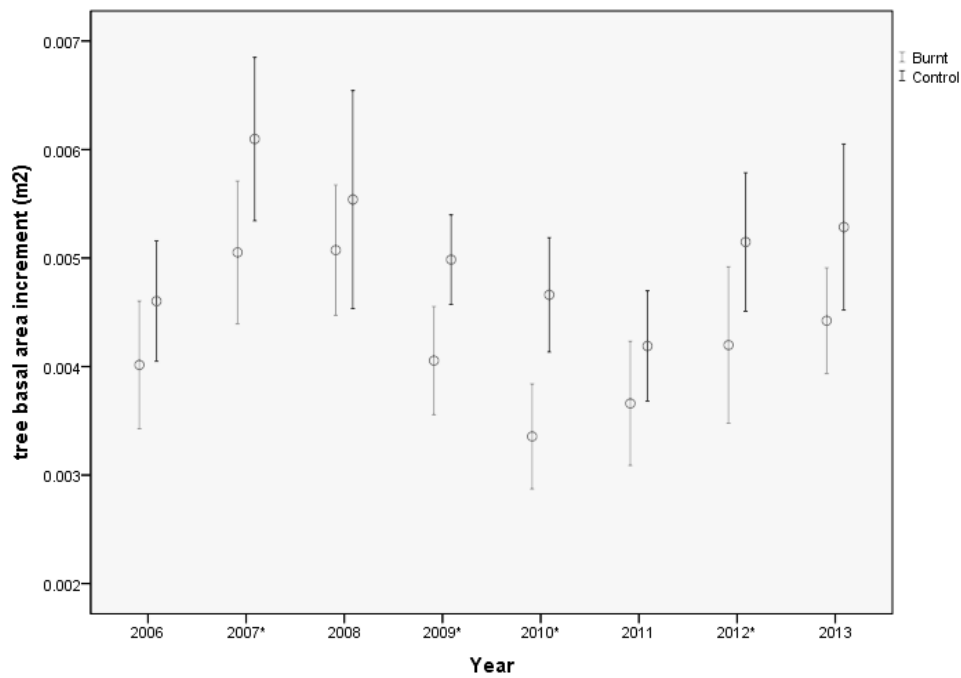


Figure 4.3: Comparison of iBA between burnt and control sites. Stars mark the years of significant difference.

Table 4.2: Differences in iBA between burnt and control site. Significant differences are highlighted in bold numbers.

Year	2006	2007	2008	2009	2010	2011	2012	2013
F (1,57)	2.211	4.572	0.667	8.690	13.94 3	1.999	4.084	3.795
P- value	0.143	<b>0.037</b>	0.417	<b>0.005</b>	<b>0.000</b>	0.163	0.148	0.056

The annual basal increment (iBA) in the control site exceeded that in the burnt site (Figure 4.3). Significant differences in iBA between the burnt and control site were recorded in 2007, 2009, 2010 and 2012 (Figure 4.3, Table 4.2). The differences in 2009 and 2010 are more pronounced compared to those observed in 2007 and 2012 (Figure 4.3). This indicates that apart from declining moisture levels, the impact of fire further decreased growth in the burnt site causing significant iBA differences between the two sites in 2009 and 2010. The lowest iBA was recorded in 2010, despite 2011 having the lowest rainfall. This indicates that the impact of the fire damage was carried over from 2009 to the following year and alongside moisture deficiency, resulted in the observed low iBA value.



The proportion of latewood to earlywood can give additional insights. Early and latewood dimensions were analysed for the core samples obtained from the DBH of both burnt and control sites (Figure 4.4, Table 4.3).

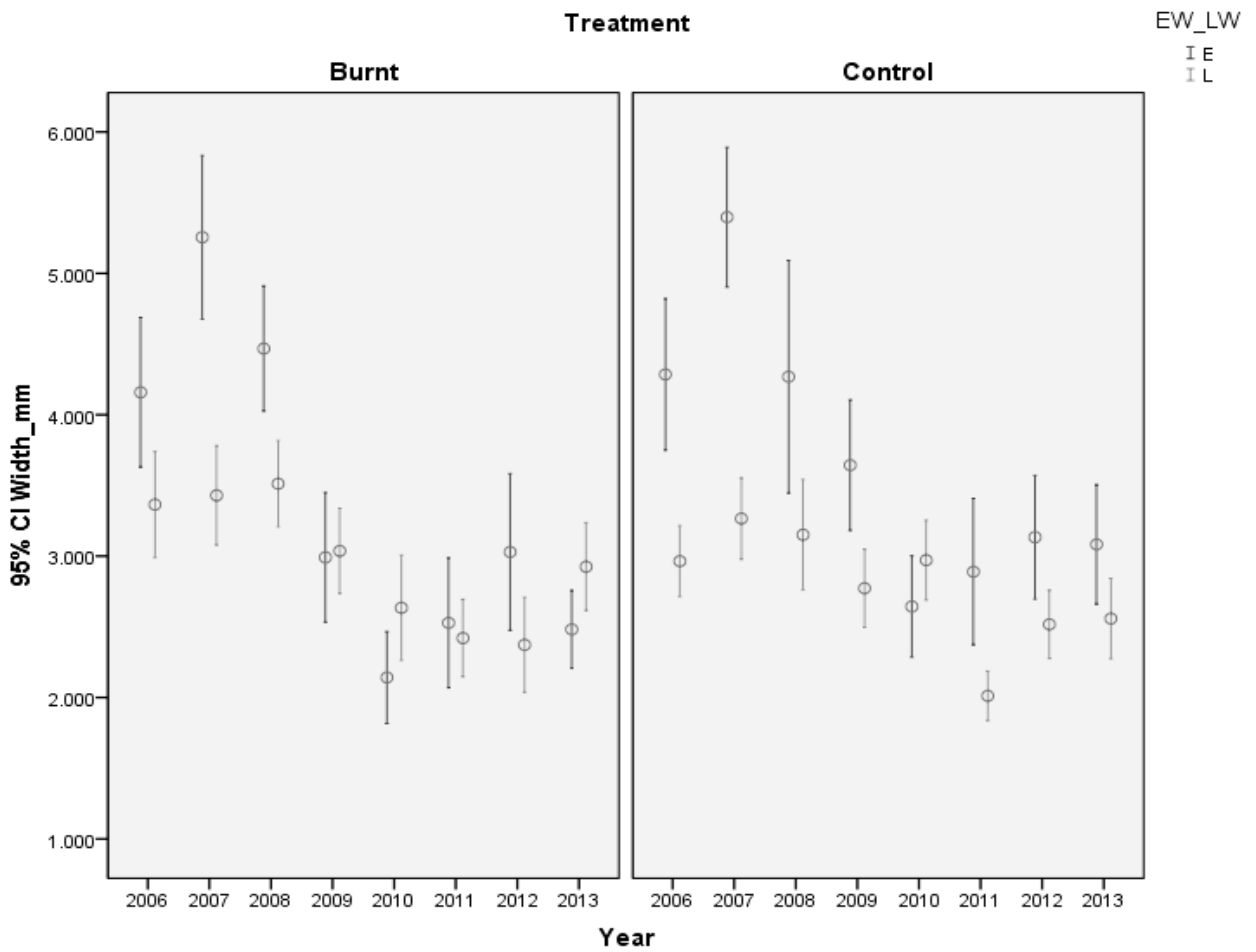


Figure 4.4: Comparison of early and late wood width in the burnt and control sites at the DBH.

Table 4.3: Significant differences between earlywood and latewood widths within the burnt trees as compared to the control.

	Year	2006	2007	2008	2009	2010	2011	2012	2013
Burnt	F (1,59)	6.286	30.426	13.201	0.029	4.161	0.170	4.288	4.767
	P- value	<b>0.015</b>	<b>0.000</b>	<b>0.001</b>	0.865	<b>0.046</b>	0.682	<b>0.043</b>	<b>0.033</b>
Control	F (1,59)	20.776	58.050	6.290	10.974	2.155	10.805	6.391	4.434
	P- value	<b>0.000</b>	<b>0.000</b>	<b>0.015</b>	<b>0.002</b>	0.148	<b>0.002</b>	<b>0.014</b>	<b>0.040</b>

Before the fire, the earlywood width significantly exceeded that of the latewood as expected in both, control and burnt trees. This trend was maintained in the control site in the fire year, 2009, but not in the burnt site in which normal growth was interrupted with a significant

decline in earlywood. This change of latewood proportion can be attributed to fire damage because 2009 was a year of above average precipitation. Negative growth impact due to the fire in 2009 was carried over to 2010 and coupled with a moisture deficiency in 2010, which affected the latewood proportions of both sites positively. While in successive years normal growth was restored at the control site i.e. earlywood width exceeding that of latewood, the burnt site showed inconsistent growth pattern of early and latewood within this period. This indicates persistence of the effect of the multiple stresses in the burnt site.

Expressing the previous relation as a latewood proportion directly, (Figure 4.5) shows that reduced growth in earlywood resulted in a higher latewood percentage in 2009 and 2010. This correlated with reduced tree growth since the earlywood occupies the biggest portion of the growth ring.

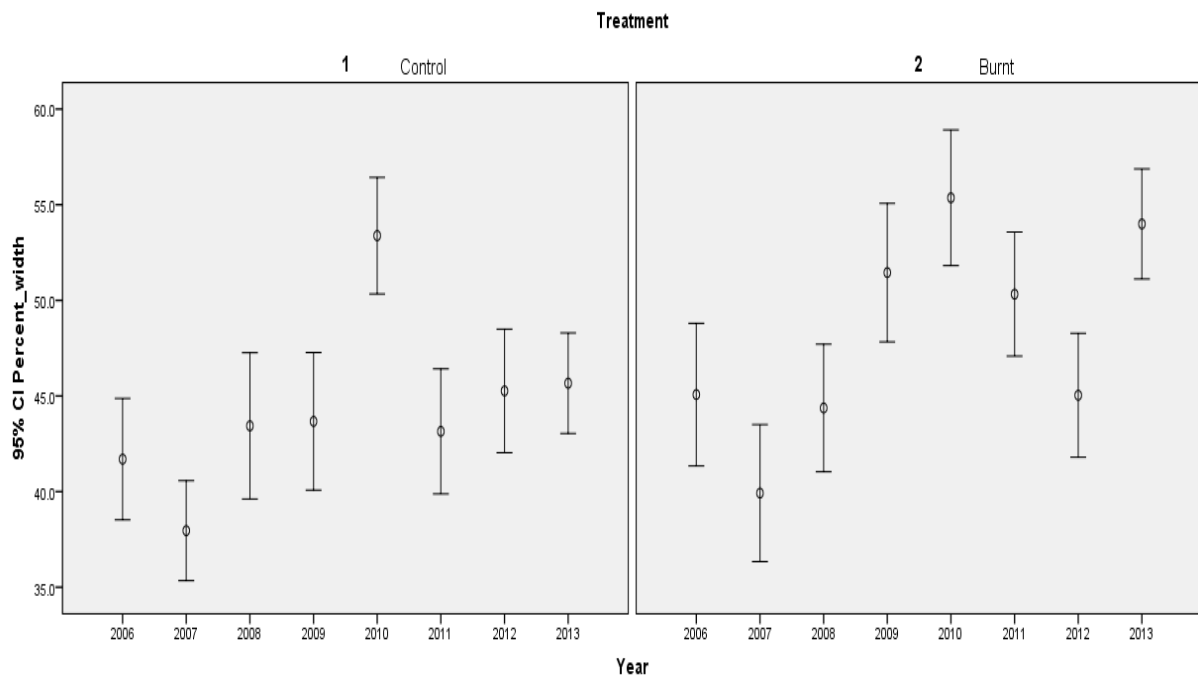


Figure 4.5: Percentage of latewood in the growth ring in control and burnt sites.

On the burnt site, the latewood percentage in the pre-fire period was similar to that in the trees of the control site indicating a similar growth pattern. However, in the fire year there was an increased latewood percentage in the burnt site as compared to the control site despite both sites experiencing the same amount of rainfall in that year. The increased latewood percentage in the burnt site in the fire year is thus to be attributed to the fire impact. Unlike in the control site in which growth (latewood percentage) returned to pre-fire levels in 2011, it took until 2012 before the latewood percentage of trees from the burnt site could

march pre-fire levels due to the impact of multiple stresses. This was helped by improved moisture levels in 2012.

The Lloret plots were used to illustrate the impact of the stresses on the trees in the burnt site and to show different reaction at stem base and at dbh.

Figure 4.6 shows the average pre- and post-fire iBAs as well as that of the fire year 2009 at breast height.

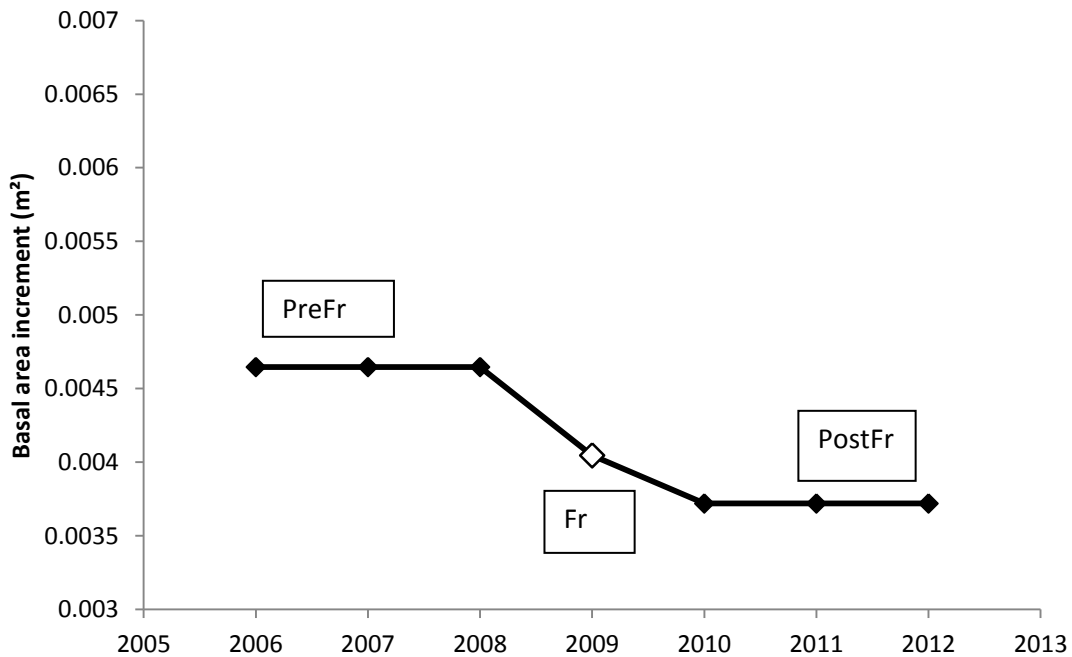


Figure 4.6: Lloret plot of iBA (m<sup>2</sup>) at the DBH.

At breast height there was average growth decline from pre- to post-fire periods. The decline from pre- to post-fire period occurred in 2009 due to the multiple stress effect resulting from moisture deficiency and fire damage in that year. The post-fire growth was lower than the pre-fire growth. This is due to the carried over effect of the fire damage and low post-fire rainfall values.

Figure 4.7 shows the average pre- and post-fire iBAs as well as that of the fire year at the charred stem base.

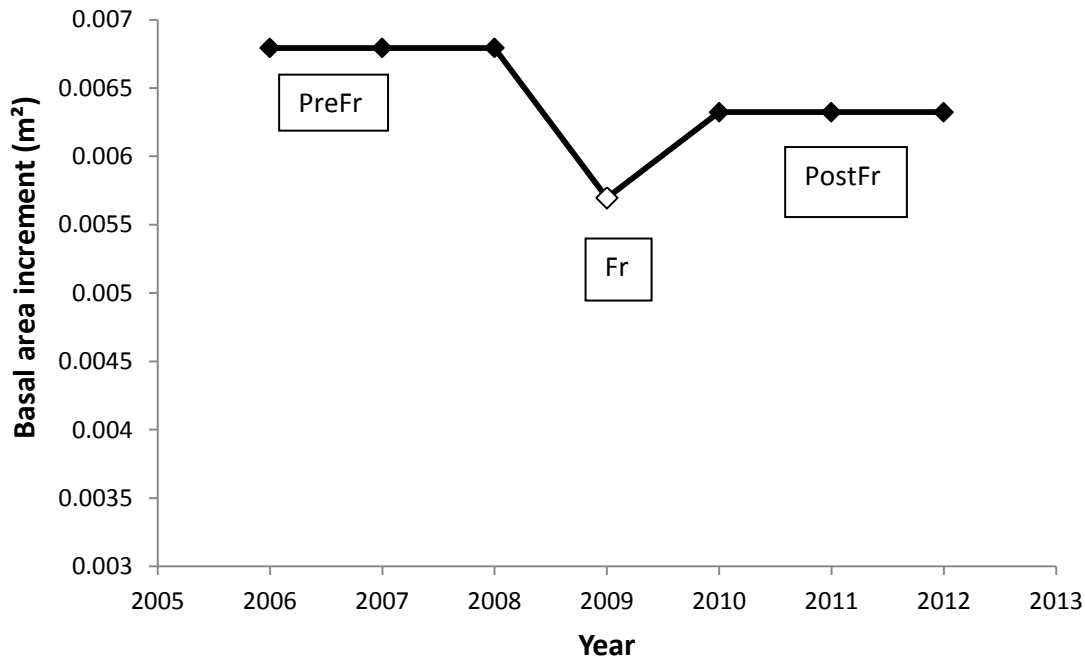


Figure 4.7: Lloret plot of iBA (m<sup>2</sup>) at the stem base.

The iBA at the stem base where the trees were charred, dipped conspicuously in the fire year, 2009. This was followed by post-fire recovery in which the iBA improved but did not match the pre-fire levels.

The growth indices provided further quantitative evidence to some of the already mentioned results. The event analysis by Lloret et al. (2011) quantifies Resistance as the decrease in iBA from the pre-stress period to the stress year;  $R_t = 1$  is complete resistance and the further the value falls below  $R_t = 1$ , the lower the resistance. The  $R_t$  index (Table 4.24) shows the trees did not resist the impact of the 2009 moisture decline and fire damage, instead there was a clear negative reaction. Resilience represents the ratio between post-stress and pre-stress iBA;  $R_s > 1$  indicates full recovery or even an increase after the episodic stress, while  $R_s < 1$  indicates growth decline and low resilience. The  $R_s$  value (Table 4.4) was used to compare recovery rate at the stem base and the DBH. The  $R_s$  value at the stem base was higher compared to that at the DBH indicating faster rate of recovery at the affected stem base as compared to the rest of the tree.

Table 4.4: Lloret's indices for the impact of the fire.

	Resistance Rt	Resilience Rs
DBH	0.8706	0.8005
Stem base	0.8386	0.9308

The recovery index was used to describe the annual growth reaction after the stress year both at the affected stem base and on the overall tree (calculated at the DBH).  $R_c = 1$  indicates persistence of a low growth level after the stress year,  $R_c < 1$  indicates a further decline and  $R_c > 1$  indicates recovery from the level reached during the stress year. The trees had recovered from the damage at the stem base by the end of the second year (2011) following the fire incident,  $R_c = 1.0803$  (Table 4.5), but the overall tree growth did only reach a complete recovery in the third year from the beginning of the stress period,  $R_c = 1.0257$  (Table 4.5). This shows a growth decline resulting from the fire, which was carried over to the following year and the trees recovered from the stem base damage in the second year following the fire. The multiple effects of fire and the moistures deficiency in both 2010 and 2011 persisted in the overall tree with recovery only realised in the third year after the fire event.

Table 4.5: Annual post-fire recovery indices.

	Recovery	
	Lower trunk	DBH
2010	0.9893	0.8323
2011	1.0803	0.8997
2012	1.2605	1.0257
2013	1.2241	1.0720

## 4.5 Discussion

The burnt and the control site comprised different sections of the same compartment. They were therefore subjected to similar environmental and site conditions. Being part of the same compartment, the two sites were likely subjected to the same management regime. Details of silvicultural operations previously conducted in the compartment were not enlisted in the compartment records provided. Growth in the control site exceeded that in the burnt site (Figure 4.8) despite a possible higher growth resource competition in the control site whose stem density (464 s/ha) exceeded that in the burnt site (344 s/ha). However, by sampling trees that showed no DBH difference on both sites a rather similar competition regime between the sampled collectives was ensured.

### 4.5.1 Basal area increment

The growth pattern in both sites conformed to the rainfall pattern (Figure 4.2). 2010 and 2011 were dry years with below average rainfall, which consequently resulted in lower growth in those two years (Figure 4.2). Generally, the two sites maintained a uniform basal area increment pattern over the years (Figure 4.8). The only differences, represented by a wider growth gap, were in 2009 and 2010 due to the influence of the fire damage.

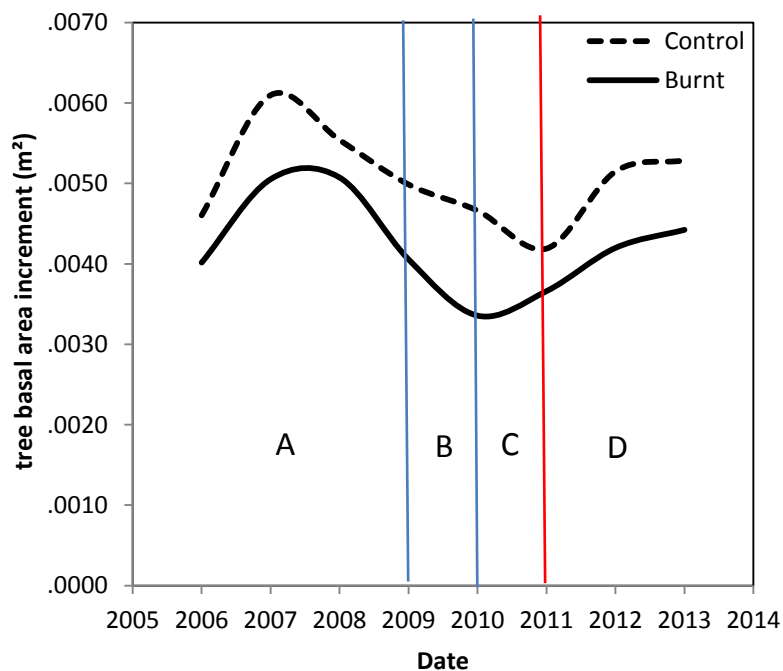


Figure 4.8: General growth pattern in both control and burnt sites. Part A: Pre-fire period, B: Fire year, C: Post-fire period when fire impact on growth is greatest, D: Post-fire recovery period.

A significant iBA difference between burnt and control site in 2009 confirmed the fire impact. 2009 experienced an average amount of rainfall, so the fire effect is the likely explanation for the decreased growth in 2009. There was further decrease in the iBA in the burnt site in 2010, which was the year with the lowest growth. There was a sharp decline in rainfall figures in 2010, which might have been the reason for this. However, the fire in 2009 might also have partially contributed to the low iBA figures in 2010. Diameter growth has been found to be most affected in the year following the fire event (Ford et al. 2010). The impact of the fire damage from 2009 might thus also have been carried over to 2010 contributing to the lowest iBA value despite 2011 recording the lowest rainfall value.

#### **4.5.2 Stress indices and Early and late wood growth**

The damage caused by fire at the stem base in 2009 resulted in sharp growth decline at that point as shown in Figure 4.3. The Resistance index (Rt) was used to measure the impact of stresses on iBA. Lower Resistance index (Rt) at the stem base compared to the DBH (Table 4.4) indicate a localised stress effect and confirm the fire damage. Although the fire impacted was at the stem base, the effect was substantial at the dbh due to systematic growth reaction. Systematic growth reaction in the tree as a result of stem base fire damage is revealed by early and latewood dimensions. In conifers, earlywood is comprised of larger lumen, vessel elements with thin walls. It forms the first and usually largest part of the annual ring as clearly revealed in the control site (Figure 4.4), and transports water and dissolved nutrients to the new leaves early in the growing season (Vaganov et al. 2004; Dieterich and Swetnam 1984). The size and density of earlywood have been shown to be related with the physiological vigour of the tree (Fonti et al. 2009b; Thomas et al. 2002). Damage to the cambium alters radial meristematic activity that include cell division, elongation and differentiation thus slowing growth (Niinemets 2010), it can also cut water and nutrient supplies to the leaves, while at the same time restricting translocation of photosynthate to the roots due to damaged phloem and xylem tissues (Rozas et al. 2011; Niinemets 2010; Ducrey et al. 1996). High temperatures are known to cause damages to plant cells either indirectly, following metabolic changes, or directly by protein denaturation, altered lipid mobility or chemical decomposition (Whelan 1995). These interruptions to normal biophysical and biochemical functions reduce the photosynthetic rate, which is manifested in the reduced earlywood width in the fire year and the year after. The reactions of a tree following trunk damage involve a series of defence processes including wound closure, compartmentalization of decay and formation of wound healing callus tissue (Seifert et al. 2010; Fink 1999; Larson 1994; Blanchette 1992). These defence and healing processes are

not only costly for the tree (Rötzer et al . 2012 ) but occur also at the expense of water transport (Schweingruber 2007) and might also impact upon the rate of photosynthesis thus contributing to the reduced earlywood growth.

The expected 'unstressed' pattern of large earlywood vs small latewood was observed before the fire in both control and burnt sites. The same pattern was maintained in the control site in the year of the fire and after the fire incident. The only difference in the control site was in 2010 which had a higher latewood percentage due to the drought. In the following year 2011, with the lowest rainfall, the trees re-adjusted to the drought conditions and restored normal growth with earlywood growth exceeding that of latewood in the control site.

At the burnt site, the expected early and latewood pattern were disrupted in 2009. In addition to decreased rainfall in that year, the effect of fire damage increased the stress levels in the trees causing reduction in earlywood growth as confirmed by increased latewood percentage (Figure 4.5). Increased latewood percentage has also been observed following crown scorch in *P. halepensis* (De Micco et al. 2013). The crowns of the trees in the burnt site were not scorched by the fire and the observed increase in latewood percentage is attributed to the cambium char. This is because in the same year, the control site which experienced the same decrease in rainfall but was not impacted by the fire had the expected growth with larger portions of the earlywood than the latewood. The earlywood width further reduced in 2010 in the burnt site due to drought and the carried over fire effect from 2009. Despite re-adjustment to the drought conditions in 2011, the multiple stress effect of the fire and drought resulted in unexpected earlywood growth in that year. Normal growth was only restored in the burnt site in 2012 following resumption of average rainfall.

The fire damage triggered a localised stress reaction at the stem base which led to faster healing at the stem base as illustrated by the Resilience index closer to 1 at the stem base compared to that at the DBH (Table 4.4). This indicates a switch from normal physiological functioning to concentrate resources in the affected area, in this case the stem base, in order to restore normality and stability in the tree. This is a common phenomenon in trees, by which they tend to react quickly to restore normal growth at the point of injury. In the event of damage to the trunk trees are known to respond by increasing bole diameter in the affected areas (Stone 1944). This fact is supported by the recovery index which shows that the trees recovered one year earlier, 2011, at the stem base before restoring normal growth to the entire tree in the following year, 2012 (Table 4.5).

Some studies have found insignificant growth impacts from surface fire damage (Hempson et al. 2014; Bauer et al. 2010; Ducrey et al. 1996). A study on *P. radiata* also found no consequences on radial growth of mature trees following surface fire damage and concluded that stem damage does not impact on merchantable wood volume (Fernandes et al. 2008).



In this study however, it was found that high intensity surface fires have a negative growth impact on *P. radiata* trees. Due to the multiple effects of both fire and moisture deficit, the impact of fire damage on iBA growth could not be estimated independently. The study was not replicated in other compartments due to lack of availability of plantations with similar type and extent of fire damage. The results therefore represent the findings in this compartment and could be used in reference to *P. radiata* sites with similar size of trees and compartment specifications. Growth reductions due to surface fire damage have however, been reported for *P. strobus* Elliott et al. (2002) and long leaf pines Ford et al. (2010). This study has shown that fire can have the same impact on *P. radiata*.

Growth reduction is realised in the fire year and also carried over to the following year after the fire event. The study has shown the trees to recover from the fire impact in the second year following the fire event. This is similar to the time lag response before complete recovery is restored to approximately pre-fire levels following crown fires (Murphy et al. 2010; Goldammer 2007; Werner 2005; Hoffmann and Solbrig 2003; Werner et al. 2006; Williams et al. 1999). Recovery from crown scorch involves regeneration from epicormic shoots (Bond and van Wilgen 1994) or leaf buds (e.g. Thies et al. 2006) to re-establish the photosynthetic capacity after the fire event. These growth re-adjustments take place at comparably the same duration as wound healing and tissue repair involved after cambial damage. This is subject to the severity of the both crown scorch and stem char but generally it can be said that both crown and cambial damage from fires can last approximately three years before pre-fire growth levels is restored.

## 4.6 Conclusions

High intensity surface fires can impact on tree growth of *Pinus radiata*. This study provided evidence that

- (1) High intensity surface fires cause reduced growth in mature stands of *P. radiata*
- (2) These growth reductions might be carried to the year following the fire event and can last a minimum of three years before pre-fire growth levels are restored.
- (3) Localised stress reactions within the tree promotes faster recovery of radial stem growth at the stem base damaged by surface fires. The recovery at stem base is attained the following year after the fire event, while it took a year longer at breast height.

## 4.7 References

- Baisan, C.H. and Swetnam, T.W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Can. J. For. Res.* 20, 1559–1569.
- Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45, 5950 -5959.
- Blanchette, R.A. 1992. Anatomical responses of xylem to injury and invasion by fungi. In: Blanchette R.A. and Biggs A.R. (eds.) *Defense mechanisms of woody plants against fungi*. Springer, Berlin, Germany, 76–95.
- Bond, W. J. and Keeley, J. E. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20(7).
- Bond, W.J. and van Wilgen, B.W. 1994. *Fire and Plants*. Chapman and Hall, London.
- Brown, P.M. and Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- Brown, P.M., Kauffman, M.R. and Shepperd, W.D. 1999. Long- term, landscape patterns of past fire events in montane ponderosa pine forest in central Colorado. *Landscape Ecology* 14,513–532.
- Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. In *Proceedings of the society of American forester’s, 1994 national convention*, pp. 171-178.
- Calvin, M. and Wettlaufer, D. 2000. *Fires in the Southern Cape Peninsula, Western Cape Province, South Africa*. IFFN No. 22:69-75.
- Cooper, R.W. and Altobellis, A.T. 1969. Fire kill in young Loblolly pine. *Fire Control Notes* 30 (4), 14-15.
- de Ronde C., Böhmer, L.H. and Droomer, A.E.C. 1986. Evaluation of wildfire damage in pine stands. *South African Forestry Journal* 138: 45-50
- de Ronde, C. and du Plessis, M. 2002. Determining the relative resistance of selected *Pinus* species to fire damage. In *Forest fire research and wildland fire safety*. Millpress, Rotterdam. pp 1-9.

de Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B. and Geldenhuys, C.J. 2004a. Fire effects on flora and fauna. In: Goldammer, J.G. and de Ronde, C. (eds). *Wildland Fire Management Handbook for Sub-Sahara Africa*: 60-87

de Ronde, C. 2008. Knowledge base in damage assessment to forests and plantations. Deliverable D3.2-7 of the Integrated project "Fire Paradox", Project FP6-018505. European Commission, pp 20.

de Ronde, C. 2008a. Guide to assess wildfire damage in Pinus stands. Deliverable D3.2-8 of the Integrated project "Fire Paradox", Project FP6-018505. European Commission, pp 18.

de Ronde, C. 2008b. Knowledge base in damage assessment to forests and plantations. Deliverable D3.2-7 Unpublished paper for FIRE PARADOX WP 3.2: European Commission, pp 20.

De Micco, V., Zalloni, E., Balzano, A. and Battipaglia, G. 2013. Fire influence on *Pinus halepensis*: wood responses close and far from the scars. *IAWA Journal* 34(4):446–458.

Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson, E.A., Miyanishi, K. (Eds.). *Forest Fires*. Academic Press, New York, 477-525.

Dieterich, J.H. and Swetnam, T.W. 1984. Dendrochronology of a fire scarred ponderosa pine. *Forest Science* 30, 238-247.

Ducrey, M., Duhoux, F., Huc, R. and Rigolot, E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Can. J. For. Res.* 26, 1366-1374.

Elliott, K.J., Vose, J.M. and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. *South J Appl For* 26:18–25.

Fernandes, P.M., Vega, J. A., Enrique, J. and Rigolot, E. 2008. Fire resistance of European pines. *Forest Ecology and management* 256(3), 246-255.

Filion, L. and Cournoyer, L. 1995. Variation in wood structure of eastern larch Subarctic Quebec, Canada. *Can. J. For. Res.* 25, 1263 – 1268.

Fink, S. 1999. Pathological and regenerative plant anatomy. *Encyclopedia of plant anatomy*, 14 (6), Gebru" der Borntre" ger, Berlin, Germany.

Fonti, P., Treydte, K., Osenstetter, S., Frank, D. and Esper, J. 2009b. Frequency dependent signals in multi-centennial oak vessel data. *Palaeogeogr palaeocl* 275, 92–99.

- Fonti, P., von Arx, G., Garcia-Gonzalez, I. and Elimann, B. 2010. Studying global changes through investigation on the plastic responses of xylem anatomy in tree rings. *New Phytologist* 185, 42–63.
- Ford, C.R., Emily, S.M. and Gordon, A.F. 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleafpine (*Pinus palustris*). *Can. J. For. Res.* 40, 1410–1420.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, London. 567pp.
- Gill, A.M. 1977. Management of fire-prone vegetation for plant species conservation in Australia. *Search* 8:20–26.
- Goldammer, J.G. 2007. *Forest Fires - A Global Perspective*. Global Fire Monitoring Center.
- Grab, S. and Craparo, A. 2011. Advance of apple and pear tree full bloom dates in response to climate change in the South western Cape, South Africa: 1973–2009. *Agric For Meteorol* 151:406–413.
- Hempson, G.P., Midgley, J.J., Lawes, M.J., Vickers, K.J. and Kruger, L.M. 2014. Comparing bark thickness: testing methods with bark– stem data from two South African fire-prone biomes. *Journal of Vegetation Science*. Available at, DOI: 10.1111/jvs.12171 [August 2014]
- Hoffmann, W.A. and Solbrig, O.T. 2003. The role of top kill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180, 273–286.
- Larson, P.R. 1994. *Springer Series in Wood Science: The Vascular Cambium*. Development and Structure. Springer-Verlag, Berlin.
- Lloret, F., Keeling, E.G. and Sala, A. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920.
- Matisons, R. and Dauškane, I. 2009. Influence of climate on earlywood vessel formation of *Quercus robur* at its northern distribution range in central regions of Latvia. *Acta Universitatis Latviensis* 753, 49–58.
- Michaletz, S.T. and Johnson, E.A. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22(6), 500–515.
- Murphy, B.P., Jeremy, R.S. and Lyndad, P. 2010. Frequent fires reduce tree growth in northern Australian savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16, 331–343.

Newton, C.A. 2007. *Forest Ecology and Conservation*. A Handbook of Techniques. Oxford university press, Oxford.

Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*. Available at DOI: 10.1016/j.foreco.2010.07.054[October 2014].

Odhiambo B.O., Meincken M. and Seifert T. 2014. The protective role of bark against fire damage: a comparative study on selected introduced and indigenous tree species in the Western Cape, South Africa. *Trees* 28(2): 555-565.

O'Donnell, A.J., Cullen, L.E., McCaw, W.L., Boer, M.M. and Grierson, P.F. 2010. Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. *Dendrochronologia* 28, 37–48.

Peterson, D.L., Sackett, S.S., Robinson, L.J. and Haase, S.M. 1994. The Effects of Repeated Prescribed Burning on *Pinus ponderosa* Growth. *International Journal of Wildland Fire* 4(4) 239 – 247.

Pretzsch, H., Schütze G. and Uhl, E. 2012. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology* 15, 483–495.

Raison, R.J. and Myers, B.J. 1992. The biology of forest growth experiment: linking water and nitrogen availability to growth of *Pinus radiata*. *Forest Ecology and Management*, 52: 279–308.

Rötzer, T., Seifert, T., Gayler, S., Priesack, E. and Pretzsch, H. 2012. Effects of stress and defence allocation on tree growth: Simulation results at the individual and stand level. In: Matyssek, R., Schnyder, H., Oßwald, W., Ernst, D., Munch, J-C., Pretzsch, H. (Eds.) *Growth and Defence in Plants*. Berlin: Springer (*Ecological Studies*, 220). 401-431.

Rozas, V., Gonzalo, P.D.L., Ignacio, G.G. and Jose, R.A. 2011. Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25, 895–905.

Schweingruber, F.H. 1993. *Trees and Wood in Dendrochronology*. Springer-Verlag Berlin Heidelberg, Berlin.

Schweingruber, F.H. 2007. Tree-ring measurements of *Picea mariana* (Black spruce) from sample QUEBEC-382. Swiss Federal Institute for Forest, Snow and Landscape Research, available online, DOI: 10.1594/PANGAEA.597213.

Seifert, T., Nickel, M. and Pretzsch, H. 2010. Analysing the long-term effects of artificial pruning of wild cherry by computer tomography, *Trees* 24(5): 797-808.

South Africa. 2011. Report on Commercial Timber resources and primary round wood processing in South Africa. Forest economic services: Pretoria.

Stahlea, D.W., Mushoveb, P.T., Cleavelanda, M.K., Roigc, F. and Haynesd, G.A. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* 124, 217-229.

Stone, E.L. 1944. Effect of fire on taper of longleaf pine. *Jour. Forestry* 42: 607.

Thies, W.G., Westlind, D.J., Loewen, M. and Brenner, G. 2006. Predicting delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. *International Journal of Wildland Fire* 15, 19–29.

Thomas, F.M., Blank, R. and Hartman, G. 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology* 32, 277–307.

Thonicke, K., Venevsky, S., Sitch, S. and Cramer, W. 2001. The role of fire disturbance for global vegetation dynamics: coupling Dynamic Global Vegetation Model. *Global Ecology and Biogeography* 10, 661–667.

Vaganov, E.A., Hughes, M.K., Silkin, P.P and Nesvetailo, V.D. 2004. The Tunguska Event in 1908: Evidence from Tree-Ring Anatomy. *Astobiology* 4(3), 391 – 399.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D. and Franklin, J.F. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524.

van Wilgen, B.W. 1982. Some effects of Post-Fire Age on the Above-Ground Plant Biomass of Fynboss (*Macchia*). *Journal of Ecology* 70:217-225.

van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78, 210-222.

Vega, J., Jimenez, E., Vegab, D., Ortizb, L. and R.Pérez, J. 2010. *Pinus pinaster* Ait. Tree mortality following wildfire in Spain. *Forest Ecology and Management* available online, DOI: 10.1016/j.foreco.2010.10.019

Wade, D.D. and Ward, D.E. 1975. Management decisions in severely damaged stands. *Journal of Forestry* 73, 573-577.

Wallin, K.F., Kolb, T.E., Skov, K.R. and Wagner, M.R. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in Northern Arizona. *Environ. Entomol* 32, 652–661.

Werner, P.A., Cowie, I.D. and Cusack, J.S. 2006. Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia: an experimental field study in Kakadu National Park. *Australian Journal of Botany* 54, 283–296.

Werner, P.A. 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees: an experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30, 625–647.

Wesolowski A., Adams M.A. and Pfautsch, S. 2014. Insulation capacity of three bark types of temperate *Eucalyptus* species. *Forest Ecology and Management* 313: 224–232.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. and Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge university press, Cambridge.

Williams, R.J., Cook, G.D., Gill, A.M. and Moore, P.H.R. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 24, 50–59.

## Chapter 5 General discussion and conclusions

Trees within an ecosystem may experience ground fires, surface fires, crown fires, a mix of any two, or all three. Crown fires involve flaming combustion of branches, buds and foliage. Crown fires are lethal and will kill the tree if they combust the entire crown (Michaletz and Johnson 2007). Usually crown fires are sustained by surface fires below, although under severe conditions crown fires can advance independently of surface fires (van Wilgen et al. 1990).

Surface fires involve flaming combustion of fine fuels accumulated on the forest floor; this include litter, leaves, twigs, branches, as well as herbaceous woody plants and shrubs. Surface fires also burn through dead plant material lying on the ground. The fires keep close to the ground leaving the foliage unaffected and can damage the trees by heating through the back and killing living tissues. Maximum temperatures are usually encountered between 0 and 50 cm above the ground (Miranda et al. 1993). A fire temperature of up to 400°C is enough to kill cambial cells and can result in the death of the tree (Gill 1995; VanderWeide and Hartnett 2011). The fires are classified as non-lethal when they damage the trees without killing them.

Ground fires involve the smouldering combustion of duff and litter on the soil surface. The fires are perpetuated by the presence of thick accumulation of duff layer (needles, leaves, and other recognizable litter on the forest floor) and generally occur after the flaming fire front on the above ground has passed. Fast moving fires along the ground, partly due to low fuel content, may not be lethal to the root system. Slower fires that consume more fuel and smoulder within the organic layer with temperatures exceeding 700°C for long periods may be lethal. Some findings have reported downwards temperature reduction within the soil, with negligible temperature rise at levels below 15 or 30 cm depth (e.g. Daubenmire 1974). Other findings show no significant rise in temperatures below 5 cm (Gignoux et al. 1997).

The damage caused to a tree is dependent on the severity of the fire which is in turn determined by the intensity and duration of the fire. Fire intensity is measured as the rate of heat energy released per unit length of fire line per unit time ( $\text{Wm}^{-1}\text{s}^{-1}$ ) (Newton 2007). Fire intensity and duration vary from place to place as a result of site differences. Topography in particular plays an important role in moderating a wide range of physical and climatic factors which influence the intensity and duration of fires. Sites with high variability in terms of slope,



aspect, stand density, evaporation rates, soil moisture, primary productivity, species distribution, decomposition rates, wind speed, fuel type, air temperature, plant temperature and relative humidity will have fire intensity and spread rate varying across a range of spatial scales (Chandler et al. 1983; Gill, 1995; Simkin and Baker 2008). Some sites experience intense heat due to large amounts of fuel loads, especially in the hot months, while the amount of fuel moisture in some places may lower the level of heat release (Fischer and Binkely 2000).

The effect of fire on trees can be direct or indirect. Direct effects occur when fire comes into contact with sections of a tree, or when fire heats the air and water vapour around the tree such that heat reaches the tree through radiation and convection. Root damage can occur directly when smouldering heat comes into contact with the roots or when soil is heated and the heat is transferred to the roots by conduction. Direct heating of cells and tissues causes damage and can result in tissue death (Hennessey et al. 1985).

Indirect effects of fires are due to the impact on soil micro-organisms, soil nutrients, and increased susceptibility to insect and disease attack. Trees that have been weakened by fire are vulnerable to insect and disease attack. This potentially may cause damage or death to the trees. The effect on soil micro-organisms depends on the type of micro-organisms, fire characteristics and changes to the soil environment. The impact of fire intensity and duration on soil organic matter, soil moisture and nutrients can result in death of some micro-organisms or a rapid population increase of others. This in turn influences tree growth. Alteration to the soil moisture, nutrients, as well as chemical changes in soil (e.g. changes in pH), all have an impact on trees growing within a specific site (Hennessey et al. 1985).

The temperature experienced by plant cells is an ultimate cause of tissue death. High temperatures can result in complete combustion which causes cell and tissue mortality (Eckmann et al. 2010). The capacity of individual cells to withstand constant exposure is not considered to vary significantly either between species or between tissues within a tree. In general, the thermal death point of typical plant cells is considered to lie between 50 and 55°C. The mortality of plant cells is complete at 60°C (Catry et al. 2010; Gignoux et al. 1997; Kobziar et al. 2006; Whelan 1995).

The time taken to cause tissue death varies from several minutes at lower temperatures to almost instantaneous death at higher temperatures (Hare 1965). Some plants cells can therefore suffer mortality at lower temperatures given sufficient exposure time (Bond and van Wilgen 1994; Catry et al. 2010; Gignoux et al. 1997). A brief and slight exposure to elevated temperatures may not result in mortality but can cause temporary disruptions. These disruptions can either be indirect, following metabolic changes, or direct by protein denaturation, altered lipid mobility or chemical decomposition (Whelan 1995). Trees that

have burnt before are likely to suffer more severe burns because previously burned wood has high chance of catching and supporting fire.

The extent of damage to which individual trees are exposed during fires is influenced by their morphological traits. Certain morphological traits offer protection against direct fire damage (Eckmann et al. 2010; Pyne et al. 1996). Pines for instance possess traits that allow survival in low to moderate intensity fires; crown damage is mitigated by large, protected buds and relatively thick scaly needles, as is the case for *P. pinaster* (Fernandes et al. 2008). Other features associated to fire resistance include long needles, tall growth habits, self-pruning and bark thickness (Climent et al. 2004).

The contribution made in this thesis addressed two key areas of tree-fire interaction through characterising the species-specific insulation capacity of tree bark based on its structural components, and by scrutinising the typical reaction pattern of tree diameter growth of trees with a stem char after surviving a fire. Both main aspects are linked to surface fires and the reaction pattern of tree growth differ significantly from patterns induced by crown fire damaged trees as will be discussed later on.

In many tree species, the bark plays a major role in protecting the vascular cambium against heat damage (Bova and Dickinson 2005; Gignoux et al. 1997; Kobziar et al. 2006; Peterson and Arbaugh 1986; Ryan et al. 1988; van Mantgem and Schwartz 2003). The probability of survival is therefore mainly dependent on the insulative capacity of the bark layers, which is determined by its thickness (Agee 1993; Catry et al. 2010; De Bano et al. 1998; Gill 1995; Pinard and Huffman 1997). Species with thicker bark have been found to offer greater resistances to fire than those with thinner bark (Mutch and Parsons 1998; Ryan and Reinhardt 1988; Stephens and Finney 2002).

In this study fire was simulated using an electric heat gun set at 400°C on fresh billets with intact bark to quantify the protective role of bark among selected indigenous and commercial species in the Cape forest region. The results were consistent with the previous findings in which *P. pinaster*, *P. elliotii*, *E. cladocalyx*, *E. capensis* and *A. mearnsii* with thick barks had higher resistance against heat damage to the cambium compared to thin barked *P. radiata*, *R. viminalis* and *O. africana*. Available moisture content in the bark of the fresh billets was found to have no significant effect on heat resistance capacity. There is therefore no adaptive trait relating to habitat that promotes resistance in indigenous species as compared to commercial species. The thin barked species are vulnerable to cambial heat damage and are often killed following fire damage. Some of them however, adapt by resprouting soon after the fire damage. Both *R. viminalis* and *O. africana* are known to be heavy resprouters and this trait enables their survival in fire prone ecosystems.

Bark thickness varies along the trunk. This study found relative stem height to be a good substitute for bark thickness for all species, where bark thickness did not change too much along the stem. The majority of broad-leaved species are known to maintain consistent bark thickness along the entire stem and have been reported to be more heat resistant along the bole (Fernandes et al. 2008). In contrast, the pines have greater bark taper with greater proportion of outer bark at the bottom than at the top. Both *P. pinaster* and *P. elliotii* form thicker bark at the bottom of the trunk and thus possess additional resistance against ground fires. The less attenuated effect of bark taper in *P. radiata* explains its inferior heat tolerance to ground fires compared with the other two pine species in the study.

In the context of bark thickness, tree size becomes an important aspect in resistance against surface fire damage. Bark thickness varies with tree size; big or adult trees have thicker bark and are more resistant to heat damage compared to the smaller trees with thin bark. Small trees are therefore more likely to suffer higher mortality in the event of fire than larger trees (Daubenmire 1974; Michaletz and Johnson 2007; Morrison 1995). Some studies (e.g. Hempton et al. 2014) have reported no consequence of heat damage on adult trees and recommended fire damage related studies on younger trees. However, due to frequent repeated burns in mature plantations, fire has become a major abiotic stress factor with potential negative consequences for growth in adult trees. Fire damage studies on older trees thus contribute substantially to understanding overall stress resistance with increasing tree size.

Bark thickness is the main determinant of the bark's insulative capacity against heat damage to the cambium. The contribution of bark thickness to heat insulation has been previously reported to be 63 % (Pinard and Huffman 1997) and 82 % (Brando et al. 2012). This study found bark thickness to contribute 85 % of insulation against cambial damage. However, there was additional resistance value in some species not explained by the bark thickness. This led to the investigation of bark density, chemical composition and topology to ascertain their role in heat resistance. Like in previous studies (van Mantgem and Schwartz 2003; Hengst and Dawson 1993; Vines 1968; Reifsnyder et al. 1967) bark density was found to have insignificant influence on heat resistance capacity. Using thermo gravimetric analytical technique (TGA), tree barks were found to comprise of the same chemical constituents which thermally degrade at the same temperatures. There were therefore no differences in the thermal degradation rates of bark of the different species due to bark chemical constituents. Bark chemical composition was thus found to have no influence on its heat resistance capacity. The amount of ash content did however differ among the species due to varying amounts of inorganic material. Ash content was also found not to have an influence on heat resistance capacity.

The distinct topological features of the tree barks were observed from billets using a microfocus CT (Computer Tomography) system. The dominant topological features among the structured barks were the fissures. Various fissure properties were tested against species-specific heat resistance capacity and fissure frequency and sizes found to have a significant influence on heat resistance capacity. Species vary in fissure frequency and sizes within their bark layer, and these variations determine the extent of their influence on heat resistance capacity. Stems with fissured bark have patterns of splitting on outer and inner bark which can allow faster heat transfer to the cambium. Increased numbers of fissures thus lowers the heat insulation ability as they create openings within the bark layer. Large size fissures, which penetrate deeper into the bark layer, further lower the heat resistance capacity. When bark thickness is constant, species with higher number of wide and deep fissures are more vulnerable to heat damage than those with fewer numbers of small sized fissures. This refines previous findings of other authors (Bauer et al. 2010; Nicolai 1986; Harmon 1984), which have reported highly structured bark with deep fissures to provide more resistance against heat damage compared to smooth barks.

Reduced growth is mostly associated with crown fires due to reduction in photosynthetic capacity. Substantial loss in photosynthetic capacity has an effect on cambial activity which is regulated by translocated food material produced by shoots. The cambium is a critical tissue containing a sensitive layer of growing cells that produces the vascular system responsible for conducting water and nutrients through the tree. The cambium also forms an important growth layer responsible for the production of bark tissue (phloem) on the outside and sapwood (xylem) on the inside of the cambial layer (Kobziar et al. 2006). The new annual layers of xylem and phloem are inserted between old layers of these tissues causing the stem, branches and major roots to increase in thickness (Kozlowski 1971). Reduced flow of assimilates from the leaves to the stem affects cambial growth which may cause marked reduction in stem diameter growth (Fritts 1976). The amount of xylem produced in the sapwood region by the cambium after a fire is reduced proportionately to the amount of crown scorch. Formation of small trachieds with non-thickened cell walls leads to abrupt growth reductions that have been observed in *P. ponderosa* and *P. sylvestris* (Schweingruber et al. 2007), *P. canariensis* (Rozas et al. 2011) and *P. taeda* (McInnis et al. 2004). If the crown is completely scorched, production of xylem stops (Kozlowski 1971), and the tree can die (Hennessey et al. 1985) or experience cessation in growth until a time when newly formed crown starts to photosynthesise (Rozas et al. 2011).

Crown fires also minimise growth through destruction of buds: early in the growing season, buds open up to begin growth and in the process produce auxins which trigger cambial division responsible for the production of xylem and phloem. The auxins are translocated downward stimulating the differentiation of new xylem and phloem from near the tips of the

twigs to the branches, trunk and roots (Fogg 1963; Kozlowski 1971). Bud damage due to crown fires, disrupts the process of cambial division, thus limiting radial growth.

High intensity surface fires can penetrate the bark layer, destroy the cambium (Michaletz and Johnson 2007; Dickinson and Johnson 2001), and possibly impact tree growth. The effect of high intensity surface fire damage on radial stem growth was investigated on a *P. radiata* plantation. The impact of the damage was measured from growth rings and analysed based on annual basal area increment (iBA). There was evidence of reduced growth resulting from the fire damage which was carried forward to the following year. This is in agreement with past studies that have reported the highest impact in the year following the fire event (e.g. Ford et al. 2010). The greatest reduction was observed at the stem base where the damage occurred and later spread through the entire tree due to systematic growth reaction. Reduced growth is attributed to cambial damage, which alters radial meristematic activity. Cambial damage prevents water and nutrient transport in the xylem and phloem respectively reducing the photosynthetic rate and restricting translocation of photosynthate to the roots. Tangential resin ducts may also form after moderate heat exposure, as observed for *P. sylvestris* (Schweingruber et al. 2007). The healing process involve wound closure and formation of wound healing callus tissue. This occurs at the expense of water transport (Schweingruber 2007) and may also impact on the rate of photosynthesis thus contributing to the reduced growth.

The majority of studies have concluded that surface fires have insignificant impacts on tree growth (e.g. Hempson et al. 2014; Bauer et al. 2010; Fernandes et al. 2008; Ducrey et al. 1996). This study has however, shown that based on basal area increments, surface fires do cause growth reductions in the short term. This is supported by the findings of Ford et al. (2010) and Elliott et al. (2002) who have also reported short term growth reductions following surface fire damage.

As mentioned earlier, recovery from bole char involves the formation of callus tissue around the damaged cambium tissue in order to protect it from further damage and infection by micro-organisms (Fogg 1963; Pinard and Huffman 1997). The callus tissue forms a fire scar (Stahlea et al. 1999) and accelerated growth around the scar creates new tissues which expand around the wound. The expanded growth occludes around the fire scar concealing it from view and effectively healing the wound (Schweingruber 1988; Rozas et al. 2011). Sometimes normal wood forming can occur on the unaffected side and little or no growth on the wounded side causing a lopsided radial profile (Vaganov et al. 2004).

The recovery index showed that it took three years for the trees to recover from the effects of the fire damage at the stem base. This duration has also been reported for crown fire damage which lasts between 1-3 years, and after which growth rates return to approximately

pre-fire levels (Murphy et al. 2010; Goldammer 2007; Werner 2005; Hoffmann and Solbrig 2003; Werner et al. 2006; Williams et al. 1999). Recovery from crown scorch involves regeneration from epicormic shoots (Bond and van Wilgen 1994) or leaf buds (e.g. Thies et al. 2006) to re-establish the photosynthetic capacity after the fire event. The severity of both the crown scorch and stem char would determine the duration taken to re-establish photosynthetic capacity as well as wound healing and tissue repair after cambial damage respectively.

Recovery was faster at the affected stem base, which had fully recovered from the effects of the damage by the end of the second year after the fire event. This is in comparison to the overall tree, which fully recovered at the end of the third year only. In the event of damage, trees seem to allocate growth resources to the affected areas and normal growth is restored once the damage is contained (Stone 1944).

The study has highlighted bark properties that contribute towards its resistance to surface fire damage. This is necessary in understanding the tolerance of various species to varying surface fire regimes. Understanding the limits of a plant's tolerance is necessary in wildfire damage assessment. Such knowledge can also be used in developing models for consistent bole damage prediction in fires of specified temperatures as determined by the prevailing fuel levels. This can be useful in defining an efficient fire management, such as in prescribed burning.

An understanding of post-fire growth impacts is of strategic economic importance for the assessment of forest tree volumes, biomass, carbon stocks and predicting the plants' potential productivity. It is also vital in making post-fire management decisions related to hazard tree removal, salvage logging and reforestation. Further studies should focus on the impacts of early and late season fires on growth and how they impact early and late wood tissues and consequently growth.

## 5.1 References

- Agee, J.K. 1993. Fire ecology of pacific north west forests. Island Press, Washington.
- Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45:5950–5959.
- Bond, W.J. and van Wilgen, B.W. 1994. Fire and plants. Chapman and Hall, London.
- Bova, A.S. and Dickinson, M.B. 2005. Linking surface-fire behaviour, stem heating, and tissue necrosis. *Canadian Journal of Forestry Research* 35: 814–822.
- Brando, P.M., Nepstad, D.C. and Balch, J.K. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behaviour. *Global Change Biology* 18:630–641.
- Catry, F.X., Rego, F., Moreira, F. and Fernandes, P.M. 2010. Post-fire mortality in mixed forests of central Portugal. *Forest Ecology and Management* 260:1184–1192.
- Chandler, C., Cheney, P., Thomas, P., Trabaud, L. and Williams, D. 1983. Fire in forestry, Vol. II. New York: John Wiley & Sons.
- Climent, J., Tapias, R., Pardos, J. and Gil, L. 2004. Fire adaptations in the Canary Islands pine (*Pinus canariensis*). *Plant Ecology* 171, 185–196.
- Daubenmire, R.F. 1974. Plants and Environment. A text book of plant autecology (3rd ed.). New York: John Wiley & Sons.
- de Bano, L.F., Neary, D.G. and Folliott, P.F. 1998. Fire's effects on ecosystems. John Wiley and Sons, New York.
- Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson EA, Miyanishi K (eds). Forest fires. Academic, New York, pp 477–525.
- Ducrey, M., Duhoux, F., Huc, R. and Rigolot, E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Canadian Journal of Forest Research* 26:1366–1374.
- Eckmann, T. C., Still, C. J., Roberts, D. A. and Joel C. M. 2010. Variations in Subpixel Fire Properties with Season and Land Covering Southern Africa. *EARTH Interactions* 6(14).

- Elliott, K.J., Vose, J.M. and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. *South J Appl For* 26:18–25.
- Fernandes, P.M., Vega, J.A., Enrique, J. and Rigolot, E. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256:246–255.
- Fischer, R.F. and Binkley, D. 2000. *Ecology and Management of Forest Soils* (3rd ed.). USA: John Wiley & sons.
- Fogg, G.E. 1963. *The growth of plants*. Mitcham, Victoria, Australia: Penguin books.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, London. 567pp.
- Ford, C.R., Emily, S.M. and Gordon, A.F. 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleafpine (*Pinus palustris*). *Can. J. For. Res.* 40, 1410–1420.
- Gignoux, J., Clobert, J. and Menaut, J. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110:576–583.
- Gill, A.M. 1995. *Plant stems: physiology and functional morphology*. Academic, New York.
- Goldammer, J.G. 2007. Wildland fires: Creeping and sudden disasters. *Crisis Response* 3:50-52, ISSN 1745-8633.
- Hare, R.C. 1965. Contribution of bark to fire resistance of Southern trees. *Journal of Forestry* 63(4): 248-251.
- Harmon, M. 1984. Survival of trees after low-intensity surface fires in the Great Smoky Mountains National Park. *Ecology* 65:796–802.
- Hempson, G.P., Midgley, J.J., Lawes, M.J., Vickers, K.J. and Kruger, L.M. 2014. Comparing bark thickness: testing methods with bark– stem data from two South African fire-prone biomes. *Journal of Vegetation Science*. Available at, DOI: 10.1111/jvs.12171 [August 2014]
- Hengst, G.E. and Dawson, J.O. 1993. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24:688–696.
- Hennessey, T.C., Dougherty, P.M., Kossuth, S.V. and Johnson, J.D. (eds). 1985. *Fire: its effects on growth and physiological processes in conifer forests*. Boston: Martinus Nijhoff publishers.



- Hoffmann, W.A. and Solbrig, O.T. 2003. The role of top kill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180:273–286.
- Kobziar, L., Moghaddas, J. and Stephens, S. L. 2006. Tree mortality patterns following prescribed fires in a mixed conifer forest. *Canadian Journal of Forestry Research* 36
- Kozlowski, T.T. (ed). 1971. *Physiological Ecology: Growth and Development of trees*. New York: Academic press.
- Lawes, M.J., Richards, A., Dathe, J. and Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212:2057–2069.
- McInnis, L.M., Oswald, B.P., Williams, H.M., Farrish, K.W. and Unger, D.R. 2004. Growth response of *Pinus taeda* L., to herbicide, prescribed fire, and fertilizer. *Forest Ecology and Management* 199:231–242.
- Rozas, V., Gonzalo, P.D.L., Ignacio, G.G. and Jose, R.A. 2011. Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25:895–905.
- Michaletz, S.T. and Johnson, E.A. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22:500–515.
- Miranda, A.C., Fatima, O.D. and Ferreira, S.D. 1993. Soil and air temperatures during prescribed cerrado fires in central Brazil. *Journal of Tropical Ecology* 9:313–320.
- Morrison, D.A. 1995. Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of NSW* 115:109–119.
- Murphy, B.P., Smith, J.R. and Priors, L.D. 2010. Frequent fires reduce tree growth in northern savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16:331–343.
- Mutch, L.S. and Parsons, D.J. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. *Forest Science* 44:341–355.
- Newton, C.A. 2007. *Forest ecology and conservation. A handbook of techniques*. Oxford university press, Oxford.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148-160.

- Pausas, J. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science* 8:703–706.
- Peterson, D.L. and Arbaugh, M.J. 1986. Postfire survival in Douglas-fir and lodgepole pine: comparing the effects of crown and bole damage. *Canadian Journal of Forestry Research* 16: 1175–1179.
- Pinard, M.A. and Huffman, J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* 13:727–740.
- Pyne, S. J., Andrews, P. L. and Laven, R. D. 1996: *Introduction to Wildland Fire*. (2nd ed.). USA: John Wiley & sons.
- Reifsnyder, W.E., Herrington, L.P. and Spalt, K.W. 1967. Thermophysical properties of bark of shortleaf, longleaf, and red pine. Bulletin no. 70. School of Forestry, Yale University, Yale.
- Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* mill. and *Pinus pinea* L. *Plant Ecology* 171:139–151.
- Rozas, V., Gonzalo, P.D.L., Ignacio, G.G. and Jose, R.A. 2011. Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25:895–905.
- Ryan, K.C. and Reinhardt, E.D. 1988. Predicting post-fire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:291–1297.
- Schweingruber, F.H. 1988. *Tree rings: Basics and applications of dendrochronology*. Dordrecht, Holland: Reidel Publishing company.
- Schweingruber, F.H. 2007. Tree-ring measurements of *Picea mariana* (Black spruce) from sample QUEBEC-382. Swiss Federal Institute for Forest, Snow and Landscape Research, available online, DOI: 10.1594/PANGAEA.597213.
- Simkin, R. and Baker, P.J. 2008. Disturbance history and stand dynamics in tall open forest and riparian rainforest in the Central Highlands of Victoria. *Austral Ecology* 33: 747–760.
- Stephens, S.L. and Finney, M.A. 2002. Prescribed fire mortality of sierra nevada mixed conifer tree species: effects of crown damage and forest floor consumption. *Forest Ecology and Management* 162:261–271.
- Stone, E.L. 1944. Effect of fire on taper of longleaf pine. *Jour. Forestry* 42: 607.

Thies, W.G., Westlind, D.J., Loewen, M. and Brenner, G. 2006. Predicting delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. *International Journal of Wildland Fire* 15, 19–29.

Vaganov, E.A., Hughes, M.K., Silkin, P.P and Nesvetailo, V.D. 2004. The Tunguska Event in 1908: Evidence from Tree-Ring Anatomy. *Astobiology* 4(3), 391 – 399.

van Mantgem, P.J. and Schwartz, M. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *Forest Ecology and Management* 178:341–352.

VanderWeide, B.L. and Hartnett, D.C. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261:1530–1538.

van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78, 210-222.

Vines, R.G. 1968. Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16:499–514.

Werner, P.A., Cowie, I.D. and Cusack, J.S. 2006. Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia. *Australian Journal of Botany* 54:283–296.

Werner, P.A. 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees: an experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30:625–647.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge university press, Cambridge.

Williams, R.J., Cook, G.D., Gil, A.M. and Moore, P.H.R. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 30:50–59.

## Chapter 6: References of Chapter 1 to 5

Abrahamson, W.G. 1984. Species responses to fire on the Florida lake wales ridge. *American Journal of Botany* 71(1):35-43.

Agee, J.K. 1993. *Fire ecology of pacific north west forests*. Island Press, Washington.

Alexandrov, V.Y. 1977. *Cells, molecules and temperature*. Springer, Berlin, p 330.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D. and McDowell, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.

Axelsson, J.N., Alfaro, R.I. and Hawkes, B.C. 2009b. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. *Forestry Chronicle* 86:87–99.

Baisan, C.H. and Swetnam, T.W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Can. J. For. Res.* 20, 1559–1569.

Bauer, G., Speck, T. and Blömer, J. 2010. Insulation capability of the bark of trees with different fire adaptation. *Journal of Material Science* 45:5950–5959.

Berg, E.E., Henry, J.D., Fastie, C.L., De volder, A.D. and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219–232.

Blanchette, R.A. 1992. Anatomical responses of xylem to injury and invasion by fungi. In: Blanchette R.A. and Biggs A.R. (eds.) *Defense mechanisms of woody plants against fungi*. Springer, Berlin, Germany, 76–95.

Bond, W.J. and Keeley, J.E. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20(7).

Bond, W.J. and van Wilgen, B.W. 1994. *Fire and plants*. Chapman and Hall, London.

- Bova, A.S. and Dickinson, M.B. 2005. Linking surface-fire behaviour, stem heating, and tissue necrosis. *Canadian Journal of Forestry Research* 35: 814–822.
- Brando, P.M., Nepstad, D.C. and Balch, J.K. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behaviour. *Global Change Biology* 18:630–641.
- Brown, P.M. and Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- Brown, P.M., Kauffman, M.R. and Shepperd, W.D. 1999. Long-term, landscape patterns of past fire events in montane ponderosa pine forest in central Colorado. *Landscape Ecology* 14:513–532.
- Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. In *Proceedings of the society of American forester's, 1994 national convention* pp. 171-178.
- Burnham, K.P. and Anderson, D.R. 2002. *Model selection and multimodel Inference. A practical information—theoretical approach*, 2nd edn. Springer science Business Media LLC, New York, pp 71, 75, 167-169.
- Burnham, K.P. and Anderson, D.R. 2004. Multimodel Inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Burrows, N.D., Woods, Y.C., Ward, B.G. and Robinson, A.D. 1989. Prescribing low intensity fire to kill wildings in *Pinus radiata* plantations in Western Australia. *Australian Forestry* 52:45–52.
- Calvin, M. and Wettlaufer, D. 2000. Fires in the Southern Cape Peninsula, Western Cape Province, South Africa. *IFFN No. 22:69-75*.
- Catry, F.X., Rego, F., Moreira, F. and Fernandes, P.M. 2010. Post-fire mortality in mixed forests of central Portugal. *Forest Ecology and Management* 260:1184–1192.
- Chandler, C., Cheney, P., Thomas, P., Trabaud, L. and Williams, D. 1983. *Fire in forestry*, Vol. II. New York: John Wiley & Sons.
- Chanyenga, T.F., Geldenhuys, C.J. and Sileshi, W.W. 2012. Germination response and viability of an endangered tropical conifer *Widdringtonia whytei* seeds to temperature and light. *South African Journal of Botany* 81:25–28.
- Christensen, J.H., Hewitson, B. and Busuioc, A. 2007. Regional Climate Projections. In Solomon S, Qin D, Manning M. (eds.), *Climate Change: The Physical Science Basis*.

Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Climent, J., Tapias, R., Pardos, J. and Gil, L. 2004. Fire adaptations in the Canary Islands pine (*Pinus canariensis*). *Plant Ecology* 171, 185–196.

Cooper, R.W. and Altobellis, A.T. 1969. Fire kill in young Loblolly pine. *Fire Control Notes* 30 (4), 14-15.

Daniels, L.D., Thomas, B.M., Amanda, B.S. and Shane, P.J.M. 2011. Direct and indirect impacts of climate change on forests: three case studies from British Columbia. *Canadian Journal of Plant Pathology* 33(2):108–116.

DAFF 2012. Report on commercial timber resources and primary roundwood processing in South Africa 2010/2011. Department of Agriculture, Forestry and Fisheries, Republic of South Africa.

Daubenmire, R.F. 1974. *Plants and Environment. A text book of plant autecology* (3rd ed.). New York: John Wiley & Sons.

Davis, K.P. 1959. *Forest fire: control and use*. McGraw-Hill Book, Michigan, pp 31–47.

de Bano, L.F., Neary, D.G. and Folliott, P.F. 1998. *Fire's effects on ecosystems*. John Wiley and Sons, New York.

de Ronde, C. 1982. The resistance of *Pinus* species to fire damage. *South African Forestry Journal* 122:22–25.

de Ronde C., Böhmer, L.H. and Droomer, A.E.C. 1986. Evaluation of wildfire damage in pine stands. *South African Forestry Journal* 138: 45-50

de Ronde, C. and du Plessis, M. 2002. Determining the relative resistance of selected *Pinus* species to fire damage. In *Forest fire research and wildland fire safety*. Millpress, Rotterdam. pp 1-9.

de Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B. and Geldenhuys, C.J. 2004a. Fire effects on flora and fauna. In: Goldammer, J.G. and de Ronde, C. (eds). *Wildland Fire Management Handbook for Sub-Sahara Africa*: 60-87

de Ronde, C. 2008a. Guide to assess wildfire damage in *Pinus* stands. Deliverable D3.2-8 of the Integrated project "Fire Paradox", Project FP6-018505. European Commission, pp 18.

de Ronde, C. 2008b. Knowledge base in damage assessment to forests and plantations. Deliverable D3.2-7 Unpublished paper for FIRE PARADOX WP 3.2: European Commission, pp 20.

de Ronde, C. 2008c. Guide to assess wildfire damage in pine stands. Deliverable D3.2-8 Unpublished paper for FIRE PARADOX WP 3.2: p 18.

de Ronde, C. 2008. Knowledge base in damage assessment to forests and plantations. Deliverable D3.2-7 of the Integrated project "Fire Paradox", Project FP6-018505. European Commission p 20.

De Micco, V., Zalloni, E., Balzano, A. and Battipaglia, G. 2013. Fire influence on *Pinus halepensis*: wood responses close and far from the scars. IAWA Journal 34(4):446–458.

Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson EA, Miyanishi K (eds). Forest fires. Academic, New York, pp 477–525.

Dickinson, M.B. and Johnson, E.A. 2004. Temperature-dependent rate models of vascular cambium necrosis. Canadian Journal of Forest Research 34:546–559.

Dieterich, J.H. and Swetnam, T.W. 1984. Dendrochronology of a fire scarred ponderosa pine. Forest Science 30, 238-247.

Donovan, L.A., Mausberg, J. and Ehleringer, J.R. 1993. Seedling size and survival for *Chrysothamnus nauseosus*. Great Basin Nature 53:237–245.

Dickinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. In: Johnson, E.A., Miyanishi, K. (Eds.), Forest Fires. Academic Press, New York, 477-525.

Ducrey, M., Duhoux, F., Huc, R. and Rigolot, E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. Canadian Journal of Forest Resources 26:1366–1374.

Eckmann, T. C., Still, C. J., Roberts, D. A. and Joel C. M. 2010. Variations in Subpixel Fire Properties with Season and Land Covering Southern Africa. EARTH Interactions 6(14).

Elliott, K.J., Vose, J.M. and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. South Journal of Applied Forestry 26:18–25.

Fahnesock, G. and Hare, R.C. 1964. Heating of tree trunks in surface fires. Journal of Forestry 62:799–805.

FAO 2003. Fires are increasingly damaging the world's forests. FAO news report, Rome.

- Fengel, D. and Wegener, G. 1984. *Wood: Chemistry, Ultrastructure, Reactions*. Walter de Gruyter, Berlin.
- Fernandes, P.M., Vega, J.A., Enrique, J. and Rigolot, E. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256:246–255.
- Filion, L. and Cournoyer, L. 1995. Variation in wood structure of eastern larch Subarctic Quebec, Canada. *Can. J. For. Res.* 25, 1263 – 1268.
- Fink, S. 1999. Pathological and regenerative plant anatomy. *Encyclopedia of plant anatomy*, 14 (6), Gebru" der Borntra" ger, Berlin, Germany.
- Fischer, R.F. and Binkley, D. 2000. *Ecology and Management of Forest Soils* (3rd ed.). USA: John Wiley & sons.
- Fogg, G.E. 1963. *The growth of plants*. Mitcham, Victoria, Australia: Penguin books.
- Fonti, P., Treydte, K., Osenstetter, S., Frank, D. and Esper, J. 2009b. Frequency dependent signals in multi-centennial oak vessel data. *Palaeogeogr palaeocl* 275, 92–99.
- Fonti, P., von Arx, G., Garcia-Gonzalez, I. and Elmann, B. 2010. Studying global changes through investigation on the plastic responses of xylem anatomy in tree rings. *New Phytologist* 185, 42–63.
- Ford, C.R., Emily, S.M. and Gordon, A.F. 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleafpine (*Pinus palustris*). *Canadian Journal of Forest Research* 40:1410–1420.
- Frazer, J.M. and Davis, S.D. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76:215–221.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, London. 567pp.
- Gignoux, J., Clobert, J. and Menaut, J. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110:576–583.
- Gill, A.M. 1977. Management of fire-prone vegetation for plant species conservation in Australia. *Search* 8:20–26.
- Gill, A.M. 1995. *Plant stems: physiology and functional morphology*. Academic, New York.
- Glitzenstein, J.S., Platt, W.J. and Streng, D.R. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monograph* 65:441-476



- Goldammer, J.G. 2007. Wildland fires: Creeping and sudden disasters. *Crisis Response* 3:50-52, ISSN 1745-8633.
- Goldammer, J.G. 1999. Forests on fire. *Science*, available online, DOI: 10.1126/science.284.5421.1782a.
- Grab, S. and Craparo, A. 2011. Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973–2009. *Agricultural and Forest Meteorology* 151:406–413.
- Grace, S.L. and Platt, W.J. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology* 83:75–86.
- Hare, R.C. 1965. Contribution of bark to fire resistance of Southern trees. *Journal of Forestry* 63(4): 248-251.
- Harmon, M. 1984. Survival of trees after low-intensity surface fires in the Great Smoky Mountains National Park. *Ecology* 65:796–802.
- Harmon, M.E. and Sexton, J. 1995. Water balance of conifer logs in early stages of decomposition. *Plant Soil* 172:141–152.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, New York.
- Hempson, G.P., Midgley, J.J., Lawes, M.J., Vickers, K.J. and Kruger, L.M. 2014. Comparing bark thickness: testing methods with bark– stem data from two South African fire-prone biomes. *Journal of Vegetation Science*, available online, DOI: 10.1111/jvs.12171.
- Hengst, G.E. and Dawson, J.O. 1993. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24:688–696.
- Hennessey, T.C., Dougherty, P.M., Kossuth, S.V. and Johnson, J.D. (eds). 1985. *Fire: its effects on growth and physiological processes in conifer forests*. Boston: Martinus Nijhoff publishers.
- Hickie, J.A., Logan, J.A., Powell, J. and Ojima, D.S. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research* 111(G2):12.
- Hobbs, R.J., Currall, J.E.P. and Gimingham, C.H. 1984. The use of “thermo-color” pyrometers in the study of heath fire behaviour. *Journal of Ecology* 72:241–250.

- Hoffmann, W.A. and Solbrig, O.T. 2003. The role of top kill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180:273–286.
- Huang, Y.F., Kuan, W.H., Chiueh, P.T. and Lo, S.L. 2011. Pyrolysis of biomass by thermal analysis–mass spectrometry (TA–MS). *Bioresource Technology* 102:3527–3534.
- Kobziar, L., Moghaddas, J. and Stephens, S. L. 2006. Tree mortality patterns following prescribed fires in a mixed conifer forest. *Canadian Journal of Forestry Research* 36.
- Kozlowski, T.T. (ed). 1971. *Physiological Ecology: Growth and Development of trees*. New York: Academic press.
- Kurz, W.A., Dymond, C.C., Stinson, G. and Rampley, G.J. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990.
- Klyosov, A.A., 2007. *Wood-Plastic Composites*. John Wiley & Sons, Inc., New Jersey.
- Larson, P.R. 1994. *Springer Series in Wood Science: The Vascular Cambium. Development and Structure*. Springer-Verlag, Berlin.
- Lawes, M.J., Richards, A., Dathe, J. and Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212:2057–2069.
- Levitt, J. 1980. *Responses of plants to environmental stresses. Vol. I: chilling, freezing, and high temperature stresses*, 2nd edn. Academic, New York.
- Lloret, F., Keeling, E.G. and Sala, A. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920.
- Lonsdale, W.M. and Braithwaite, R.W. 1991. Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* 16:363–374.
- Martin, R.E. 1963. Thermal properties of bark. *Forest Products Journal* 3:419–426.
- Matisons, R. and Dauškane, I. 2009. Influence of climate on earlywood vessel formation of *Quercus robur* at its northern distribution range in central regions of Latvia. *Acta Universitatis Latviensis* 753, 49–58.
- Matthew, B.D. and Johnson, E.A. 2004. Temperature-dependent rate models of vascular cambium cell mortality. *Canadian Journal of Forest Research* 34:546–559.
- McCloskey, S.P.J., Daniels, L.D. and McLean, J.A. 2009. Evaluation of the role of climate in driving western hemlock looper outbreaks. *Northwest Science* 83:225–238.

- McHugh, C.W., Kolb, T.E. and Wilson, J.L. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32:510–522.
- McInnis, L.M., Oswald, B.P., Williams, H.M., Farrish, K.W. and Unger, D.R. 2004. Growth response of *Pinus taeda* L., to herbicide, prescribed fire, and fertilizer. *Forest Ecology and Management* 199:231–242.
- Michaletz, S.T. and Johnson, E.A. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22:500–515.
- Miranda, A.C., Fatima, O.D. and Ferreira, S.D. 1993. Soil and air temperatures during prescribed cerrado fires in central Brazil. *Journal of Tropical Ecology* 9:313–320.
- Morrison, D.A. 1995. Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of NSW* 115:109–119.
- Murphy, B.P., Smith, J.R. and Priors, L.D. 2010. Frequent fires reduce tree growth in northern savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16:331–343.
- Mutch, L.S. and Parsons, D.J. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. *Forest Science* 44:341–355.
- Newton, C.A. 2007. *Forest ecology and conservation. A handbook of techniques.* Oxford university press, Oxford.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148-160.
- Nikolova, P., Blaschke, H., Matyssek, R., Pretzsch, H. and Seifert, T. 2009. Combined application of computer tomography and light microscopy for analysis of conductive xylem area of beech and spruce coarse roots. *European Journal of Forest Research* 128(2):145 – 153.
- Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*. Available at DOI: 10.1016/j.foreco.2010.07.054[October 2014].
- Odhiambo, B.O., Meincken, M. and Seifert, T. 2014. The protective role of bark against fire damage: a comparative study on selected introduced and indigenous tree species in the Western Cape, South Africa. *Trees* 28(2):555-565.

- O'Donnell, A.J., Cullen, L.E., McCaw, W.L. and Boer, M.M. 2010. Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. *Dendrochronologia* 28:37–48.
- Pausas, J. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science* 8:703–706.
- Pereira, H., Graca, J. and Rodrigues, J.C. 2003. Wood chemistry in relation to quality. In: Barnett, J.R., Jeronimidis, G. (Eds.). *Wood Quality and its Biological Basis*. Blackwell Publishing, Oxford pp 53–83.
- Peterson, D.L. and Ryan, K.C. 1986. Modeling post-fire conifer mortality for long-range planning. *Journal of Environmental Management* 10:797–808.
- Peterson, D.L., Sackett, S.S., Robinson, L.J. and Haase, S.M. 1994. The Effects of Repeated Prescribed Burning on *Pinus ponderosa* Growth. *International Journal of Wildland Fire* 4(4) 239 – 247.
- Pinard, M.A. and Huffman, J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* 13:727–740.
- Poorter, L. and Hayashida-Oliver, Y. 2000. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology* 16:481–498.
- Pretzsch, H., Schütze G. and Uhl, E. 2012. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology* 15, 483–495.
- Pyne, S. J., Andrews, P. L. and Laven, R. D. 1996: *Introduction to Wildland Fire*. (2nd ed.). USA: John Wiley & sons.
- Raison, R.J. and Myers, B.J. 1992. The biology of forest growth experiment: linking water and nitrogen availability to growth of *Pinus radiata*. *Forest Ecology and Management*, 52: 279–308.
- Reifsnyder, W.E., Herrington, L.P. and Spalt, K.W. 1967. Thermophysical properties of bark of shortleaf, longleaf, and red pine. Bulletin no. 70. School of Forestry, Yale University, Yale.
- Rego, F. 2005. General introduction to forest fires in the Mediterranean environment. *Mediterranean Forests* 26(3):204-206.
- Richardson, D.M. 1998. Forestry trees as invasive aliens. *Conservation Biology* 12:18–26.

Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* mill. and *Pinus pinea* L. *Plant Ecology* 171:139–151.

Rogerson, P.A. 2001. *Statistical methods for geography*. Sage, London.

Rötzer, T., Seifert, T., Gayler, S. and Priesack, E. 2012. Effects of stress and defence allocation defence on tree growth: simulation results at the tree and stand level. In: Matyssek R, Schnyder H, Ernst D, Munch J-C, Pretzsch H (eds) *Growth and defence in plants: resource allocation at multiple scales*. *Ecological studies* 220. Springer, Heidelberg, pp 401–432.

Rowell, R.M., 2005. *Handbook of Wood Chemistry and Wood Composites*. CRC Press, Madison, USA.

Rozas, V., Gonzalo, P.D.L., Ignacio, G.G. and Jose, R.A. 2011. Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25:895–905.

Ryan, K.C. and Reinhardt, E.D. 1988. Predicting post-fire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:291–1297.

R Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, version 2.15.1. Vienna, Austria. <http://www.R-project.org>

Safranyik, L., Shrimpton, D.M. and Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. In D.M. Baumgartner (Ed.) *Management of lodgepole pine ecosystems*. Pullman, WA, Washington State University Cooperative Extension, 406–428 pp.

Sanchez-Silva, L., López-González, D., Villaseñor, J., Sánchez, P. and Valverde, J.L. 2012. Thermogravimetric–mass spectrometric analysis of lignocellulosic and marinebiomass pyrolysis. *Bioresource Technology* 109: 163–172.

Schabenberger, O. and Pierce, F.J. 2002. *Contemporary statistical models for the land and soil sciences*. Taylor and Francis, New York.

Schoennagel, T., Turner, M.G. and Romme, W.H. 2003. The influence of fire interval and serotiny on post-fire lodgepole pine density in Yellowstone National Park. *Ecology* 84:2967–2978.

Schoonenberg, T., Pinard, M. and Woodward, S. 2003. Responses to mechanical wounding and fire in tree species characteristic of seasonally dry tropical forest of Bolivia. *Canadian Journal of Forest Research* 33:330–338.

Schweingruber, F.H. 1988. *Tree rings: Basics and applications of dendrochronology*. Dordrecht, Holland: Reidel Publishing company.

Schweingruber, F.H. 1993. *Trees and Wood in Dendrochronology*. Springer-Verlag Berlin Heidelberg, Berlin.

Schweingruber, F.H. 2007. Tree-ring measurements of *Picea mariana* (Black spruce) from sample QUEBEC-382. Swiss Federal Institute for Forest, Snow and Landscape Research, available online, DOI: 10.1594/PANGAEA.597213.

Seifert, T., Nickel, M. and Pretzsch, H. 2010. Analysing the long-term effects of artificial pruning of wild cherry by computer tomography. *Trees* 24(5):797-808.

Simkin, R. and Baker, P.J. 2008. Disturbance history and stand dynamics in tall open forest and riparian rainforest in the Central Highlands of Victoria. *Austral Ecology* 33: 747–760.

Smith, D.M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. Forest Products Laboratory, Forest Service, U. S. Department of Agriculture.

South Africa. 2011. Report on Commercial Timber resources and primary round wood processing in South Africa. Forest economic services: Pretoria.

Stahlea, D.W., Mushoveb, P.T., Cleavelanda, M.K. and Roigc, F. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* 124:217-229.

Stephens, S.L. and Finney, M.A. 2002. Prescribed fire mortality of sierra nevada mixed conifer tree species: effects of crown damage and forest floor consumption. *Forest Ecology and Management* 162:261–271.

Stone, E.L. 1944. Effect of fire on taper of longleaf pine. *Jour. Forestry* 42: 607.

Swezy, M.D. and Agee, J.K. 1991. Prescribed-fire effects on fineroot and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21:626–634.

Thies, W.G., Westlind, D.J., Loewen, M. and Brenner, G. 2006. Predicting delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. *International Journal of Wildland Fire* 15, 19–29.

- Thomas, F.M., Blank, R. and Hartman, G. 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology* 32, 277–307.
- Thonicke, K., Venevsky, S., Sitch, S. and Cramer, W. 2001. The role of fire disturbance for global vegetation dynamics: coupling Dynamic Global Vegetation Model. *Global Ecology and Biogeography* 10:661–667.
- Uhl, C. and Kauffman, J.B. 1990. Deforestation, fire susceptibility and potential tree responses to fire in the eastern Amazon. *Ecology* 71:437–449.
- Vaganov, E.A., Hughes, M.K., Silkin, P.P and Nesvetailo, V.D. 2004. The Tunguska Event in 1908: Evidence from Tree-Ring Anatomy. *Astobiology* 4(3):391 – 399.
- van Mantgem, P.J. and Schwartz, M. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *Forest Ecology and Management* 178:341–352.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C. and Daniels, L.D. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.
- VanderWeide, B.L. and Hartnett, D.C. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261:1530–1538.
- van Wilgen, B.W. 1982. Some effects of Post-Fire Age on the Above- Ground Plant Biomass of Fynbos (macchia). *Journal of Ecology* 70:217–225.
- van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78, 210-222.
- Vega, J., Jimenez, E., Vegab, D., Ortizb, L. and R.Pérez, J. 2010. *Pinus pinaster* Ait. Tree mortality following wildfire in Spain. *Forest Ecology and Management* available online, DOI: 10.1016/j.foreco.2010.10.019
- Vines, R.G. 1968. Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16:499–514.
- Vines, R.G. 1981. Physics and chemistry of rural fires. In: Gill AM, Groves RH, Noble IR (eds). *Fire and the Australian biota*. Australian Academy of Sciences, Canberra, pp 129–150.

- von Richter, L., Little, D. and Benson, D.H. 2005. Effects of low intensity fire on the resprouting of the weed African Olive (*Olea europaea* subsp. *cuspidata*) in Cumberland plain woodland, western Sydney. *Ecological Management and Restoration* 6:230–232.
- Wade, D.D. and Ward, D.E. 1975. Management decisions in severely damaged stands. *Journal of Forestry* 73, 573-577.
- Wallin, K.F., Kolb, T.E., Skov, K.R. and Wagner, M.R. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in Northern Arizona. *Environ. Entomol* 32, 652–661.
- Walters, M.B. and Reich, P.B. 1999. Research review. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist* 143:143–154.
- Werner, P.A., Cowie, I.D. and Cusack, J.S. 2006. Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia. *Australian Journal of Botany* 54:283–296.
- Werner, P.A. 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees: an experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30:625–647.
- Wesolowski, A., Adams, M.A. and Pfautsch, S. 2014. Insulation capacity of three bark types of temperate Eucalyptus species. *Forest Ecology and Management* 313: 224–232.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R. and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943.
- Whelan, R.J. 1995. *The ecology of fire*. Cambridge university press, Cambridge.
- Wicht, C.L. 1971. The Task of Forestry in the Mountains of the Western and Southern Cape Province. *Proceedings of the Annual Congress of the Grassland Society of South Africa* 6:20–27.
- Williams, R.J., Cook, G.D., Gil, A.M. and Moore, P.H.R. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 30:50–59.
- Woodman, M. and Rawson, R. 1982. *Fuel Reduction Burning in Radiata Pine Plantations*. Res. Rep. No. 14. Victoria: Department of Conservation and Environment, Fire Management Branch.



Wooldridge, J.M. 2000. Introductory econometrics: a modern approach. South Western College, p 824.

zu Castell, W., Schrödl, S. and Seifert, T. 2005. Volume Interpolation of CT Images from Tree Trunks. *Plant Biology* 7:737 – 744.