

**THE SPATIAL DIMENSIONS
OF SAVANNA FIRE ECOLOGY
IN KRUGER NATIONAL PARK, SOUTH AFRICA**

A Thesis presented to
the Faculty of the Graduate School
at the University of Missouri

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Biological Sciences

by
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DEC 2015

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THE NESTED SPATIAL DIMENSIONS
OF SAVANNA FIRE ECOLOGY IN KRUGER NATIONAL PARK, SOUTH AFRICA

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ACKNOWLEDGMENTS

I would like to thank Dr. Ricardo Holdo for his support and guidance throughout this process, as well as the rest of my committee. I would also like to thank Navashni Govender and the staff at Kruger National Park for their assistance during my field research. The friendship and camaraderie of Tucker 2nd floor has provided a home for me here in Columbia, and has made this whole process much easier. I would also like to thank Moose, the medium brown dog who taught me to never leave food within reach but out of sight. Lastly, I would not be here without the love and support of my partner, Katie, my parents, and my brother. Thank you.

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ABSTRACT

Savannas are thought to be bistable with forests potentially occurring above 650 mm yr⁻¹ of Mean Annual Precipitation (MAP) due to the limiting effects of fire on tree cover. This is predicated on two assumptions: 1) fires increasingly limit woody cover in more mesic (≥ 650 MAP) savannas and 2) increasing tree cover produces feedbacks that reduce fire intensity. These assumptions are investigated in a spatially explicit framework. We use Kruger National Park (KNP), South Africa as our study system, in part due to the wide range of frequency of fires, the large variation in natural communities and rainfall, and the large body of previous research for comparisons and modeling efforts. To investigate whether tree cover produces feedbacks on fire intensity, we measured fire behavior as a function of grass fuel load and woody cover in experimental burns within KNP. We found weak but positive relationships (not negative, as assumed) between woody cover and fire intensity, independent of grass fuel load, and no relationship between tree cover and grass fuel load. At a landscape scale, we modeled the factors predicted to drive fire severity in KNP. We observed that fireline intensity is a strong predictor of many estimations of fire severity in small fires, but across larger fires, rainfall and woody cover likewise can predict impacts on herbaceous consumption and woody cover, respectively. Lastly, to investigate whether trees escape fire less often in more mesic savannas, we used a stochastic model parameterized with real data. After a review of published growth rates, we modeled fire escape probability using mean annual precipitation, fire frequency, and fireline intensity values across KNP. When accounting for species turnover across rainfall gradients, we found a nearly flat relationship between the

probability of individuals escaping fire and rainfall. Our research challenges two key assumptions for fire-mediated bistability of mesic savannas.

Chapter 1

Introduction

1.1 Savanna Fire Ecology

The presence and associated functions of trees are a fundamental structural component of terrestrial ecosystems (Brudvig and Asbjornsen, 2009; Hoffmann et al., 2012). In savannas, which are intermediate between fully tree-dominated forests and tree-free grasslands, an additional (and related) challenge is posed by the issue of tree-grass coexistence. Briefly, the failure of trees or grasses to completely exclude the other in savannas remains poorly understood (Sankaran et al., 2005; Sarmiento, 1984; Sankaran et al., 2004; Scholes and Archer, 1997). Furthermore, the spatial distribution of most terrestrial biomes can be predicted from climatic and soil variables, but savannas challenge this model, often occurring where forests and grasslands are predicted (Bond, 2005, 2008; Whittaker, 1975).

1.1.1 Bistability of Mesic Savannas

In general, tree cover in savannas increases with rainfall up to 650 mm yr^{-1} , where it saturates at 80% (Sankaran et al., 2005; Staver et al., 2011b). Below 650 mm yr^{-1} , maximum tree cover in savannas is thought to be resource limited (Sankaran et al., 2005). Water limitation improves competitiveness of grasses relative to the more water-demanding trees. Additionally, fire frequency and intensity, which are related to grass availability (Govender et al., 2006a), are reduced by the overall lower productivity of the grasses in these drier savannas. This reduction in fire frequency and intensity is thought to reduce the ability for fires to constrain woody cover (Sankaran et al., 2005).

Savannas are thought to be bistable with forests above 650 mm yr^{-1} (Sankaran et al., 2005; Staver et al., 2011b). Increases in rainfall, and thus soil water, are thought to reduce competition for soil water between trees and grasses. This increases overall grass productivity (Govender et al., 2006a) and, potentially, tree growth rates (Higgins et al., 2000). This increasing grass productivity allows both more frequent and intense fires and greater herbivore biomass, which in turn constrain tree cover (Sankaran et al., 2005; Staver et al., 2011b). In the absence of fire, trees are thought to be no longer constrained and quickly “fill in” a savanna, resulting in a conversion to forest (Staver et al., 2011b; Sankaran et al., 2005). This process is thought to be accelerated by proposed feedbacks from increasing tree cover, which could reduce the ability for fire to spread either through increases in grass fuel moisture (Hoffmann et al., 2011) or reductions in grass fuel load (Scholes and Archer, 1997).

Mechanistically, fire in savannas is believed to limit recruitment of woody species through the top-killing (aboveground mortality) of seedlings and saplings (Hanan

et al., 2008; Higgins et al., 2000; Scholes and Archer, 1997). The top-killed trees may be suppressed by subsequent fires for many years, despite resprouting back following each fire event (Higgins et al., 2000). Grass production during the growing season produces a large, roughly contiguous fuelscape during the dry season, which helps propagate frequent fires. During periods of diminished fire activity, some trees are able to grow sufficiently to escape the so-called “fire trap”, characterized by this cycle of resprouting followed by topkill (Laris, 2008; Scholes and Archer, 1997). Tree survival is thus linked to stochastic events such as fire occurrence and deterministic traits such as tree size and bark thickness (Higgins et al., 2000; Lawes et al., 2011). Fire may therefore provide a mechanism for the coexistence of trees and grass by favoring herbaceous species at the expense of woody species. This process continues until variations in the fire regime provide opportunities for trees to grow sufficiently to survive a fire (Hoffmann et al., 2012; Scholes and Archer, 1997).

1.1.2 Assumptions of Bistability

The concept of bistability of “wetter” savannas ($\geq 650 \text{ mm yr}^{-1}$) is predicated on two key assumptions: 1) the ability for trees to escape fire is reduced with increasing rainfall and 2) trees produce feedbacks to reduce fire intensity around them. The initial contention is predicated on an assumption that increasing frequency or intensity of disturbance, particularly fire, overwhelms the ability for trees to effectively escape these constraints. However, studies of the long term Experimental Burn Plots at Kruger National Park, South Africa, which span the gradient between xeric and mesic savannas, show unclear relationships between woody cover and fire frequency (Higgins et al., 2007). Furthermore, tree growth rates may increase in response to

rainfall (*i.e.*, as assumed in Higgins et al., 2000), which could potentially offset the parallel effects of increasing disturbance.

The second assumption is likewise understudied: at the local scale, the spatial dynamics of tree-grass-fire interactions have not been well characterized, and these have been suggested by modeling studies to have profound qualitative effects on tree dynamics (Calabrese et al., 2010; Hochberg et al., 1994b; Holdo, 2007; Jeltsch et al., 1996). Trees can both negatively and positively affect grass productivity in savannas at various scales (Belsky, 1994; Belsky et al., 1993; Riginos, 2009; Riginos et al., 2009; Riginos and Grace, 2008). Although once thought to only negatively impact production, the effects of trees on grass appear to be both species- and rainfall-dependent, as well as influenced by whether the trees are grouped or not (Belsky, 1994). Grass production in more xeric sites appear to benefit more from trees than in more mesic sites (Belsky et al., 1993). This rainfall-linked neighborhood effect could contribute to variable tree survival by changing fire behavior through effects on fuel biomass and moisture.

1.2 Objectives

These assumptions are critical for our current understanding of bistability of mesic savannas, but have not been systematically studied in meaningful ways. This project will investigate these two key assumptions through a spatially explicit framework.

Specifically, we propose to:

1. At the local scale, investigate how tree neighborhoods may affect fire intensity.

If we observe reduced fire behavior around trees, this supports the prevailing

narrative that trees produce feedbacks to reduce fire intensity in savannas.

2. At the landscape scale, identify drivers of categorical fire severity using fire occurrence records and experimental fire data. Fire severity is the ecological effect of a fire, and is often – but not always – linked to fireline intensity (Keeley, 2009a). We will use expert assessments of fire severity and model what variables predict these assessments. This can help identify drivers of fire severity in southern African savannas, which to date have not been investigated meaningfully.
3. At the regional scale, model the relationship between three rainfall-linked processes: tree growth, fire frequency, and fire intensity. All three are often described as increasing with mean annual precipitation, but this is counter-intuitive to the observed increase in woody cover at higher rainfall sites (Sankaran et al., 2005). Modeled decreases in probability of escape with higher rainfall would support the hypothesis that fire is more important at maintaining savanna tree / grass coexistence in wetter savannas. Likewise, these models can improve our understanding of what factors really matter in escaping the “fire trap.”

1.2.1 Study System

Landscape of Kruger National Park

Kruger National Park serves as an ideal study system for questions of savanna fire ecology. Kruger NP is located in eastern South Africa, sharing its eastern borders with Mozambique and northern border with Zimbabwe. The park is over 2 million ha,

and spans 350 km from north to south. To the west are a series of game reserves, both public and private (Wolmer, 2003). A north-south rainfall gradient spans the park, peaking at 800 mm yr^{-1} in the southwest and $\leq 400 \text{ mm yr}^{-1}$ at Pafuri in the northeast (Wolmer, 2003). The parks soils vary in productivity based on their parent material: in the west, low fertility granite, and to the east, high fertility basalt (Wolmer, 2003).

Fire Management in Kruger National Park

Fire is common in Kruger NP, and much of it is anthropogenic in origin (van Wilgen et al., 2003). Fires vary in seasonality, intensity, and frequency, and are used by Kruger NP managers to meet specific and general objectives (Govender, 2003; Govender et al., 2006a). Kruger NP is the site of a long-term fire experiment in which plots located across the park are burned at varying frequencies and seasons (Biggs et al., 2003).

Chapter 2

Tree Neighborhood Effects on Fire Intensity and Behavior

2.1 Introduction

Savannas are a terrestrial biome comprised of a discontinuous overstory of trees and a continuous understory of grasses (Scholes and Archer, 1997). Savannas are widespread, covering approximately 20% of the terrestrial surface. The mechanisms that control the coexistence of trees and grass in savannas remain contested, and are generally divided into two broad categories: top-down and bottom-up explanations (Scholes and Archer, 1997). The former argues that disturbances, primarily fire and herbivory, suppress tree recruitment from earlier life stages and periodically trap trees in a cycle of growth, topkill, and resprouting (Scholes and Archer, 1997). The latter argues that root-niche partitioning allows for coexistence between trees and grasses due to differential rooting depth (Ward et al., 2012). Grass-driven surface fires are

frequent in savannas, affecting tree demography by introducing size-class bottlenecks through topkilling of woody stems (Lawes et al., 2011; Higgins et al., 2000). Fires vary in size, frequency, and intensity (Govender et al., 2006a; Archibald et al., 2010b,a). In southern African savannas, fire frequency and intensity increase with mean annual precipitation due to increased grass production throughout the year, contributing to a highly flammable, continuous fuel bed (Govender et al., 2006a). Fire frequency and intensity are often used to explain how tree densities vary across rainfall gradients (Govender et al., 2006a). In wetter savannas ($\geq 650 \text{ mm yr}^{-1}$), fire may suppress tree cover that would otherwise “fill in” to convert savannas into forests (Sankaran et al., 2005).

The majority of fire research in African savannas has focused on meso- and macro-scale measurements of fire intensity (Trollope and Potgieter, 1985; Govender et al., 2006a). These measurements are primarily based on estimates of Byrams fireline intensity, which is an estimate of energy release along a flaming front (Byram, 1959). Byrams fireline intensity is useful for providing an estimate of absolute energy released from a given fire, but this method does not account for smaller spatial variation in intensity (Keeley, 2009b).

Local-scale variation in fire intensity has been shown to be an important factor in understanding fire effects on trees in frequent-fire environments. Small changes in the fuel microenvironments (structure, loading) increased shrub mortality in Pine savannas in the Southeastern US (Thaxton and Platt, 2006), while changes in fire type (backing vs. head fires) also affected resprouting vigor of fire-adapted oak seedlings in the same region (Hmielowski, Unpublished Data 2014). Changes in fuel structure, such as clusters of trees, can also reduce downwind fire intensity by reducing available

oxygen (van Langevelde et al., 2014). Burn patchiness and fire severity, a measure of ecological impact, were found to be related to fire season and vegetation structure in tropical savannas in Australia (Heward et al., 2013).

Implicit in our understanding of fire effects on trees and grass in savannas is a process of positive and negative feedbacks of canopy coverage on grass biomass. At high canopy coverage, trees are thought to reduce fire intensity and grass biomass in a neighborhood around them (Hoffmann et al., 2011, 2009). However, canopy coverage and tree density have shown to have both positive and negative effects on grass biomass (Belsky et al., 1993; Belsky, 1994; Belsky et al., 1989; Kalwij et al., 2010; Riginos et al., 2009). This relationship appears to be species specific, community specific, and density-dependent (Belsky et al., 1993). Because fire intensity in savannas is known to be highly responsive to available grass biomass, savanna trees may therefore, in principle, differentially either increase or decrease local fire intensity in a neighborhood around them. Some research has supported this (Holdo, 2005; van Langevelde et al., 2014; Gambiza et al., 2000), but for a process that is crucial to our understanding of how fire is thought to variably mediate tree / grass interactions in savannas, there is a startling lack of scholarship on this relationship.

Large-scale models predict bistability between forests and savannas, and this bistability is often described as being driven by negative feedbacks of trees on fire behavior, grass production, or both (Sankaran et al., 2005; Staver et al., 2011a; Higgins et al., 2000). However, these relationships have rarely been tested at the scale of the individual tree. Consequently, it remains unknown on what scale these feedbacks may occur and to what degree to they may pattern fire effects. Despite the acknowledged importance of understanding local-scale fire intensity variation, little is known about

it in southern African savannas. We investigate the scale of the effects of canopy on grass fuel load and fire intensity in southern African savannas by analyzing time-integrated temperature flux (an estimation of local intensity) and maximum observed fire temperatures within experimental prescribed fires in savannas at Kruger National Park, South Africa. Specifically, we asked: 1) How does fire intensity vary with canopy cover? 2) How does fire intensity vary at small spatial scales, independently of variation in grass biomass?

Addressing these questions will improve our understanding of the factors governing spatial controls on fire intensity in savannas, and thus the conditions that affect the feedbacks that may control tree cover in savannas.

2.2 Methods

2.2.1 Study Site

Research was conducted in Kruger National Park, South Africa, a savanna ecosystem on the eastern border of South Africa (Mabunda et al., 2003). Mean annual precipitation varies across the park: in the south, rainfall exceeds 750 mm y^{-1} , while it is as low as 450 mm y^{-1} in the northern portion of the park. The western half of the park has granitic soils and the eastern half has basaltic. These variations in rainfall and soil fertility contribute to variation in savanna plant communities and fire frequency (Smit et al., 2013). Savannas in Kruger experience multiple interacting disturbances, including elephants, grazers, browsers, planned and unplanned fire, frost, and wind events (Mabunda et al., 2003).

In Kruger, a long-term fire experiment has been conducted since 1954 (Biggs et al., 2003). The experiment, known as the Kruger Experimental Burn Plots, manipulates the season and frequency of prescribed burns in four blocks distributed across the park. Plots are ~7 ha in size. Data for the current study were collected in plots with annual and biannual August burns, before and immediately after burns occurred over the period 2012-2014 (Table 2.1 and fig. 2.1). We focused on late dry season fires (*i.e.*, August, October) because these most resemble the higher intensity fires we were interested in (Govender et al., 2006a).

2.2.2 Experimental Design

Our unit of analysis was a subplot (roughly 1 m²) in which we placed temperature sensors and collected data on grass fuel load and canopy cover. We also used these as the focal point for assessing woody cover at three neighborhood sizes. Subplots (so-named to reduce their confusion with the Experimental Burn Plots) were located within each of the plots. The number of subplots per site varied based on the field season and between sites due to availability of temperature sensors. At the corner of each Experimental Burn Plot, 100-m transects with random starting bearings between 0-90 were extended. Along these semi-randomized transects, subplots were placed at 10-m intervals, with the assumption that autocorrelated fire behavior would be reduced at this distance; available temperature sensors were evenly distributed between subplots. Earlier burn trials had fewer subplots due to limitations on the number of available temperature sensors (Table 2.1). Previous research has suggested that roads have substantive impacts on vegetation and fire behavior (Smit and Asner, 2012). To reduce potential edge effects of the firebreak, 15-m buffers were applied to perimeter

roads before transects were established.

Within each subplot, grass fuel loads and canopy cover were quantified. Grass fuel loads were measured using a disc pasture meter calibrated for Kruger National Park (Zambatis et al., 2006). Four disc pasture meter values were sampled in cardinal directions around each temperate sensor and mean grass biomass was calculated. Trials from the first field season included clipped and dried grass samples; these data were transformed to the same unit of g m^{-2} as the disc pasture meter results. Disc pasture meter values are calibrated to clipped grass biomass, and are effectively interchangeable ($r=0.979$, $r^2=0.951$, $P < 0.0005$, Zambatis et al. 2006). Four canopy cover values were recorded at right angles to each other using a crown densitometer (Forestry Suppliers, Jackson, MS, USA) and mean crown cover values (0 – 100%) calculated.

Because it was unclear at what scale the potential feedbacks of trees on fire might occur at, we included additional neighborhoods analyses of woody cover. We assessed tree neighborhoods at varying distances around each subplots. Aerial images were collected from Google Earth to maximize visible contrast of woody cover at each Experimental Burn Plot (Goo, 2015). Tree canopies were defined using a binary tree / no tree supervised classification in ArcGIS 10.2 (ESR, 2015). For each subplot, percent tree cover was calculated for 10, 20, and 30 m^2 neighborhoods by summing percent of woody cover in that radius around each subplot (TC_10, TC_20, and TC_30, respectively).

Prior to planned prescribed burn, temperature sensors were deployed. iButton temperature sensors were placed within stainless steel pipes (30 cm long by 5 cm in diameter). The setup consisted of an iButton integrated datalogger and temperature

sensor (Model DS1922T, Maxim Integrated, San Jose, CA, USA) placed inside a sand-filled galvanized steel pipe. The iButtons were placed on top of the sand, top side up, with care taken to make sure it is centered within the pipe. More sand was poured over the iButton to provide additional insulation, filling the pipe to the brim. The sand provided insulation for the sensor while the metal provided a conductor for radiant and convective heat. These pipes were placed within the grass sward and buried vertically 5 cm into the ground, leaving 25 cm above ground. iButtons were placed 5 cm below the top of the pipe and covered with sand. Sand was collected on site and sifted through a 5 mm sieve. Temperature values were collected every five seconds during the planned controlled burns. Data were downloaded in the field following the fires.

The insulated pipe and iButton sensor package was conceptually similar to the deployment of iButtons during fires used by Thom et al. (2015), which capture reliable measurements of fire temperatures. We acknowledge the difficulties of capturing fire temperature data reliably, but note that similar work in savanna systems have successfully deployed and interpreted fire metrics using various tools for measuring temperature or intensity (Ellair and Platt, 2013; Iverson et al., 2004; Engle et al., 1989; Thaxton and Platt, 2006; Gagnon et al., 2015; Ryan, 2011; Thom et al., 2015).

Fire temperature time series were collected at 5-s resolution. We calculated three temperature metrics per fire that were compatible with other studies on fire intensity: maximum recorded temperature above (*i.e.*, Gagnon et al., 2015; Ryan, 2011; Thom et al., 2015), time duration between the onset of observed temperature change and the peak (duration, Gagnon et al. 2015), and the partial differential between onset of fire temperature change and the peak (Engle et al., 1989; Thom et al., 2015). Onset of

the fire was identified by analyzing fire temperature time series per plot and selecting values above visually identified critical background temperature. Recorded ambient air temperature for each fire was subtracted from all temperature values to calculate a temperature flux value for the variables *maxTemp* and *sumTemp*.

2.2.3 Statistical Analyses

Our analysis sought to test for the effects of tree canopies on fire behavior variables, maximum temperature, duration, and temperature sum, independent of grass fuel loads. Response variables and grass fuel load were log transformed to meet the assumptions of linearity. Linear mixed effects models were fit to the data using the *nlme* package (Pinheiro et al., 2012). Due to highly variable nature of fires, each plot, and thus each individual burn, was treated as having a random effect on the calculated intercepts. For each temperature metric, we fit models with fixed effects of grass fuel load (GFL), canopy coverage (CC), the additive effects of grass fuel load and canopy coverage (GFL + CC), and the same interactions using the tree canopy neighborhoods (TC-10, TC-20, TC-30). We also tested what, if any, of our variables might explain grass fuel loads around trees to test for a possible mechanism whereby tree cover may drive observed relationships with fire. All models were fit using maximum likelihood. AIC was used for model selection. Because subplots vary in terms of distance to each other, and because of potential about spatial autocorrelation in fire behavior, we had concerns about potential non-independence of model components. We first fit models that assumed independence among subplots, and tested model residuals using the *ncf* R package (Bjornstad, 2013). The various lag distances per site were calculated using Sturges Rule (Legendre and Legendre, 2012). Had a large number of models (≥ 3)

shown evidence of significant spatial autocorrelation, we would have fit Generalized Least Squares (GLS) models, but this was unnecessary. We did not fit GLS models initially because these models do not accommodate random effects.

2.3 Results

Deployed iButtons had an 86.9% success rate (temperature - time values were recovered post-fire) at capturing temperature data during fires. In three fires, programmed start time of data logging occurred after the ignition had taken place (Table 2.1). Experimental burns were considered within the normal range of variation by the fire management personnel on site, with relative humidities ranging between 20.5% – 88.0% and wind speeds ranging between 0.61 – 3.2 m s⁻¹.

2.3.1 Canopy Coverage and Woody Cover

Canopy cover from the densitometer and woody cover from aerial imagery varied by subplot and site (Figure 2.2). Aerial imagery was not of sufficient quality (low spatial resolution for all published years) to calculate neighborhood woody cover for Lindanda 4 and Mooiplaas 5 (Figure 2.2).

2.3.2 Grass Fuel Load

There was substantial variation in canopy coverage, woody cover, and grass fuel loads between plots (Figures 2.2 and 2.3). No model explained grass fuel load (log transformed) better than a null model, suggesting no clear relationship between canopy

cover or woody cover and grass cover at the scales examined.

2.3.3 Maximum Temperatures

Maximum temperatures varied with canopy coverage, grass fuel load, and canopy neighborhood (Figure 2.4). Maximum temperature values were best explained by a model including both woody canopy neighborhoods at 20 meters (TC_20) and log Grass Fuel Load (TC_20 + GFL, Table 2.2). These relationships were positive (Table 2.3).

2.3.4 Duration

Fire durations varied with recorded variables (Figure 2.5). Neither grass fuel load (GFL) nor canopy coverage (CC) predicted fire duration better than a null model (Table 2.2). All of the models including woody cover neighborhoods (*e.g.*, TC_10) slightly performed better than a null model; the model with a 30 m neighborhood (TC_30) performed the best, although the low dAIC values make distinguishing among the models difficult. The best fit model showed a positive relationship between neighborhood woody cover and fire duration (Table 2.3).

2.3.5 Summed Temperatures

Like duration, neither models with grass fuel load nor canopy coverage explained summed temperatures better than a null model (Table 2.2). Ultimately, summed temperatures were best explained by models grass fuel load and 10 m tree canopy neighborhoods (GFL + TC_10, Tables 2.2 and 2.3 and fig. 2.6).

2.3.6 Random Effects

Residual standard errors of the random effects were higher than the residual errors for *maxTemp* (0.31 and 0.13, respectively) and *Duration* (0.73 and 0.32), and were roughly equal for *sumTemp* (0.59 and 0.56).

2.3.7 Spatial Autocorrelation

For the most part, spatial correlograms of raw fire response variables did not indicate significant spatial autocorrelation at the lag distances examined, although *maxTemp* and *sumTemp* from the two Biyamiti experimental burns did exhibit significant autocorrelation at lags less than 100 m (Figures A.1 to A.4). This autocorrelation in those plots was still apparent in the residuals of the best-fit models. No clear autocorrelation was apparent in measured duration or the residuals (Figures A.5 and A.6). This suggests that the treatment of subplots within plots as independent samples was reasonable.

2.4 Discussion

Many savanna dynamics models rely on an assumption that at greater canopy cover, the ability for fire to limit trees is suppressed either through reductions in grass production or an increase in fuel moisture, and that this (Higgins et al., 2000; Scholes and Archer, 1997; Sankaran et al., 2005). This is thought to create a feedback loop, in which increased tree cover produces reductions in fire intensity, which in turn supports more tree cover (Higgins et al., 2000; Scholes and Archer, 1997). To investigate this

claim, we measured fire behavior at various levels of grass biomass and canopy cover. We found that for our three fire metrics, variation was best explained by models that combined both grass fuel load and some measurement of woody cover (Table 2.2). These models always showed a positive relationship between grass fuel load, woody cover, and the fire metric (Table 2.3). This is contrary to the expectations of many savanna models, which would expect decreasing fire intensity with increasing woody cover at a local scale. Although others have established that grass biomass varies either positively (Belsky et al., 1989) with individual trees or negatively (Mordelet and Menaut, 1995) with woody cover, and that fire intensity varies substantially at both fine scales (Ryan, 2011) and downwind of woody patches (van Langevelde et al., 2014), we present evidence that links these processes in a novel way, showing that fire behavior likewise increases with both grass and, weakly, woody cover. Our models indicate a strong plot-level random effect that explains more variance than within-plot residual error, suggesting a great deal of stochastic within and between fires.

Maximum observed fire temperatures are often used as a comparative metric for linking fire behavior to fire effects (Gibson et al., 1990; Kimuyu et al.; Thom et al., 2015). Although our method, like others, does not capture an absolute fire temperature, but rather an index relative to the sensor system we used to measure the heat flux of the fire, our results are intriguing. We show positive relationships between woody cover and grass fuel load and fire metrics (Table 2.3). This does not support the negative feedbacks between trees and fire intensity often supposed (Higgins et al., 2000; Scholes and Archer, 1997).

Fire duration, or residence time, has been identified as a key driver of fire effects in many grassland and savanna systems (Gagnon et al., 2015; Engle et al., 1989;

Ryan, 2011). We show a disconnection between both grass fuel load, canopy coverage and fire duration (Table 2.2, Fig. 5). The positive relationship between tree canopy neighborhood and fire duration (Table 2.3) may be potentially driven by a decrease in stand wind speed, which decreases the rate of combustion and thus increases fire duration (Rothermel, 1972). Further research on how stand density and architecture may drive fire behavior dynamics could help our understanding of how fire behavior may feedback into driving savanna structure.

Partial summed temperature, or temperature-time, has likewise been identified as an important metric of fire severity and fire effects (Thom et al., 2015; Gagnon et al., 2015). All model fits are poorly distinguishable for partial summed temperature, although models that include grass fuel load and a tree canopy neighborhood value performed better than those without (Table 2.2). This positive relationship may be driven by greater amounts of larger size fuel particles in the understory as a result of greater canopy coverage. This process may be better understood through a more nuanced understanding of fire environment in savannas. Much of the previous research has focused on using grass fuel load as the primary explanatory variable of fire behavior, and thus fire effects, in southern African savannas (Trollope and Potgieter, 1985; Higgins et al., 2000; Govender et al., 2006a). However, larger size class (*i.e.*, 100-hr, 1000-hr, using Rothermel fuel size class distribution) fuels are found in Kruger National Park (personal observation); these larger fuels can contribute to smoldering combustion in lower intensity fires or even be directly consumed in higher intensity fires (Rothermel, 1972). This may explain the persistent spatial autocorrelation we observe in our results (Figures A.1 to A.6). More complex fuelbed modeling, such as fuel models that include particle size, may be able to better account for this variation

and better predict partial summed temperatures.

Like Moustakas et al. (2013) and February et al. (2013) who both also worked in KNP, we observe no strong relationship between grass biomass and woody cover or canopy coverage (Moustakas et al., 2013; February et al., 2013). Moustakas et al. (2013) did observe increasing grass biomass with tree height, which we did not measure. We know that grass species vary in flammability (Calitz et al., 2015). There may be associated grass species changes on sites with greater neighborhood canopy coverage. These species may be more or less flammable relative to those associated with lower neighborhood canopy coverage. Alternatively, just as savanna trees have positive effects on grass nutrition (Treydte et al., 2007), there could be additional effects of trees the on flammability of grasses. Additional research on variation in flammability of grass species, and how these species vary in space relative to other biotic and abiotic factors, could help better explain these dynamics.

Our research quantitatively investigates the relationship of tree cover with fire behavior in a southern African savanna. Previous research focused more on aggregate intensity metrics rather than understanding factors that may control local interactions. Because many processes of interest in savannas occur at the individual-level (*e.g.*, topkill, complete mortality, etc.), local-scale fire effects research is important for directly linking the fire behavior to these outcomes. We provide one of the first attempts at understanding how fire varies at the local scale in savannas. Our findings suggest that assuming negative feedbacks between trees and both grass fuel load and fire intensity. Future research in savanna fire effects must not only relate local-scale fire behavior to local-scale effects, but also to the larger scale processes (firing patterns, weather, climate, etc.) that may drive the distribution of these local effects.

At a coarse scale, we understand how fire affects tree mortality in savannas. We have quantitative models linking tree height, Byrnes fireline intensity, species, and probability of topkill (Higgins et al., 2012). However, our understanding of how fire behavior varies within a fire, the drivers of this variation, and in what way this may structurally pattern tree survival in savannas remains critically limited.

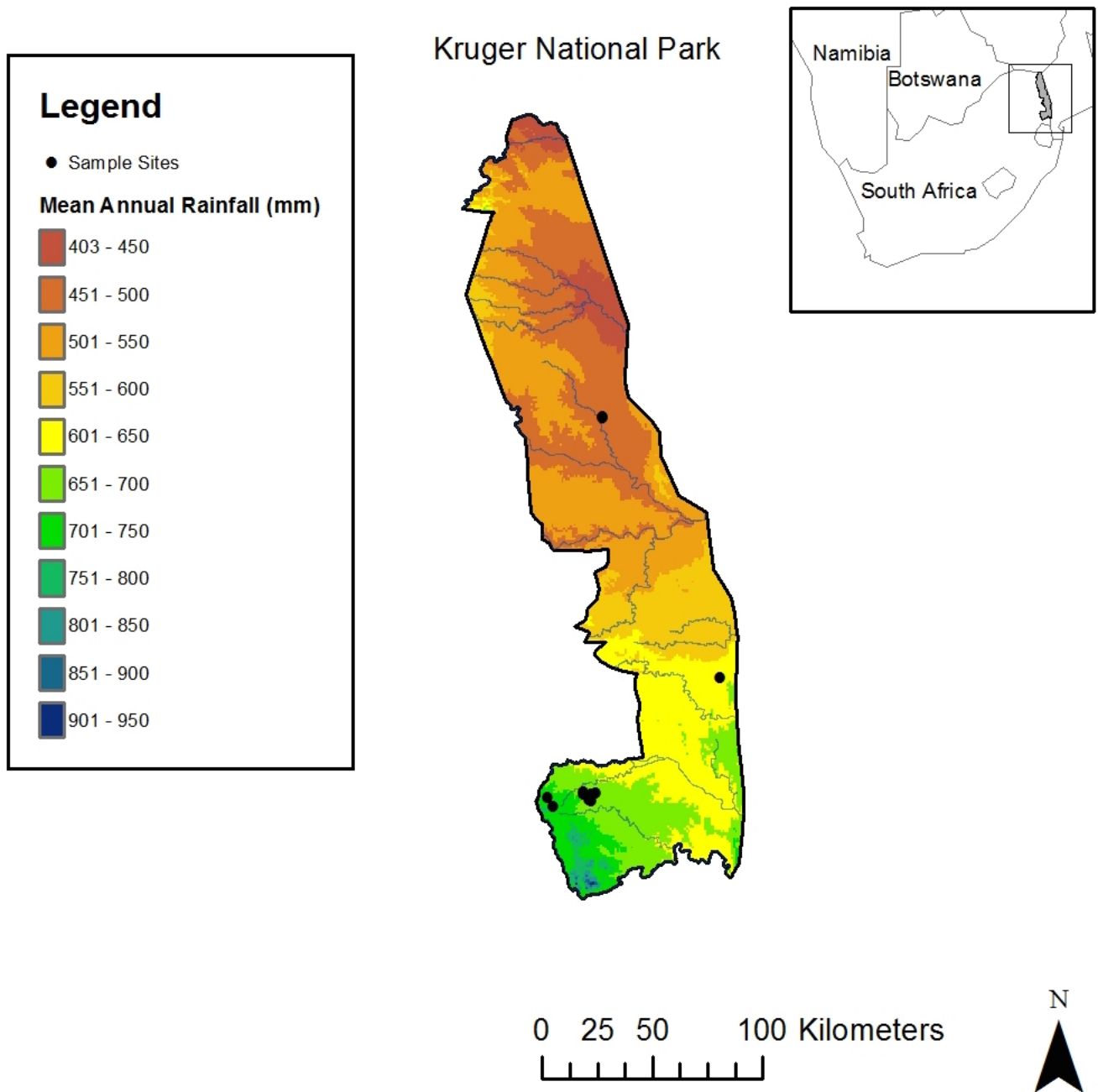


Figure 2.1: Locations of Experimental Burn Plots (EBPs) used in this study within Kruger National Park, South Africa. Mean annual precipitation from WorldClim.

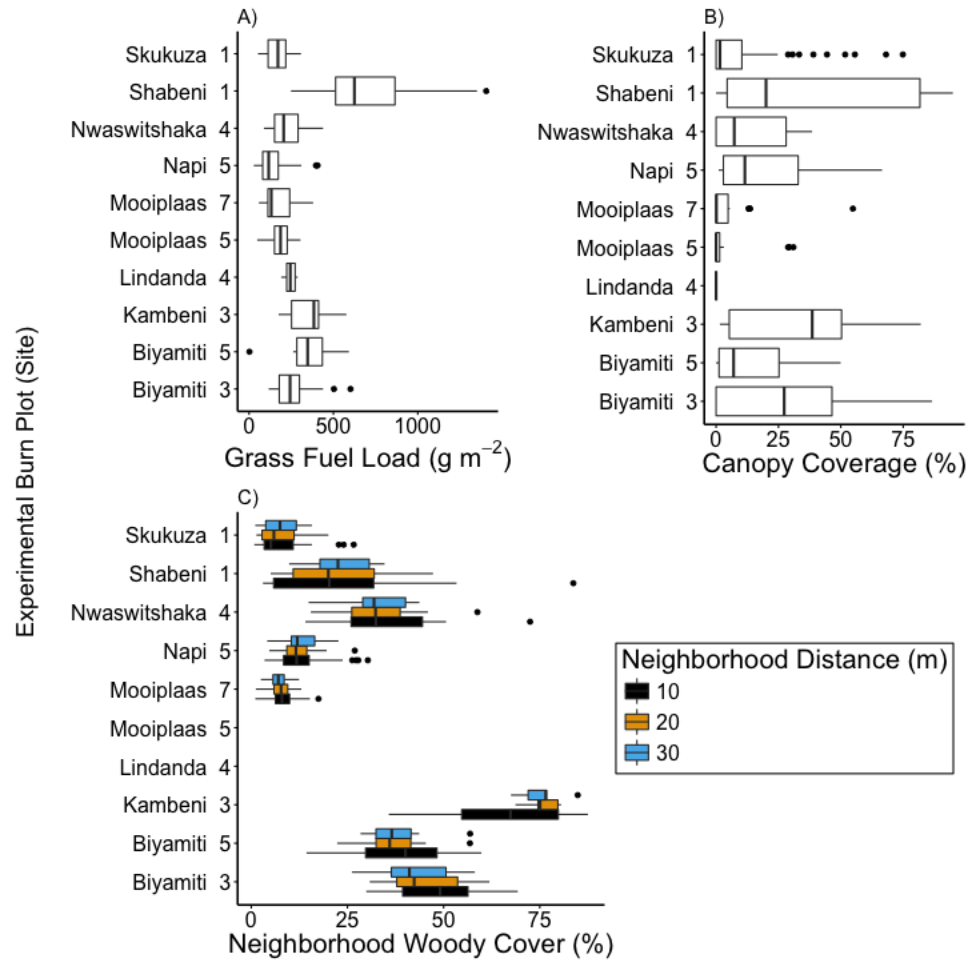


Figure 2.2: A) Grass Fuel Load, B) canopy cover as measured by crown densitometer at each subplot, and C) neighborhood woody cover at three distances from subplot centers across subplots within Experimental Burn Plots in Kruger National Park. Interior boxes represent first, second, and third quartiles. Lines extend to $1.5 \times \text{IQR}$. Outliers are plotted as points.

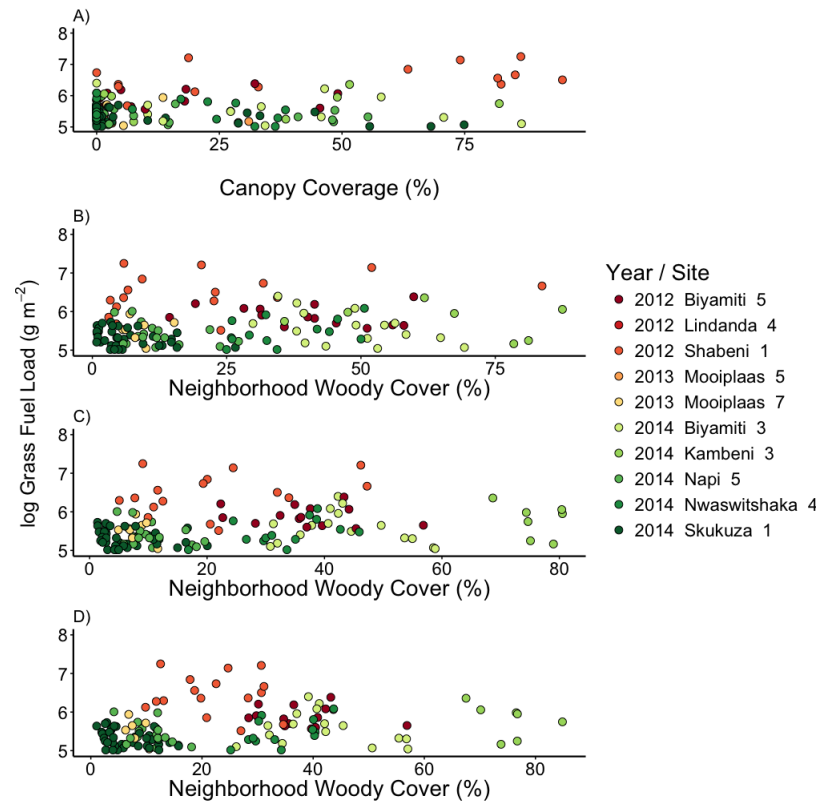


Figure 2.3: Relationship between log grass fuel load and A) canopy coverage, and the same relationship with woody cover at B) 10 m, C) 20 m, and D) 30 m neighborhoods.

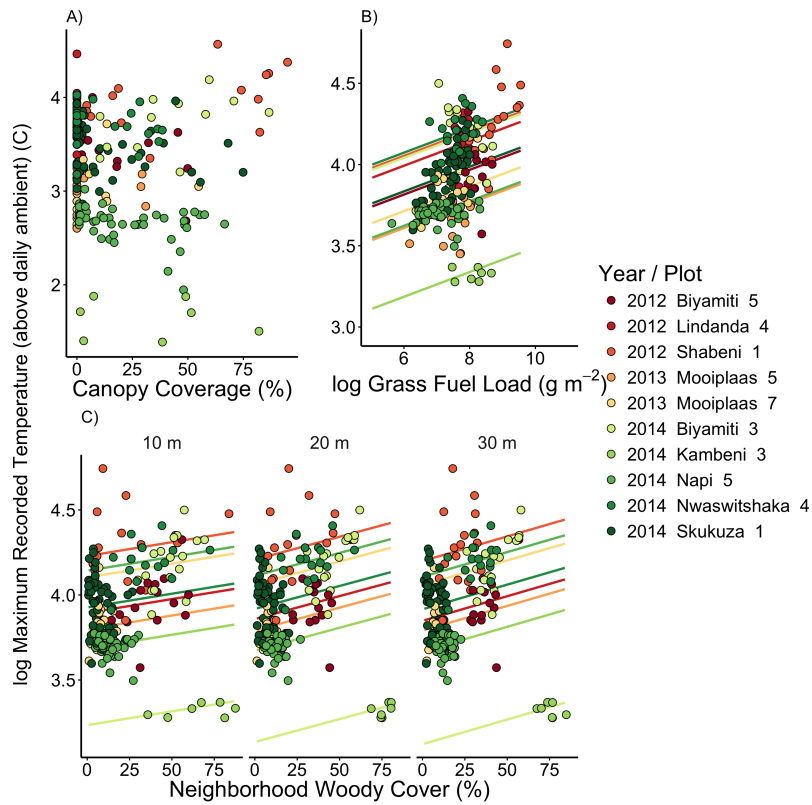


Figure 2.4: $maxTemp$ plotted against A) tree canopy coverage, B) grass fuel load, and C) woody cover at different neighborhood distances. Best fit model lines from linear mixed effect models of bivariate relationships are shown unless, as in $maxTemp \sim CC$, the model did not perform better than a null model ($maxTemp \sim 1$)

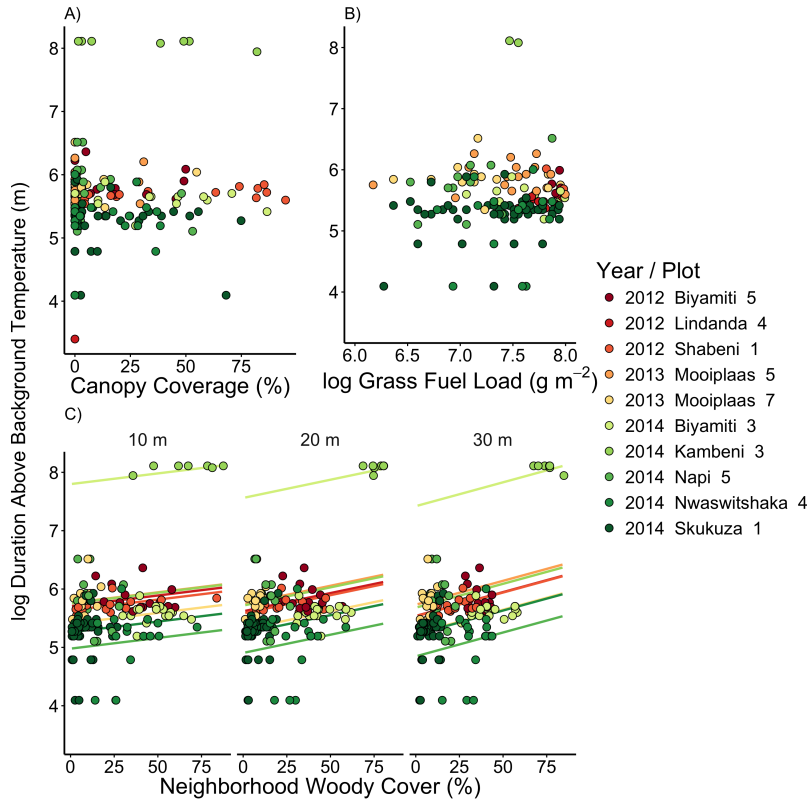


Figure 2.5: *Duration* (log min) plotted with A) tree canopy coverage, B) grass fuel load, and C) neighborhood woody cover. *Duration* was calculated as the amount of time between onset of warming above a critical temperature (identified manually per burn) and the time at which the maximum recorded temperature occurred. Best fit model lines from linear mixed effect models of bivariate are shown unless, as in $\text{Duration} \sim \text{CC}$ and $\text{Duration} \sim \text{GFL}$, they did not perform better than a null model ($\text{maxTemp} \sim 1$)

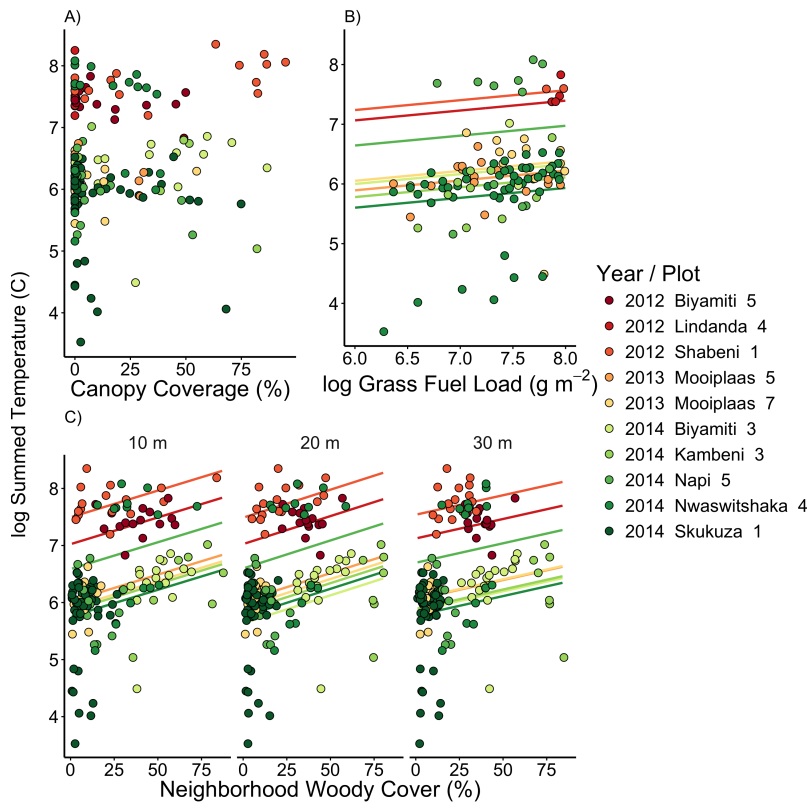


Figure 2.6: Summed temperature ($sumTemp$) plotted with A) tree canopy coverage, B) grass fuel load, and C) neighborhood woody cover. Best fit model lines from linear mixed effect models of bivariate are shown unless, as in $sumTemp \sim CC$, the model did not perform better than a null model ($sumTemp \sim 1$)

Table 2.1: Experimental Burn Plots in which data were collected and associated attributes. Mean annual precipitation (MAP) is based on long-term averages from the nearest rain gauges to the site in KNP.

Experimental Burn Plot	MAP (mm)	Burn Month	Subplot Count	Successful iButtons
Lindanda 4	507	August	16	12
Biyamiti 3	572	October	32	17
Biyamiti 5	572	August	16	15
Mooiplaas 5	451	August	19	19
Mooiplaas 3	451	October	18	18
Napi 3	572	August	24	0
Napi 5	572	October	55	55
Nwaswitshaka 4	572	October	40	40
Nwaswitshaka 7	572	August	18	0
Shabeni 1	705	August	20	17
Kambeni 3	705	October	53	53
Skukuza 1	572	October	54	54
Total:			365	300

Table 2.2: Response variable, fixed effects, and dAIC values from model selection process investigating potential drivers of fire behavior. All models have a random intercept effect per experimental burn. Each column indicates a different model being compared per response variable. Models with lowest dAIC values are in bold.

Fixed Effects	Response Variables		
	<i>maxTemp</i>	<i>Duration</i>	<i>sumTemp</i>
<i>Null</i>	19.5	2.0	5.6
<i>CC</i>	21.0	3.5	7.5
<i>GFL</i>	3.3	3.2	3.3
<i>CC + GFL</i>	4.3	4.8	5.3
<i>TC_10</i>	18.4	1.2	1.9
<i>TC_10 + GFL</i>	2.3	2.5	0.0
<i>TC_20</i>	17.5	0.3	4.3
<i>TC_20 + GFL</i>	0.0	1.5	2.0
<i>TC_30</i>	18.4	0.0	6.4
<i>TC_30 + GFL</i>	0.6	1.2	4.2

Model variable definitions: *maxTemp* = log Maximum observed temperatures above ambient (C). *Duration* = log time (minutes) between onset of heating and the peak temperature observed. *sumTemp* = sum of the temperatures recorded during Duration. *TC_10*, *TC_20*, *TC_30* = neighborhood calculations (% m⁻²) of woody cover from Google Earth imagery. *CC* = canopy cover as measured with crown densitometer (%). *GFL* = log Grass Fuel Load (g m⁻²).

Table 2.3: Direction of fixed effects for best fit models of fire metrics.

Fixed Effects	Response Variables		
	<i>maxTemp</i>	<i>Duration</i>	<i>sumTemp</i>
<i>GFL</i>	+		+
<i>TC_10</i>			+
<i>TC_20</i>	+		
<i>TC_30</i>		+	

Model variable definitions: *maxTemp* = log Maximum observed temperatures above ambient (C). *Duration* = log time (minutes) between onset of heating and the peak temperature observed. *sumTemp* = sum of the temperatures recorded during Duration. *TC_10*, *TC_20*, *TC_30* = neighborhood calculations (% m⁻²) of woody cover from Google Earth imagery. *CC* = canopy cover as measured with crown densitometer (%). *GFL* = log Grass Fuel Load (g m⁻²).

Chapter 3

Fire Intensity and Fire Severity in Kruger National Park, South Africa

3.1 Introduction

Savannas cover close to a fifth of the terrestrial land area, and are characterized by the coexistence of trees and grass (Scholes and Archer, 1997). Savannas experience frequent fire, and although fire is highly stochastic, it is thought to play a substantive, deterministic role in patterning the structure and interactions of herbaceous and woody plant species (Higgins et al., 2000; Frost and Robertson, 1987; Scholes and Archer, 1997; Hochberg et al., 1994a). Frequent fires have contributed substantial evolutionary pressure on savanna trees (Bond and Midgley, 2001), and consequentially many savanna trees have traits that are thought to help them survive frequent fires, such as thick bark, life histories that promote the ability to escape fires, and

a pronounced ability to resprout (Scholes and Archer, 1997; Hoffmann and Solbrig, 2003; Higgins et al., 2012).

Savanna fire research has focused in part on understanding the drivers of tree topkill (*e.g.* Higgins et al., 2000, 2012; Holdo, 2005; Hoffmann et al., 2009). This process, defined as the persistence of belowground after the aboveground mortality of an individual, creates demographic bottlenecks by repeatedly topkilling individuals into smaller size classes, creating large populations of small trees and fewer larger trees (Mayer and Khalyani, 2011; Scholes and Archer, 1997). Reductions in fire frequency (Higgins et al., 2007), spatial patterns of fire (van Langevelde et al., 2014), or rainfall-driven fuel loads (Higgins et al., 2000) can provide opportunities for recruitment of these smaller individuals into larger size classes. Although generally the fastest growing species may be able to escape this cycle of topkill (Wakeling et al., 2011) mass recruitment events are theorized to account for landscape level woody cover patterns (Frost and Robertson, 1987).

Savanna fire research has focused primarily on fire intensity, the energy released from a fire, and ecosystem responses (CN). Fire intensity is generally calculated as a unit of energy released in a given amount of time per a spatial unit, whether linear or areal. Fire intensity can be calculated many ways, but savanna literature overwhelmingly calculates intensity using Byram’s fireline intensity equation (Govender et al., 2006b,a; Higgins et al., 2000; Stocks and van Wilgen, 1996). Byram calculated fireline intensity (I) as a product of H , the heat yield (kJg^{-1}) of combusted fuel, the mass (w) of combusted fuel within a headfire, and (r) the rate of spread given in ms^{-1} (Equation (3.1)). This calculation thus estimates heat transfer along the head fire of a given fire in units of kWm^{-1} . Note that this is a linear measurement and

does not account for heat transfer within the backing fires (fires moving against the wind) or flanking fires (fires moving at a right angle to the wind).

$$I = Hwr \tag{3.1}$$

Fireline intensity has been repeatedly identified as key predictor of the probability of an individual tree being topkilled (Higgins and Scheiter, 2010; Trollope and Potgieter, 1985). This provides a predictive link between the energy released from the fire and an ecosystem response. Although useful, the link between energy released and ecological responses is often difficult to determine post fire when direct observations of fireline intensity were not made. The concept of fire severity arose as a tool to link energy released – fire intensity – to ecological responses through post-fire estimations of organic matter consumption (Keeley, 2009a). Organic matter consumption generally increases linearly with metrics of fire intensity, particularly fireline intensity (Ryan and Noste, 1985). Categorical indices linking organic matter consumed to fireline intensity often follow a scale (*i.e.* Ryan and Noste, 1985) from “Unburned” to “Deep burn or crown fire”, with increasing levels of organic matter consumption at each level (Keeley, 2009a). After calibration to local conditions, these rankings allow post-fire estimations of fireline intensity as well as a standardized index for linking post-fire effects to ecosystem responses.

Fire severity is often conceptually combined with *burn severity*, which is an estimation of fire severity derived from satellite remote sensing (Keeley et al., 2011). Research in savannas on burn severity is likewise limited, due in part to limitations of satellite platforms Smith:2005ck. Work in Kruger National Park in South Africa has shown the potential for linear spectral unmixing for developing burn severity

mapping as a function of ash production (Landmann, 2003), but this application has seen little use. Work in structurally similar woodland systems in Oklahoma, USA has suggested that standard tools for assessing burn severity (*i.e.* Key and Benson, 2005) in Western forests in the USA can provide accurate and meaningful burn severity mapping (Stambaugh et al., 2015), but this has not been applied to data in other systems. Similarly, some burn severity mapping has been completed in Australian savannas, but this is also limited by inconsistent definitions (Roy et al., 2006; Heward et al., 2013). Ultimately, fire severity in savannas must be understood in order to provide a consistent framework for linking post-fire observations to ecosystem responses (Keeley, 2009a).

Our understanding of fire severity in savannas suffers from inconsistent category definitions and a wide variation in natural communities classified as *savannas*. To constrain our discussion, we will focus on investigating estimations of fire severity in Kruger National Park, South Africa. This research focuses on expanding our limited understanding of the interrelationship of fireline intensity and fire severity in southern African savannas, providing a quantitative link between energy released and various estimates of organic matter consumed. Specifically, we investigate what biotic and abiotic factors predict in-field estimates of fire severity. To address these questions, we use subject matter expert assessments of post-fire organic matter consumption and relate these to fuel and environmental conditions. We then outline a roadmap for future research into developing more nuanced understanding of these topics.

3.2 Methods

3.2.1 Study System

To investigate questions of fireline intensity and fire severity in savannas, we focused on Kruger National Park in South Africa. Kruger National Park (KNP) serves as an ideal study system for questions of savanna fire ecology (Figure 3.1). KNP is located in eastern South Africa, sharing its eastern borders with Mozambique and northern border with Zimbabwe. A north-south rainfall gradient spans the park, peaking at $\sim 800 \text{ mm yr}^{-1}$ in the southwest and $\leq 400 \text{ mm yr}^{-1}$ at Pafuri in the northeast (Mabunda et al., 2003). The park's soils vary in productivity based on their parent material: in the west, low fertility granite, and to the east, high fertility basalt (Mabunda et al., 2003).

The park is over 2 million ha, and spans 350 km from north to south. To the west are a series of game reserves, both public and private (Wolmer, 2003). It is embedded within a larger transfrontier protected area complex, the Great Limpopo Transfontier Park (Wolmer, 2003).

Fire is common in KNP, and much of it is anthropogenic in origin (van Wilgen et al., 2003). Fires vary in seasonality, intensity, and frequency, and are used by KNP managers to meet specific and general objectives (Govender, 2003; Govender et al., 2006a). KNP is the site of a long-term fire experiment in which plots located across the park are burned at varying frequencies and seasons (Biggs et al., 2003). We use data collected from these Experimental Burn Plots (EBPs) for our second analysis.

3.2.2 Qualitative Savanna Fire Severity Observations

Fire Occurrence Data

We used two datasets for addressing questions of fire severity. The first is spatially explicit fire occurrence records for Kruger National Park (the same ongoing dataset as used in Smit et al. (2013)), collected between 2004 – 2011. These data were collected by KNP Rangers, who work as both fire management personnel and law enforcement officers and have extensive experience in the field. Data were subset to only include those fire records that included observations of fire effects on woody vegetation (“Woody Impact”, scaled from “None” to “Very severe”) and rates of herbaceous biomass consumption (“Herbaceous Consumption”, scaled from “Clean” to “Very Patchy”), both potential proxies for fire severity through their descriptions of vegetative biomass consumption. We investigated several different potential predictor variables based on *a priori* knowledge of drivers, largely informed by Govender et al. (2006a): season, MAP, percent woody cover, and MAP + percent woody cover, season + MAP, season + woody cover. To account for seasonal differences in fire intensity (described in Govender et al. (2006a)), we assigned a value of “dry season” to all fires observed between July and September and “wet season” to all other months, following Higgins and Scheiter (2010). We extracted and calculated the mean values within the fire perimeters for both continuous canopy cover (from the 30 m Bucini and Hanan (2007) dataset for KNP) and mean annual precipitation (from the 1 km global Hijmans et al. (2005) dataset) using the *raster* package in R (Hijmans, 2015).

Experimental Burn Plot Data

The second dataset comes from the Experimental Burn Plots (EBPs) at KNP (Figure 3.1). Weather variables (relative humidity, air temperature, wind speed), fuel moisture content (%), and grass fuel load (kg ha^{-1}) and post-fire estimations of Byram’s fireline intensity (kW m^{-1}) were recorded with each fire. For response variables, we investigated relationships with two categorical assessments and one continuous assessments of severity: 1) percent of plot burnt, 2) “success” of burn, both of which are assessments of organic matter consumed, and 3) “type” of burn, which is roughly analogous to herbaceous consumption from the first dataset. Type of burn index levels were recoded from bilingual values (Afrikaans and English) to the English ranking (“Clean”, “Moderately clean”, “Moderately dirty”, “Dirty”, and “No burn”). Ambiguous values were removed, *i.e.* the description was not recorded or did not follow these standards. Success of fire rankings were recoded as: “Highly”, “Successful”, “Moderately”, “Unsuccessful”. For predictor variables, we investigated models including all the weather data individually and combined (*i.e.*, Wind, Speed, Temperature... and Wind Speed + Temperature + Relative Humidity), the weather variables and grass fuel load, fuel moisture content, season (calculated as in the first dataset), and fireline intensity.

For categorical response variables, we used multinomial regression using the *nnet* R package (Ripley, 2011). Models were compared against a null model (*i.e.*, Woody Impact = 1) and against each other using ΔAIC as a selection criterion (Sakamoto et al., 1986, Table 3.1). We compared models with lowest ΔAIC and models with ΔAIC differences ≤ 5 with Chi-square tests to determine if significant improvements in model fits were observed. For the multinomial regressions, we chose reference

factor levels that most closely matched responses that were intermediate between high and low impacts (Table 3.1). These reference factor levels, following Qian et al. (2012), are used for calculating the rate of change of the ratios of the prevalence of a given factor level to another. Probabilities of category assignment were predicted across ranges of the best fit model predictors for each respective best fit model. For the continuous variable “percent consumed,” generalized linear models were fit to the data (Table 3.1), compared with ΔAIC , and the best fit model used to predict responses. Models were fit using a binomial distribution with a *logit* link function.

3.3 Results

3.3.1 Qualitative Savanna Fire Severity Observations

Fire Occurrence Data

Of the 162 fire occurrence footprints during the period of record, 84 had comments on either consumption of herbaceous material or the fire’s impact on woody cover, or both. Of these 84, relative to herbaceous consumption, nearly half were described as burning moderately cleanly (46%, Table 3.2). Similarly, nearly half of fires recorded were described as having a “moderate” effect on woody plants in the fire (44%, Table 3.2). Fire size ranged from 0.31 - 53,767 ha, with a mean size of 6181.6 (1213.5 SE) ha. Mean percent woody cover within each footprint ranged between 5.6% and 58.2%, with a mean across all fires of 35.1% (1.3% SE). Mean MAP values within fire footprints ranged from 405 - 745 mm yr⁻¹, with a mean across all fires of 571 (9.9 SE) mm yr⁻¹.

The model with the lowest ΔAIC (Table 3.3) for models with woody impact as a response variable had MAP and percent woody cover as the predictor (Woody Impact $\sim$ MAP + Woody Cover (%), Table 3.1). The model performed significantly better than a null model ($\chi^2(8,324)=188.9$, LR stat. = 46.1, $p \leq 0.01$). The resulting probability of category assignment varied across percent woody cover and MAP gradients (Figure 3.2a). As both MAP and percent woody cover increased, likelihood of a severe impact on woody cover decreased (Figure 3.2a).

The multinomial regression models with lowest ΔAIC (Table 3.3) with herbaceous consumption as a response variable had both percent woody cover and mean annual precipitation as predictor variables (Herbaceous Consumption $\sim$ Woody Cover + MAP, Table 3.1). However, this model was poorly differentiable from one in which MAP was the sole predictor variable (Herbaceous Consumption $\sim$ MAP, $\Delta\text{AIC} = 1.4$, Table 3.1) and a Chi square test showed that the addition of percent woody cover to the models did not significantly improve model fit ($\chi^2(3,243)=189.8$, LR stat. = 7.4, $p = 0.059$). A model including only MAP as the predictor fit significantly better than a null model ($\chi^2(3,246)=197.2$, LR stat. = 10.3, $p \leq 0.05$). Predicted probability assignment varied across rainfall gradient, with a general increase in consumption with increasing rainfall (Figure 3.2b).

Experimental Burn Plot Data

For the period of 1982 - 2012, 1230 experimental burns were conducted and data recorded. Independent of all variables, nearly half of all fires were described as a “clean” type of burn and being “highly successful” (Table 3.2). Visualizations did not suggest a strong relationship between either success of fires or types of fires

and weather or fuel variables (Figures 3.3 and 3.4), although both categories showed positive trends with Byram’s Fireline Intensity, plot rate of spread, and grass fuel load. Both categories are visually collinear with percent of plot burnt, although we did not test models due to non-independence of variables (Figures 3.3h and 3.4h), *i.e.* post-burn estimation of these variables may have influenced the others.

Like with the fire occurrence datasets, multinomial regression models fit to the categorical variables (type of fire and success of fire) for the Experimental Burn Plots were compared (separately) using ΔAIC . For both, models that included Byram’s Fireline Intensity as the predictor variable had the lowest ΔAIC values (Tables 3.1 and 3.4). Both of these models predicting type of burn and success of burn with fireline intensity performed significantly better than associated null models (Type - $\chi^2(3,3684)=2233.6$, LR stat. = 510.8, $p \leq 0.01$; Success - $\chi^2(3,3684)=2407.9$, LR stat. = 562.6, $p \leq 0.01$). Generally, success of burn and type of burn increased with fireline intensity (Figures 3.3a and 3.4a). At intensities $\geq 4000 \text{ kW m}^{-1}$, a “successful” and “clean” burn is very probable.

Percentage of plot burnt, a continuous variable recorded for each experimental burn plot, was also best predicted by Byram’s fireline intensity (Figure 3.5 and table 3.4). The model performed significantly better than a null model ($\chi^2(3,1228)=344.2$, $p \leq 0.01$). Predicted completeness of burn saturated at 100% above 4000 kW m^{-1} (Figure 3.6c).

3.4 Discussion

This research presents the first quantitative analysis of qualitative descriptions of fire severity metrics in southern African savannas. We present evidence that fireline intensity predicts two categorical estimations and one continuous estimation of fire severity.

We also investigate broader drivers of estimations of fire severity. We show a negative relationship between woody cover and MAP and the likelihood of categorizing a fire as impacting woody cover (Figure 3.2a and table 3.1). Fires categorized as having very severe impacts on woody cover were more likely to occur in areas of lower woody cover and lower mean annual precipitation. Although our inference space is limited by the smaller sample of fires ($n = 84$), this relationship provides some support for the hypothesis that at greater tree densities, trees produce feedbacks to suppress fires that may limit their dominance, and conversely, that at low tree densities, higher grass fuel loads increase the impact of fire on trees (Higgins et al., 2007; Sankaran et al., 2005).

Herbaceous consumption categories tended to track with mean annual precipitation (Figure 3.2b and table 3.1). This is consistent with previous work at KNP that showed that grass biomass increases with mean annual precipitation, and, as a consequence, so does average fireline intensity (Govender et al., 2006a). The increasing rainfall does not appear to cause a limiting increase in relative humidity, which could reduce herbaceous consumption through patchier fires.

The larger EBP dataset provides an opportunity for a more nuanced understanding of fire severity. Byram’s fireline intensity consistently predicted type of burn, success of burn, and percent of plot burnt, but individual weather and fuel variables

were weakly related to these categories (Figures 3.3 to 3.5). In general, increasing grass fuel loads increased the success and completeness of burns (Figures 3.3d, 3.4d and 3.5d), as did plot rates of spread (Figures 3.3c, 3.4c and 3.5c). The disconnection between individual fire weather variables and estimations of burn completeness and severity is surprising, and may be explained by variations in firing strategies (*e.g.*, strip-head firing patterns being used when wind or fuel continuity reduces fire spread) being used to overcome the limitations imposed by varying weather and fuel conditions. It also provides evidence of how fire-adapted savanna systems are: despite varying weather and fuel conditions, almost every fire was successful. This, however, is tempered by a bias in the data: fires are only attempted on days in which it seemed likely that they would be successful or safely managed.

The EBP data provide general breakpoints for understanding fire severity as a function of fireline intensity. Fires with fireline intensity above 4000 kW m^{-1} are all likely to burn completely, cleanly, and successfully, according to the multinomial regressions. Between $2000 - 4000 \text{ kW m}^{-1}$, a burn has a greater than 50% chance of a clean, successful, complete burn. Fireline intensities below 2000 kW m^{-1} are decreasingly likely to burn cleanly. Patchiness of fires has been suggested as a desirable management outcome in savannas (Parr and Andersen, 2006; Parr, 2008); these values can be operationalized in burn planning by choosing weather and fuel conditions to achieve particular objectives.

We note that the results as described may be difficult to apply broadly due to lack of clear definitions of categorical severity estimations. Future research could focus on creating clear processes for assessing these categorical estimations. Despite the unclear definitions of each severity class, the fact that they are predictable from

variables with known mechanistic links to organic matter consumption (*i.e.*, fireline intensity) suggests that these severity class definitions may be effectively capturing their intended assessment.

Although the estimations of fire severity in KNP can be explained by fireline intensity, we lack a strong link between these severity categories and ecological effects in savannas. We know that fireline intensity can be used to explain probability of topkill across species (Higgins et al., 2012), but we know little about effects on herbaceous species (aside from consumption), soil effects, or fauna. More focused research tying fireline intensity and post-facto fire severity categories to individual- and community-level effects could lead to a broader understanding of how these continuous and categorical variables link to actual ecosystem responses. Our knowledge of fire effects has long been limited to coarse studies of topkill or limited metrics of a small number of fires. Ultimately, we must expand our understanding of how fireline intensity can vary within a fire and how this affects both fire severity and fire effects.

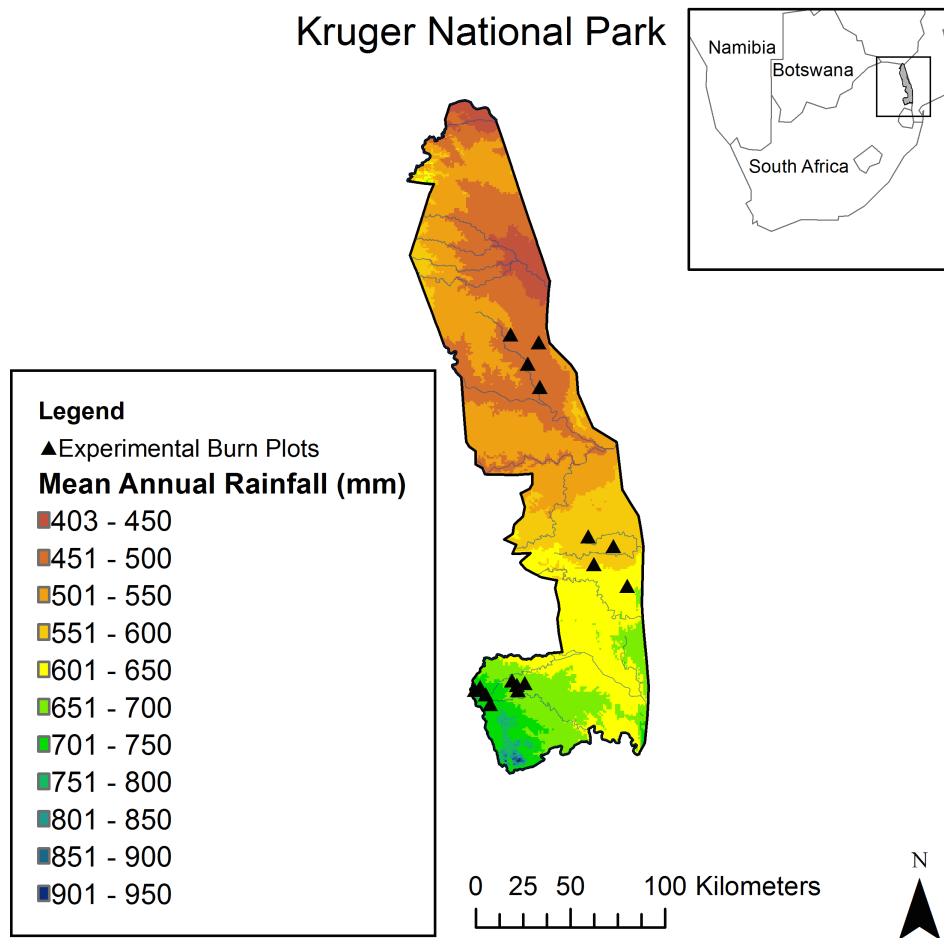
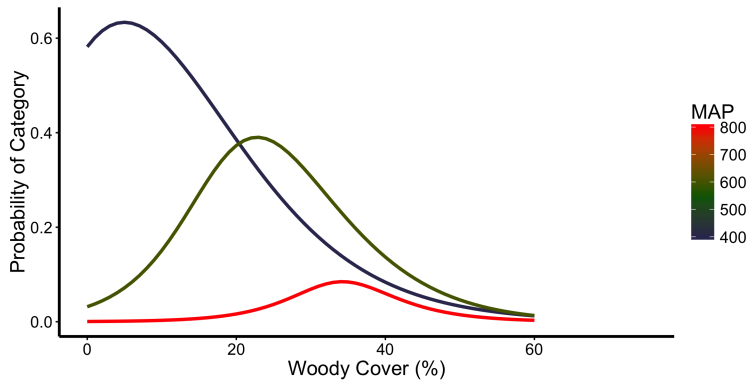
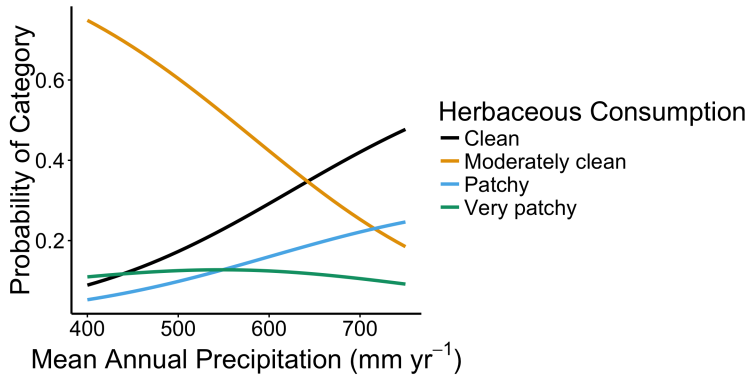


Figure 3.1: Fire severity, fireline intensity and weather data were collected during controlled burns in the Experimental Burn Plots across Kruger National Park, South Africa. Fire occurrence data spanned the park but was excluded from the map to aid in readability.



(a)



(b)

Figure 3.2: Predicted probability of “severe” impacts on woody cover relative to Mean Annual Precipitation (color and lines) and percent woody cover. This relationship represents a surface of variation; for simplicity, only three relationships with MAP are shown. B) Predicted probability of a fires herbaceous biomass consumption category by mean annual precipitation.

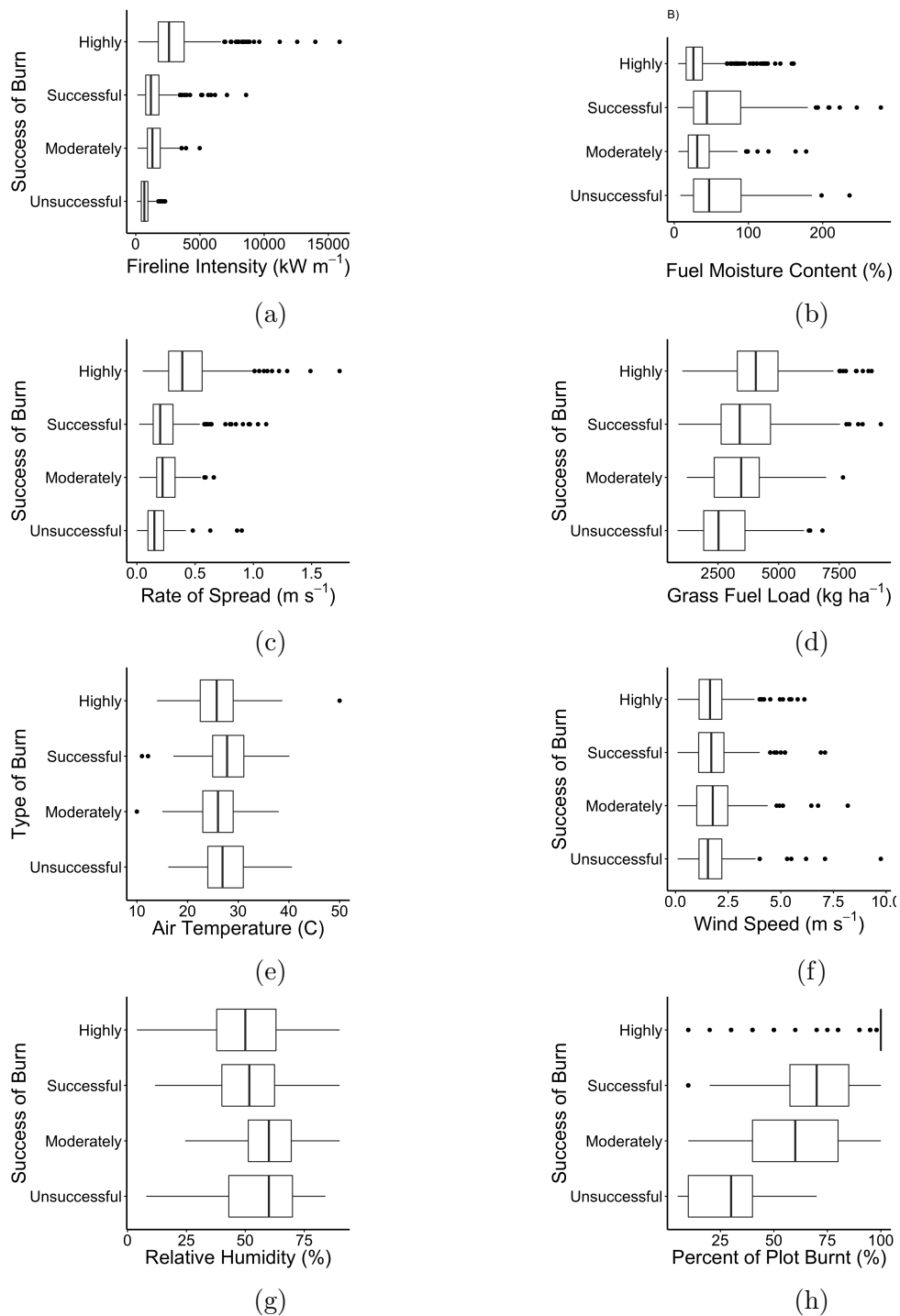


Figure 3.3: Relationship between reported “success” of fires in Kruger National Park’s Experimental Burn Plots and accompanying weather, fire behavior, and fuel variables.

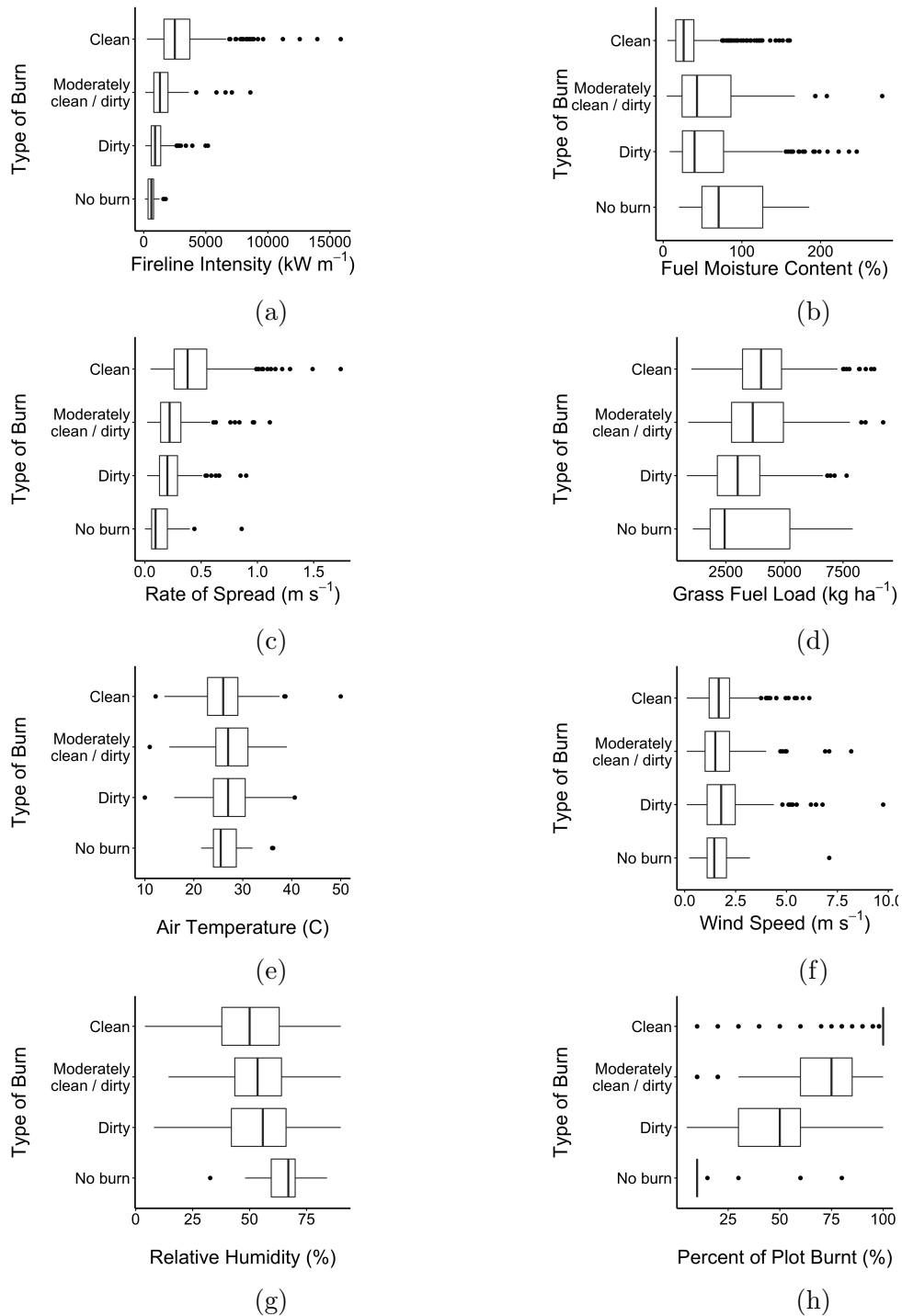


Figure 3.4: Relationship between reported “type” of fires in Kruger National Park’s Experimental Burn Plots and accompanying weather, fire behavior, and fuel variables.

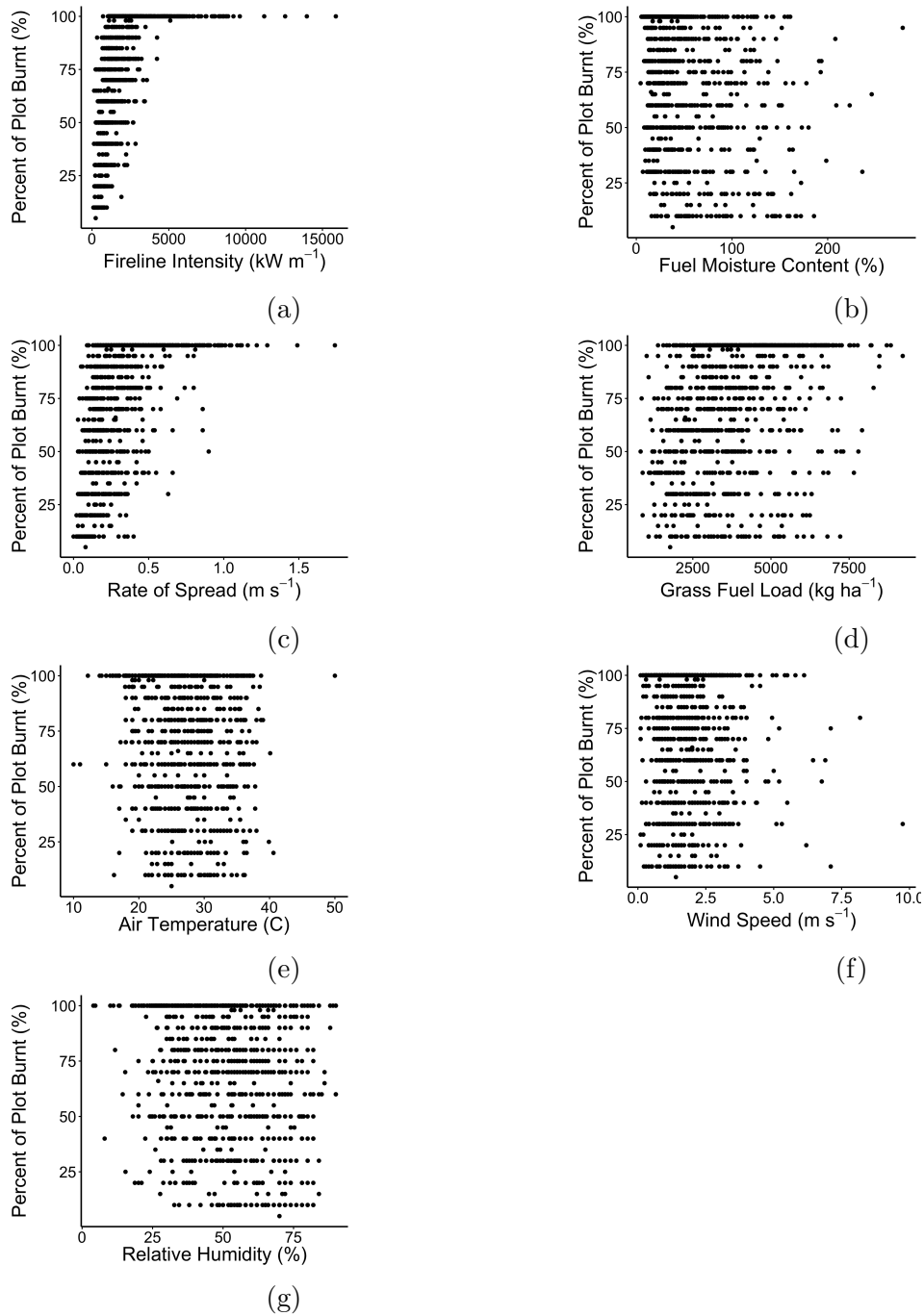
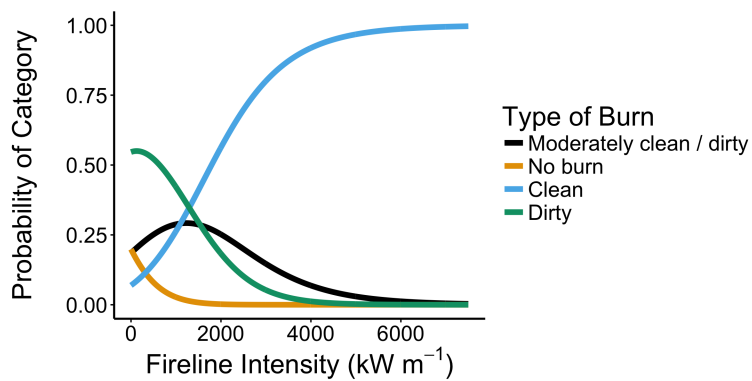
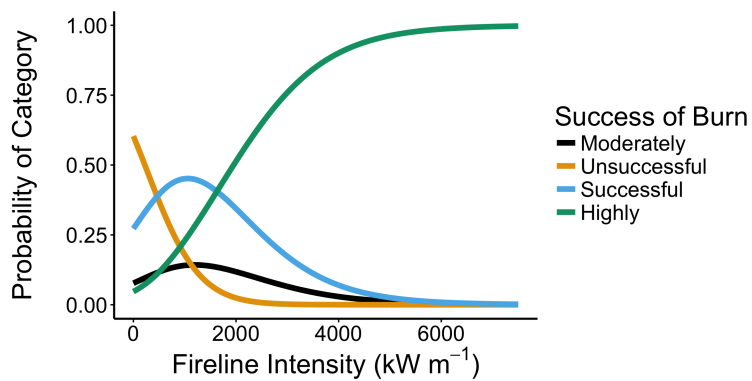


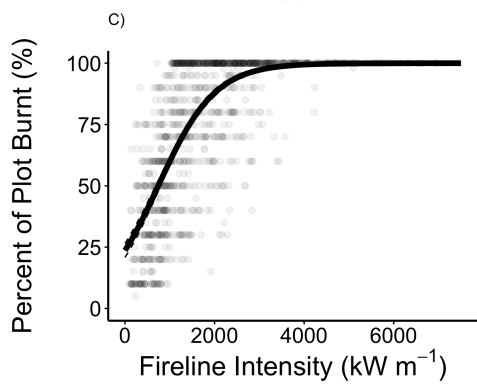
Figure 3.5: Relationship between reported percent area burnt of fires in Kruger National Park's Experimental Burn Plots and accompanying weather, fire behavior, and fuel variables.



(a)



(b)



(c)

Figure 3.6: A) Categorical predictions of type of burn, B) success of burn, and C) percent of plot burnt by Byram's fireline intensity (kW m⁻¹).

Table 3.1: Response variables, category levels, and predictor variables. Reference levels for multinomial regressions are noted in bold.

Dataset	Response Variable	Factor Levels	Predictor Variables
Fire Occurrence	Woody Impact	Very Severe, Severe, Moderate , Slight, None	Season, MAP, MAP + Season, Woody Cover, Woody Cover + MAP, Woody Cover + Season (%)
		Clean, Clean , Patchy, Very Patchy	Season, MAP, MAP + Season, Woody Cover, Woody Cover + MAP, Woody Cover + Season
	Herbaceous Consumption		FI, FMC, ROS, GFL, Temp, WS, RH, Season, RH + WS + Temp, RH + WS + Temp + GFL
EBPs	Type Of Burn	Clean, Clean , Moderately Dirty, Dirty, None	FI, FMC, ROS, GFL, Temp, WS, RH, Season, RH + WS + Temp, RH + WS + Temp + GFL
	Success Of Burn	Highly, Successful, Moderately , Unsuccessful	Temp, WS, RH, Season, RH + WS + Temp, RH + WS + Temp + GFL
	Percent of Plot Burnt	(Continuous)	FI, FMC, ROS, GFL, Temp, WS, RH, Season, RH + WS + Temp, RH + WS + Temp + GFL

Model variable key: MAP: Mean Annual Precipitation (mm yr^{-1}). Season: Season of fire (dry / wt). GFL: Grass Fuel Load (kg ha^{-1}). FI: Byram's Fireline Intensity (kW m^{-1}). FMC: Fuel Moisture Content (%). ROS: Rate of Spread (m s^{-1}). Temp: Temperature (C). WS: Wind speed (m s^{-1}). RH: Relative humidity (%).

Table 3.2: Distribution of severity estimations between datasets.

Dataset	Categorical Variable	Factor Levels	Count	Percent
Fire Occurrence	Herbaceous Consumption	Clean	22	26%
		Moderately clean	40	47%
		Patchy	12	14%
		Very patchy	10	11%
	Woody Impact	None	8	9%
		Slight	17	20%
		Moderate	37	44%
		Severe	17	20%
		Very Severe	5	5%
EBPs	Type of Fire	No Burn	28	22%
		Dirty	322	26%
		Moderately clean / dirty	267	21%
		Clean	613	49%
	Success of Fire	Highly	570	46%
		Successful	387	10%
		Moderately	126	12%
		Unsuccessful	147	31%

Table 3.3: Multinomial models fit to the Kruger National Park fire occurrence dataset and associated ΔAIC values.

Response Variable	Predictor Variables	ΔAIC
Impact on Woody Cover	Null	30.2
	Season	34.6
	Season + MAP	24.3
	Season + Woody Cover	17.0
	MAP	20.0
	Woody Cover	12.5
	Woody Cover + MAP	0.0
Herbaceous Consumption	Null	5.7
	Season	10.4
	Season + MAP	5.9
	Season + Woody Cover	11.1
	MAP	1.4
	Woody Cover	6.4
	Woody Cover + MAP	0.0

Table 3.4: Multinomial models fit to the Kruger National Park Experimental Burn Plot dataset and associated ΔAIC values.

Response Variable	Predictor Variables	ΔAIC
Type of Burn	Null	504.8
	Season	375.8
	MAP	424.7
	FI	0.0
	RH	476.6
	FMC	357.2
	WS	502.9
	ROS	187.5
	GFL	406.0
	Temp	489.0
	RH + WS + ROS	406.6
	RH + WS + ROS + GFL	298.5
Percent of Plot Burned	Null	498.7
	Season	460.8
	MAP	479.3
	FI	0.0
	RH	491.5
	FMC	453.6
	WS	500.1
	ROS	200.3
	GFL	418.9
	Temp	495.4
	RH + WS + ROS	472.9
	RH + WS + ROS + GFL	384.9
Success of Burn	Null	556.6
	Season	427.8
	MAP	470.6
	FI	0.0
	RH	521.3
	FMC	374.5
	WS	557.6
	ROS	236.1
	GFL	436.8
	Temp	516.3
	RH + WS + ROS	452.27
	RH + WS + ROS + GFL	314.9

Chapter 4

Simulated Effects of Fire on Topkill Across Rainfall Gradients Are Driven by Species Turnover

4.1 Introduction

Tree cover varies across biomes, and some biomes appear to be capable of supporting greater tree cover than they currently contain (Bond, 2008). Savannas, a biome defined by its coexistence between trees and grasses, in particular may be able to support greater tree cover (Sankaran et al., 2005). An ongoing debate in the ecological literature concerns the extent to which the savanna biome primarily owes its existence to top-down (primarily fire) vs. bottom-up (primarily soil moisture) factors (Sankaran et al., 2005). A prevailing thesis posits that the relative influence of these factors shifts along precipitation gradients, with water and fire being the key drivers at the arid and mesic extremes of the biome, respectively (Sankaran et al., 2005). Maximum

woody cover saturates above a mean annual precipitation (MAP) of about 650 mm, but savannas persist well above this threshold. Implied within this hypothesis is that maximum tree cover in the wetter savannas is limited by fire, and that in the absence of fire, tree cover would increase. Because savanna fires are fueled by grasses, and grass primary production increases with MAP (Dublin et al., 1990; Govender et al., 2006a; Smit et al., 2013; McNaughton, 1985), the greater frequency and intensity of fires due to increased grass biomass in more mesic savannas may drive this tree cover limitation (Archibald et al., 2010a; Govender et al., 2006a). The influence of fire on tree demography has not been systematically studied across MAP gradients, and this comprises a significant gap in our understanding of savanna dynamics.

Central to the role of fire in tree demography is the notion of escape from the so-called fire trap. Trees are frequently topkilled in savannas because they are unable to grow sufficiently to become resistant to fire between disturbance events, although whole tree mortality from fires is very low (Holdo, 2005). Trees caught in the fire trap are rarely killed, but instead persist in a cycle of growth, aboveground mortality, and subsequent resprouting (Hoffmann et al., 2009). Although bark thickness (which is correlated with tree size) and other factors play a role in topkill resistance, it has been well established that resistance to fire is size-dependent (Dantas and Pausas, 2013; Holdo, 2007; Trollope and Trollope, 2002). When fire is intense, the minimum size required to acquire resistance (and thus avoid topkill) increases. Likewise, frequent fire reduces the window of opportunity for escape between fires.

A missing piece of the escape equation concerns growth. Growth rates are generally thought to increase with precipitation, but this generalized response lacks nuance (Higgins et al., 2000). In water-limited systems, growth rate may be assumed increase

with MAP, and this increase in growth could in principle offset the negative effects of fire along a gradient of increasing MAP. A key question, then, is can the effects of MAP on growth limit or cancel out the effects of MAP on fire? Resolving this question is particularly important because it is generally assumed that fire and other disturbances are more important for controlling woody cover in mesic savannas, and that resource limitation is more important in drier savannas (Sankaran et al., 2005). If this is true, in the absence of tree effects on fire, we would expect the probability of escape to decrease as a function of MAP.

Prior work has shown that fire frequency increases with MAP (Dublin et al., 1990; Govender et al., 2006a; McNaughton, 1985; Smit et al., 2013). For fire intensity, the evidence is less clear. Intensity, or the rate of energy released by a fire, is driven by a number of factors, including wind, fuel arrangement, fuel load, fuel moisture, and other factors (Rothermel, 1972; Byram, 1959). Although over short time scales fire frequency and intensity may be inversely related (frequent fires reduce fuel accumulation and thus the potential for high intensity fires), in general both tend to increase with rainfall due to the dominant effect of rainfall on grass production and fuel continuity (Govender et al., 2006a).

To understand how fire and tree demography interact across the rainfall gradient and to better understand the role of fire in limiting tree cover in mesic and semi-arid savannas, we seek to understand how three key variables associated (or potentially associated) with MAP interact to determine the probability of trees escaping the fire trap along a savanna MAP gradient. To do so, we use a dynamic model to combine the effects of MAP on fire frequency, fire intensity, and tree growth rates (Section 4.6). We ignore the potential for feedbacks between tree cover limiting grass production

or facilitating increased grass production as it is beyond the scope of this model (Belsky, 1994; Belsky et al., 1993; Riginos, 2009). We focus on the Kruger National Park ecosystem of South Africa as a case study, given the abundance of data suitable for parameterizing the model in this well-studied system. We specifically test the hypothesis that the probability of escape decreases with MAP. We also investigate which of the three variables (fire intensity, fire frequency, or growth) play the dominant role on escape probability.

4.2 Methods

4.2.1 Study System

Kruger National Park (KNP hereafter) is located in eastern South Africa, bordering Mozambique and Zimbabwe. The park extends over 2 million ha, and spans 350 km from north to south. KNP serves as a compelling system for this study because it spans a MAP gradient (400 - 800 mm y⁻¹) that captures a significant fraction of the savanna range in sub-Saharan Africa (Figure 4.2). Furthermore, KNP has a long record of detailed fire monitoring. These features of the system make it an appropriate unit of analysis for understanding fire trap dynamics in savannas across the continent.

In addition to variation in MAP and fire, KNP exhibits wide variation in geology and soils. The latter vary in productivity based on their parent material: the western two thirds of the park are dominated by sandy soils of granitic origin with low fertility, while the eastern third is dominated by more fertile, soils of basaltic origin with a higher clay fraction (Mabunda et al., 2003). These soils are associated with dis-

tinct vegetation communities, with broad-leafed vegetation dominated by *Terminalia sericea* and *Sclerocarya birrea* savanna occurring on granite and *Acacia nigrescens* and other fine-leafed species being common on basalt. The dry northern portion of the park is largely dominated by *Colophospermum mopane*, regardless of parent material.

Fire is pervasive in KNP, and much of it is anthropogenic in origin (van Wilgen et al., 2000). Fires vary in seasonality, intensity, and frequency, and are used by KNP managers to meet both specific and general management objectives (Govender, 2003; Govender et al., 2006a; van Wilgen et al., 2000). Despite this, an analysis of 65 years of fire records across KNP shows that fire frequency is effectively determined by two factors: MAP (which has a positive effect) and geology (fire is more frequent on basalt, Smit et al. 2013). This suggests that fire across the system is largely fuel- rather than ignition-limited, and provides strong support for a role of MAP as a key driver of fire frequency.

4.2.2 Model Description

The dynamic model tracks simulated growth and fire-induced topkill of trees occurring along a precipitation gradient ranging from 400 to 900 mm y^{-1} (Figure B.1). Three variables are simulated as a function of MAP: tree growth, fire occurrence (a stochastic function of frequency), and fire intensity. The relationship between MAP and each of the variables is derived from empirical relationships. We sample directly from the range of MAP and fire frequency values, whereas the relationship between tree growth and intensity and MAP are simulated using models fit to the data. To the extent possible, the data were KNP-specific, although growth data included research from

outside of KNP to extend the range of values. The model is completely stochastic, with realizations for each process of interest either sampling from the full known population or following appropriate statistical distributions. We assumed that only one fire event occurs in a given year. Fire occurrence is generated with a Bernoulli distribution with probability determined by the empirical relationship between fire frequency and MAP for KNP (Smit et al., 2013). If a fire occurs, the intensity of the fire is a stochastic function of MAP, and the probability of topkill for each stem in the cohort is a function of tree height and fire intensity (Higgins et al., 2012). Topkilled trees are reset to a height of 0 and resprout the following year, continuing to grow. For trees that do not experience fire in any given year, the model simulates growth as a function of MAP. All analyses were conducted in R (R Core Team, 2015).

4.2.3 Tree Growth

There is a surprising lack of tree growth data for the savanna biome, particularly relative to environmental gradients. To attempt to better understand tree / fire dynamics across the range that KNP represents, we chose three common species. The first, *Colophospermum mopane*, is common in the dryer north of Kruger (Scholtz et al., 2014). The second, *Terminalia sericea*, is most common in the wetter south of the park, but is still found across Kruger. The third, *Combretum apiculatum* and *Combretum zeyhari*, were binned as *Combretum* sp. (following Holdo 2007). Together, these species cover much of the park (Figure 4.4). We used studies that allowed us to relate diameter or radial increments to MAP to develop intraspecific relationships between growth and precipitation (Holdo, 2005; Prior and Cutler, 1996; Mushove et al., 1995; Shackleton, 2001; Gaugris et al., 2008; Calvert, 1993; Childes, 1984).

After standardizing circumference or radius to diameter increments (Table B.2), we fit linear models to the relationship between annual diameter increment Δd and MAP. With these species-specific models, our growth model tracked cumulative diameter growth by sampling each time step from the estimated distribution of diameter growth increments for a given species and MAP. These increments were added annually. We estimated height from cumulative diameters at each time step in the model using allometric relationships for KNP trees (K. Cummings, unpublished data).

4.2.4 Fire Frequency

We overlaid a MAP layer from WorldClim (Hijmans et al., 2005) across a raster layer of mean fire return interval (MFRI) of KNP (Smit et al., 2013). We sampled paired fire frequency (the inverse of MFRI) and mean annual rainfall from this dataset as inputs into the model (Figure 4.3b). The actual occurrence of fire (b) in each year was given by the outcome of a Bernoulli random variable ($0 = \text{not burned}$, $1 = \text{burned}$) with mean f (fire frequency between 0 and 1) and number of trials equal to 1, as follows:

$$b \sim \text{Bernoulli}(f) \tag{4.1}$$

4.2.5 Fire Intensity

Based on a sample of 30 years of experimental burning, Govender et al. (2006) found a positive relationship between MAP and calculated Byrams fireline intensity in KNP in the Experimental Burn Plots. Govender et al., following standard methods,

calculated Byrams fireline intensity using $I = Hwr$, where I is intensity (kW m^{-1}), H is the energy content of KNP grasses ($16,890 \text{ J g}^{-1}$), w is standing grass biomass (kg ha^{-1}), and r is the rate of spread of the head fire (Govender et al., 2006a; Byram, 1959). Because the distributions of intensity are constrained to only fires in the burn plots, it was necessary to model the relationship between the distribution of intensity relative to MAP. We reanalyzed this relationship by fitting a generalized linear model linking I to MAP across the different burn plots. We investigated Gamma, normal, and log-normal distributions for this relationships, and compared them to a null model using AIC and model likelihood ratio tests. For each fire event in the model, we used this relationship to draw a random value of I from within the 95th percentiles of the distribution generated by MAP.

4.2.6 Probability of Topkill and Probability of Escape.

For those trees that experience fire in a given year, we assumed that the probability of topkill per tree per year (p) is a function of stem height (h), fireline intensity (I), and season (M) following Higgins et al. (2012):

$$\text{logit}(p) = \beta_{0,S} + \beta_{1,S}\log(h) + \beta_{2,S}\sqrt{I}\beta_{3,S}M \quad (4.2)$$

In Equation (4.2), the parameters vary across species (S). The Higgins et al. (2012) model was fitted to a multi-species dataset of monitored individuals of contrasting height in the KNP Experimental Burn Plots. After an experimental fire treatment, individual-level topkill was recorded and associated with the Byrams fireline intensity of the fire. Higgins et al. included season (M) as a covariate in their

model; we hold this constant, assuming dry season fires, which exert the strongest effects on tree mortality. We parameterized the model with composite, non-species specific terms (Table B.1). The occurrence of topkill (m) is then given by:

$$m = \begin{cases} 0 & \text{if } b = 0 \\ \sim \text{Bernoulli}(p) & \text{if } b = 1 \end{cases} \quad (4.3)$$

The probability of escape is given by the proportion of trees that grew to heights of at least 3 m per model run for each model run, following the escape cutoff height for African savannas defined by Bond and Midgley (2001). Mean, 2.5th, and 97.5th percentile values were calculated for each 10 mm yr⁻¹ rainfall bin across returned values.

We also investigated how MAP-linked species turnover (with slower-growing species dominating dry areas and fast-growing species dominating mesic areas) may drive variation in probability of escape. Using an extensive dataset of tree species distribution within 20 x 20 m plots across KNP, we determined relative frequency by calculating what percent of Venter plots had our study species within 10 mm yr⁻¹ rainfall bins (Venter, 1992; Hijmans et al., 2005). We multiplied these relative frequencies by predicted probability of escape per rainfall bin to calculate weighted mean probabilities of escape. We then mapped this across KNP using the WorldClim data.

4.2.7 Variability Analysis

Following runs of our models, we conducted a simple test to determine the extent to which the observed escape vs. MAP relationship was driven by associations between MAP and tree growth, fire frequency, or fire intensity. We decoupled the relationships

between MAP and each of these variables in turn and reran the escape model. To decouple growth rates, we fit a null linear model to all the growth rate data. We then sampled from this uniform distribution. For fire frequency, we sampled values separately from MAP and fire frequency values, as opposed to paired. For fire intensity, we used the intercept models. We then compared the predicted probability of escape across rainfall gradients between the standard models for each species and the three MAP-decoupled models using R^2 .

4.2.8 Model Run Parameters

Each model runs 10000 times, with 500 trees in each sampled fire frequency / MAP pairing from the Smit et al. 2012 dataset for 100 year time steps (Figure B.1). We also analyzed the effect of model time limit on probability of escape by comparing the 25, 50, 75, and 100 year time steps on the probability of escape of *Terminalia sericea*. We assumed no whole-tree mortality in the model, due in part to the relatively low background mortality rates and direct tree mortality from fires (Holdo, 2005). Although this reduces the realism somewhat, we note that the model does not intend to capture the full range of demographic processes in the system (such as recruitment from seed), but rather intends to investigate how growth, topkill, rainfall, and fire all interact.

4.3 Results

4.3.1 Tree Growth

T. sericea demonstrated a non-significant positive growth response to rainfall ($p = 0.504$, $F = 0.5732$, $DF_{1,3}$) whereas *Colophospermum mopane* ($p = 0.5590$, $F = 0.4829$, $DF_{1,2}$) and *Combretum sp.* ($p = 0.06365$, $F = 8.004$ $DF_{1,3}$) both demonstrated negative growth trends (Figure 4.3c). *T. sericea* overall grew faster than both *C. mopane* and *Combretum sp.*

4.3.2 Fire Intensity

Maximum likelihood estimation was used to fit fire intensity data to MAP for the Experimental Burn Plots. A Gamma distribution was found to be a good fit for the fire intensity data, and fit better than normal or log-normal distributions. A likelihood ratio test showed that fire intensity estimations as a function of MAP produced significantly better fits than a null model (Fire Intensity ~ 1 , $\chi^2 (1, 1235) = 26.809$, $p \leq 0.01$), and the relationship was positive (Figure 4.3a).

4.3.3 Effect of Rainfall on Probability of Escape

The probability of a tree escaping the fire trap varied by species across the rainfall (Figure 4.5). *T. sericea*, common in wetter sites, showed a relatively flat probability of escape (Figure 4.5a). *C. mopane*, the slow growing, dry site specialist, showed a steeper decline of escape probability with rainfall than the other two species and overall had a lower probability of escape (Figure 4.5b). *Combretum sp.* decreased

in probability of escape linearly across the rainfall gradient in which it was found (Figure 4.5c).

When accounting for species turnover and variation in growth rates across a rainfall gradient, probability of escape varied across Kruger (Figure 4.7a). Generally speaking, there was a North-to-South gradient of escape probability, increasing as mean rainfall increases. Although the relationship was not entirely linear, there was an overall increase in probability of escape as mean annual precipitation when accounting for species distribution (Figure 4.7b).

4.3.4 Variability Analysis

When all but one factor was held constant relative to MAP, species-specific variation in predicted probability of escape was observed (Table 4.1 and fig. 4.6). When only fire frequency or intensity varied with rainfall, weak effects on probability of topkill were observed (Figures 4.6a and 4.6b). The likely controlling factor for probability of escape for the three species varied. For *T. sericea*, no clear factor stood out, whereas the probability of escape *C. mopane* was most explained by models in which only fire frequency varied. For *Combretum* sp., escape was most explained by models in which growth varied. Variability models were not distinguishable by AIC for *T. sericea*, although they were for the other species.

4.3.5 Time Analysis

Varying the model simulation period for the escape probability resulted in little change in the probabilities of escape (Figure B.2). Although escape was significantly

lowered at shorter time scales, there was not a clear trend of increasing escape past 100 years. The curves ultimately approached the same shape.

4.4 Discussion

The probability of trees escape fire appears to be dependent on growth rate, though the way in which this was expressed varied. The faster growing *T. sericea* had an overall higher escape probability which overwhelmed the effects of fire frequency and fire intensity. Probability of escape of *C. mopane* decreased dramatically with increased rainfall; *Combretum* sp. decreased less so, and overall was more resistant to fire than *C. mopane*. This suggests an interaction of fire frequency, fire intensity, and growth that varies by site and species.

The results of the variability analysis were intuitive. When only tree growth rates varied with rainfall and all other variables were held constant, probability of escape varied by species (Figure 4.6c). *C. mopane* was largely unable to escape the fire trap, whereas *T. sericea* increased in escape probability with rainfall and *Combretum* sp. decreased in escape probability with rainfall. Conversely, when only intensity varied with rainfall, probability of escape was relative flat (Figure 4.6b), which may be driven by the wide range of potential intensities across the rainfall gradient. When only fire frequency varied with rainfall (Figure 4.6a), probability of escape decreased with MAP, which, in turn, may be driven by the stronger linkage between MFRI and MAP.

Our model suggests that probability of escape is highly sensitive to mean fire return intervals and tree growth rates, although fire intensity does play an important

role, as well (Table 4.1). Intensity can vary a great deal within a MAP scenario, which may drive this weak linkage. Weather (wind, relative humidity, etc.) and fuel moisture scenarios greatly affect fire behavior and consequently fire intensity, even when combustible fuel is held constant (Rothermel, 1972; Trollope and Potgieter, 1985). It is possible to see a wide variety of different fire intensities even with the same fuel load, which may account for the variation in intensities found within the EBPs sampled.

Our study, along with many others on savanna fire dynamics, may be influenced by the research coming from the Kruger National Park Experimental Burn Plots. The commonly cited relationships between fire weather variables and fire intensity, as well as the relationship between intensity and topkill, are all derived from experimental burns (e.g. Govender et al., 2006a; Higgins et al., 2000, 2012). These prescribed fires upon which these studies are based are naturally more conservative than wild-fires. Fire managers are more likely to light fires on days where control is easy; this necessarily excludes days with lower relative humidity, higher wind speeds, or lower fuel moistures across size classes. Thus the sampling space is biased towards more tame fires. Although there have been recent efforts to experiment with higher intensity fires in savannas, the bulk of the literature focuses on fires of relatively lower intensity (Browne and Bond, 2011). These fires may be of little impact to highly fire adapted species such as savanna trees; only larger, more intense fires may provide the necessary changes to truly affect tree dynamics. Previous literature has emphasized the importance of growth rates for escaping fire (Dantas and Pausas, 2013; Higgins et al., 2012; Werner, 2012; Bond and Midgley, 2001), though largely from a theoretical perspective. Compared to many areas, savanna tree growth rates are understudied.

This in part due to difficulties in measuring tree rings in many tropical trees and an otherwise paucity of dendrometer studies (Worbes, 1995; Lilly, 1977). Lacking this quantitative basis, we are limited in our understanding of how growth rates affect tree dynamics in savannas. Notably, our results are not replicated with more species on the wetter or drier end. These results should be further explored with more species with varying growth rates and species distributions.

Empirical descriptions of the effects of fire frequency and rainfall on tree dynamics show a variety of results (Shackleton and Scholes, 2000, 2011; Higgins et al., 2007; Smit et al.). After sampling at one of the more arid Experimental Burn Plots (Satara), Shackleton and Scholes (2000) found tree heights decreased with fire frequency. Higgins et al. (2007) found similar results, noting that fire frequency affects tree biomass and structure, but not density. This was supported by Smit et al., who found that fire had greater absolute effects at reducing biomass in wetter, denser savannas, but relative effects were greater in drier sites. Across a rainfall gradient from 484 ± 32 to 1161 ± 225 mm yr⁻¹, Shackleton and Scholes (2011) found evidence for increasing tree biomass, density, and height with increasing MAP. Interestingly, our modeled decreases in probability of escape occur around 650 mm yr⁻¹ MAP, which is also approximately the cutoff between drier, resource limited savannas and wetter, disturbance limited savannas (Guyette et al., 2015; Sankaran et al., 2005). Overall, these support our general findings that fire limits tree recruitment more in wetter savannas than in drier savannas as well as the observed effects of fire frequency.

A key element that is not included in this model, and remains a difficult component to include, is the interacting roles of fire and herbivores, which has been noted in previous research. Tree growth rates in both dry and wet savannas have been shown

to increase when herbivory was reduced (Staver et al., 2009; Staver and Bond, 2014), thus suggesting that in drier sites, trees may be growth limited by both resource availability and herbivory. Periods of decreased herbivore pressure could thus allow otherwise suppressed woody individuals to escape the fire trap. Similarly, the interactions of elephants and fire has been long shown to increase tree mortality across size classes and change the structural composition of savannas (Holdo, 2007; Baxter and Getz, 2005; Sankaran et al., 2008; Levick et al., 2012, 2014). Interactions between animal populations (and thus herbivore pressure), longer term rainfall patterns, and fire frequency are likely to exist, but the complexity of the interactions may make it difficult to understand in what ways they may provide opportunities for cohort recruitment of trees in savannas.

4.5 Conclusions

Our study shows that trees may increase in escape probability with rainfall, suggesting that trees are able to compensate for increased intensity and frequency of fires in areas of higher rainfall. We demonstrate evidence to support the importance of growth rates, fire frequency, and fire intensity, and that these may have interacting species-level effects on probability of escape. Although previous work has focused on these drivers individually, few have integrated them into a model that explicitly addresses the role of mean annual rainfall as a parallel driver of growth, fire frequency, and fire intensity. Ultimately, more research must be done on the factors that control growth rates of savanna trees to truly understand how this may affect tree dynamics. This remains a key area in which we still know very little, yet is crucial to our understanding

of this important biome.

4.6 Acknowledgments

We would like to thank Navashni Govender, Scientific Services, Kruger National Park, as well as the rest of the staff their for their support in our data analysis efforts.

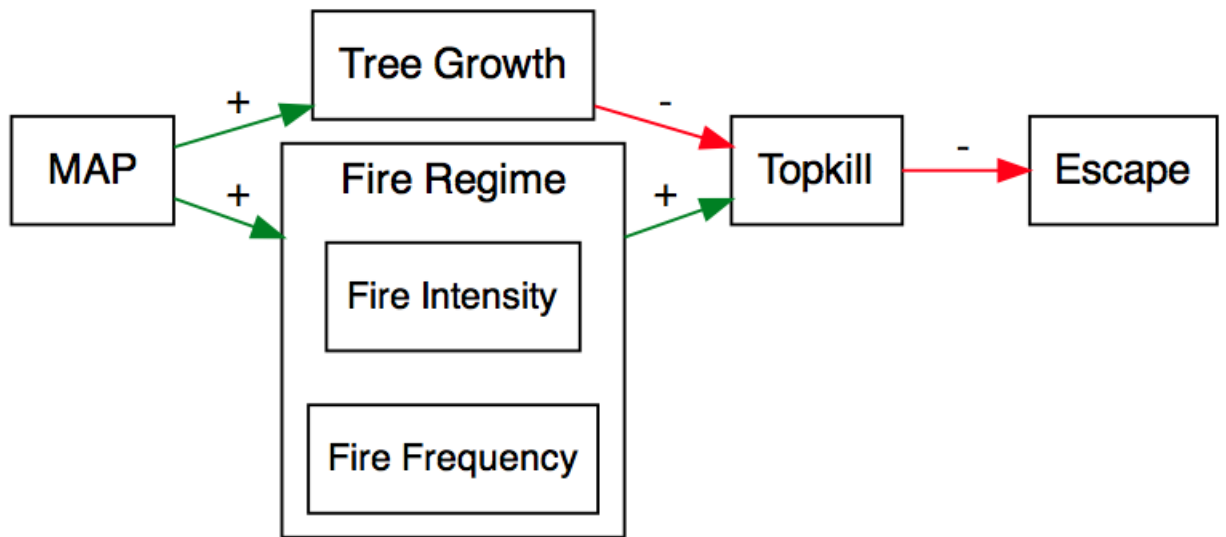


Figure 4.1: Model links fire frequency, fire intensity, and growth to probability of topkill, and thus probability of escaping the fire trap. Green lines are positively linked variables. Red lines are negatively linked variables.

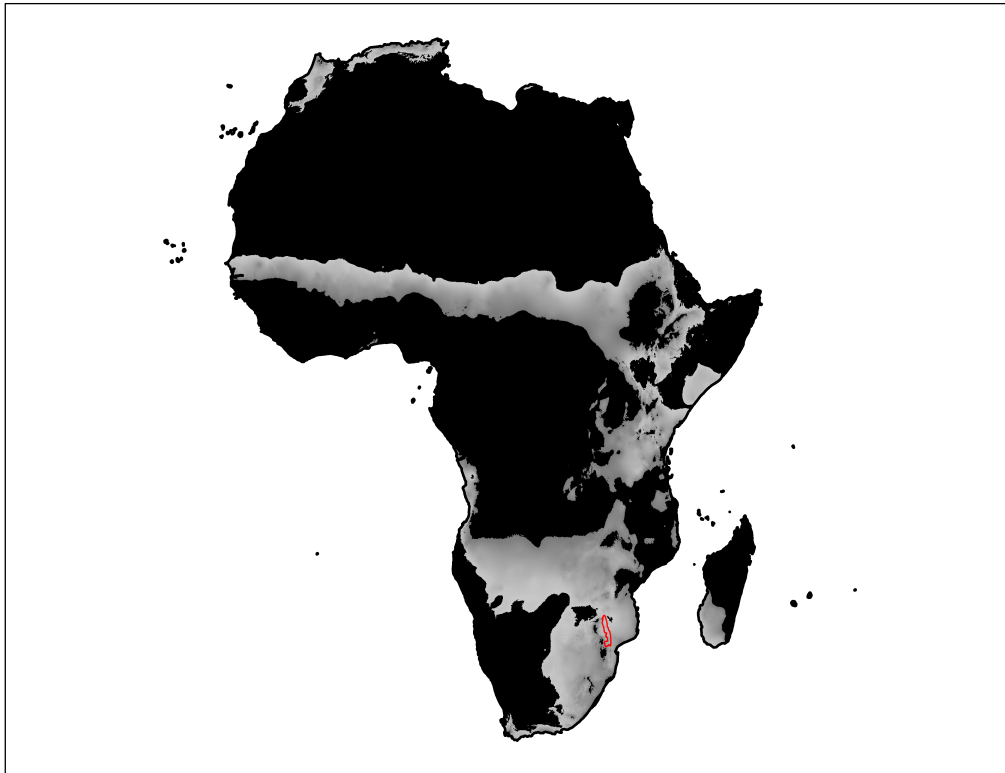


Figure 4.2: Kruger National Park, South Africa (red) serves as an ideal model system for capturing rainfall-linked variation across the savanna biome in Africa by spanning a wide mean annual precipitation gradient (gray, 450 - 900 mm yr⁻¹). Precipitation data from WorldClim

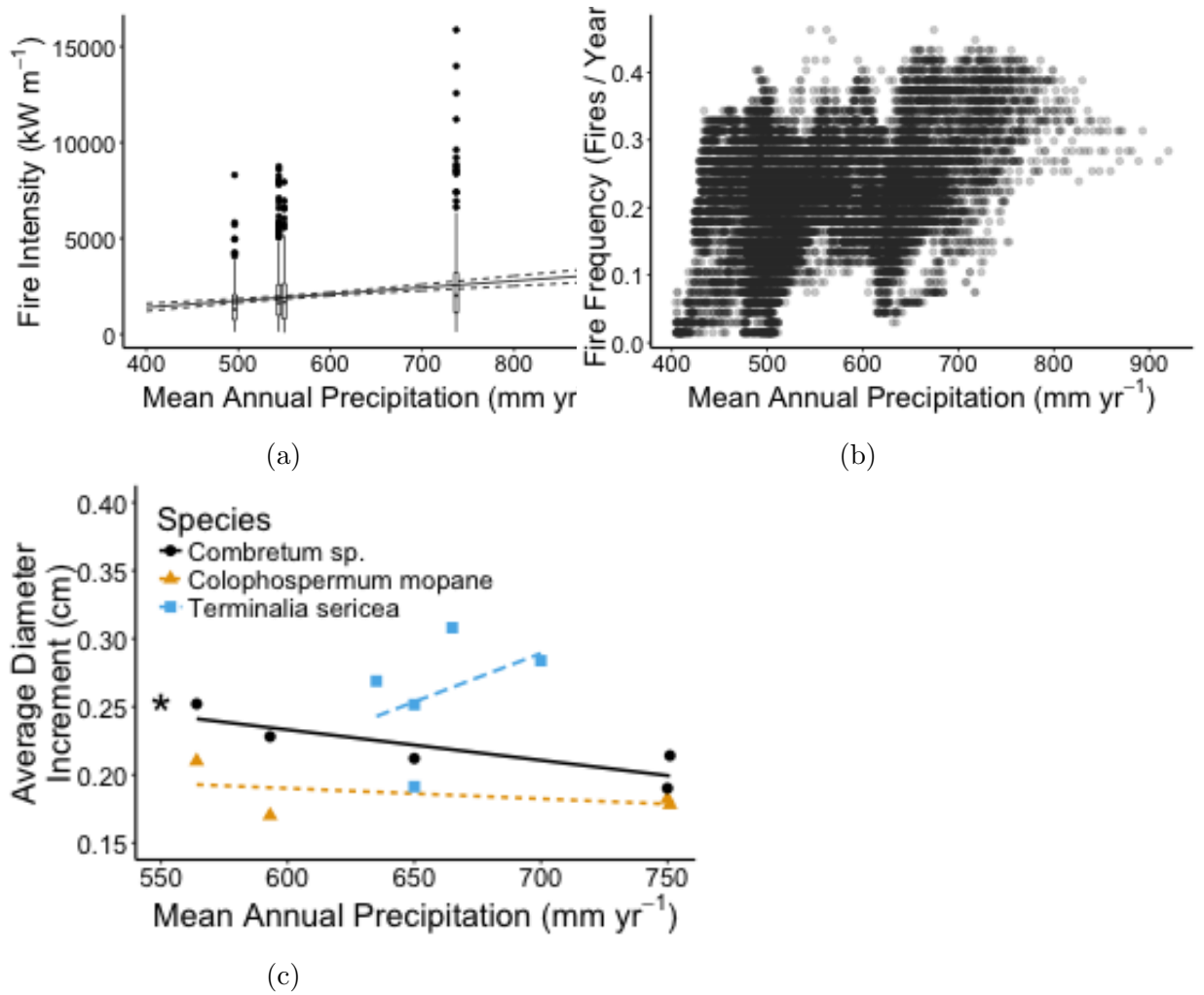


Figure 4.3: A. Byram's fireline intensity values reported from fires in the Experimental Burn Plots at Kruger National Park. Solid line is a gamma-distributed GLM (dashed lines are 95% CI) fit to the relationship between $I \sim \text{MAP}$. B. Distribution of fire frequency across MAP as derived from Smit et al. 2013. C. Reported average diameter increments (cm) of study species and the associated mean annual precipitation of the site. *Combretum* sp. relationship (denoted by asterisks) is significant at $p \leq 0.05$.

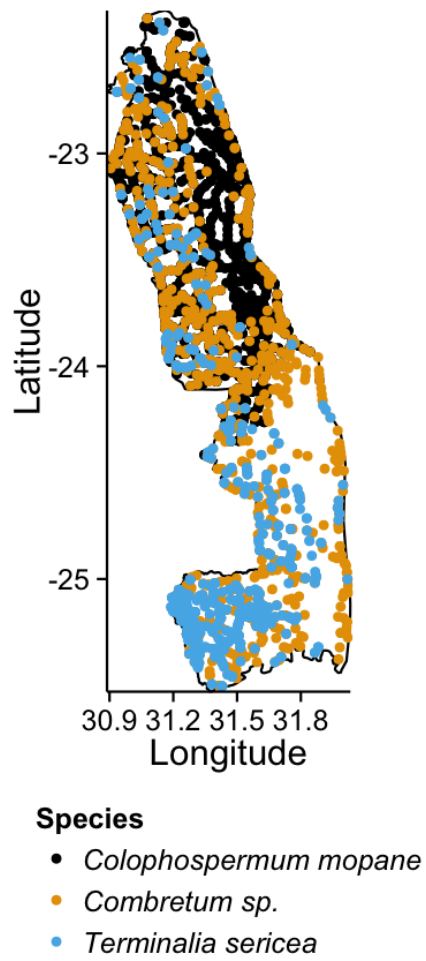


Figure 4.4: The species of study (*Terminalia sericea*, *Colophospermum mopane*, and *Combretum apiculatum* and *Combretum zeyhari*, coded as *Combretum sp.*) are widely distributed across the rainfall gradient present at Kruger National Park, South Africa.

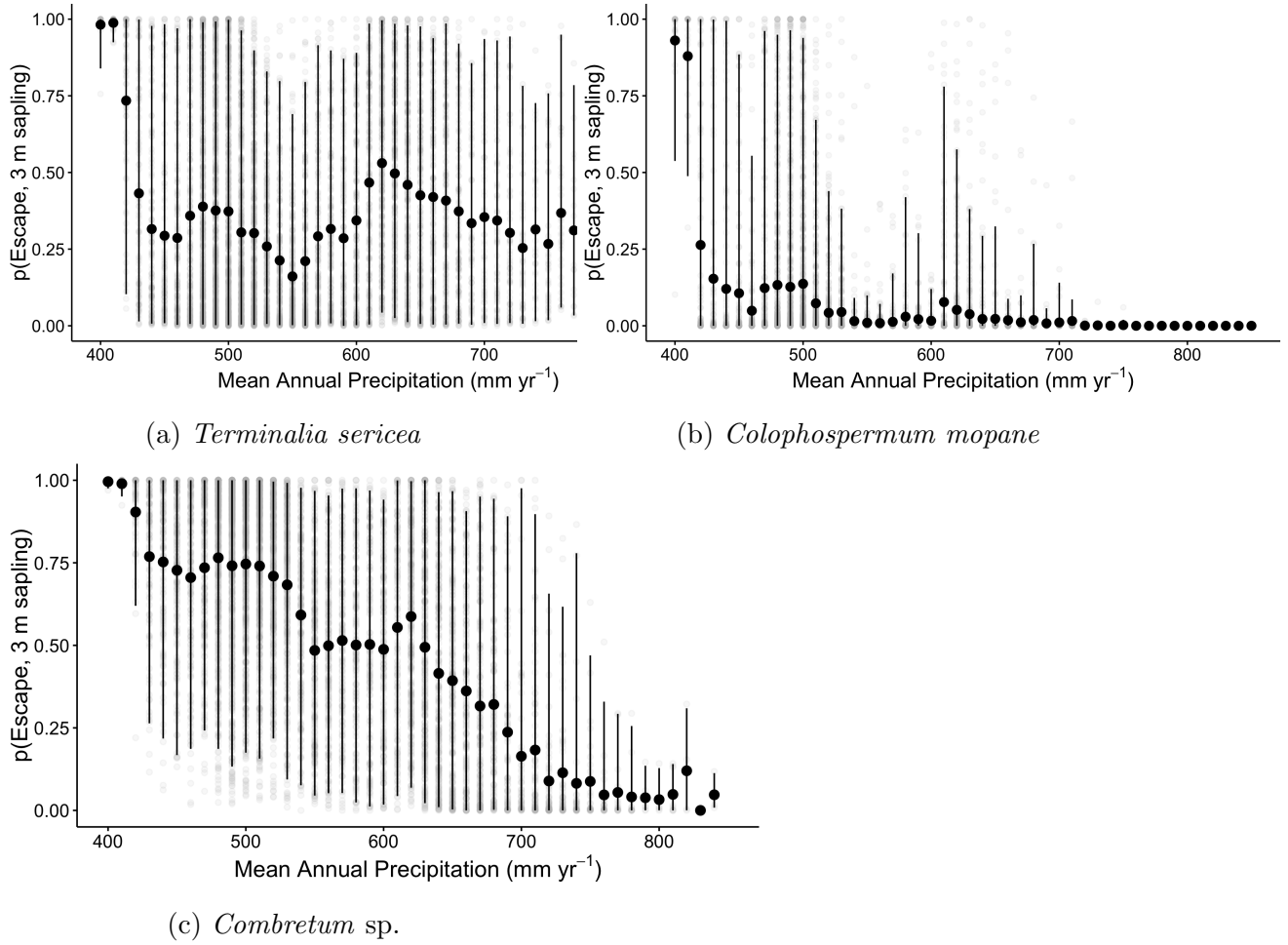
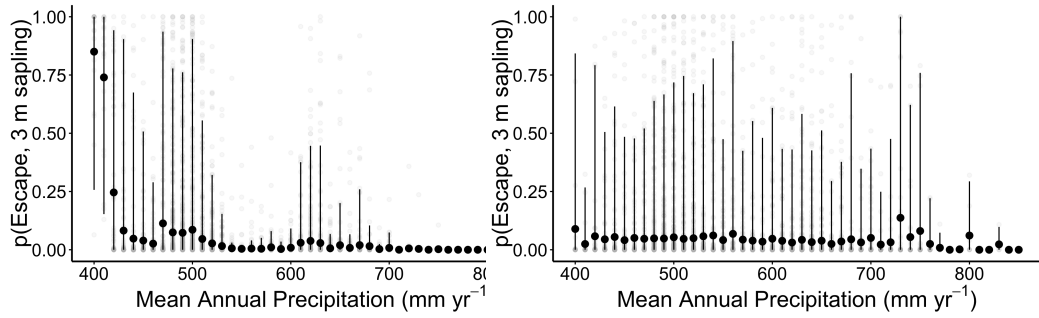
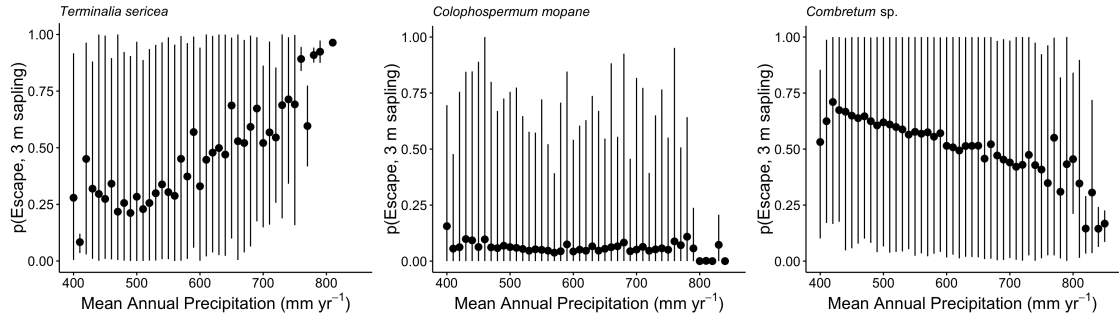


Figure 4.5: Variation in probability of topkill as a function of rainfall with three different growth-responses relative to rainfall: A) *Terminalia sericea*, B) *Colophospermum mopane*, and C) *Combretum sp.* Points are averages and lines show ranges of values in 2.5% - 97.5% quantiles as calculated in 10 mm yr⁻¹ rainfall bins.

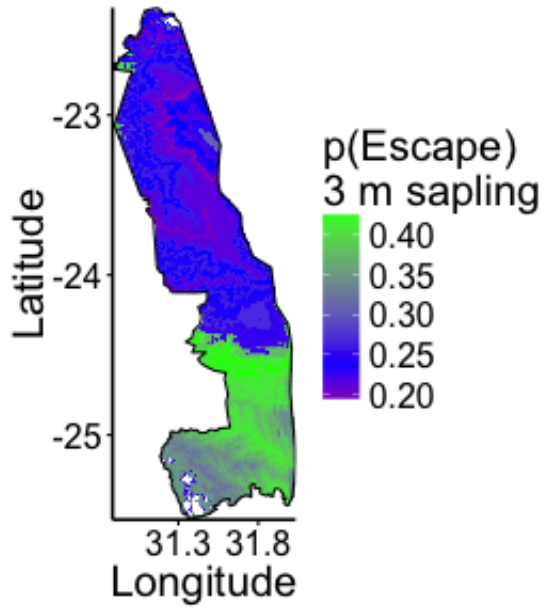


(a) Only fire frequency varies with MAP (b) Only fire intensity varies with MAP

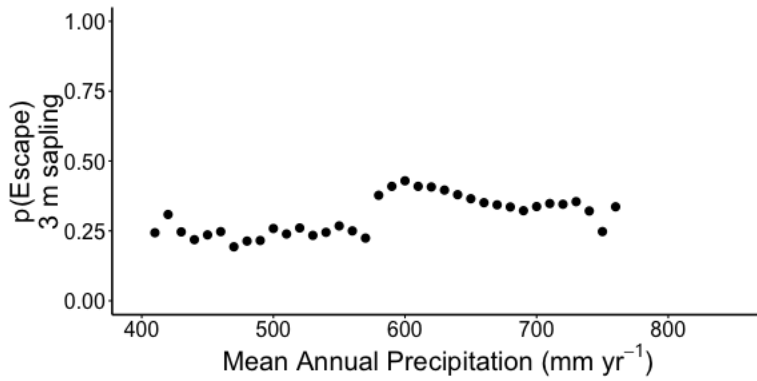


(c) Only growth varies with MAP

Figure 4.6: Predictions from variability analysis. Model was rerun with only (A) fire frequency, (B) intensity, and (C) growth rates by species varying with rainfall. Points are averages and lines show ranges of values in 2.5% - 97.5% percentiles as calculated in 10 mm yr^{-1} rainfall bins.



(a)



(b)

Figure 4.7: Spatial distribution of probability of escape A) mapped and B) plotted across Kruger National Park, South Africa. Weighted mean probability of escape was predicted based on relative abundance of *Terminalia sericea*, *Combretum* sp., and *Colophospermum mopane* in 10 mm yr⁻¹ rainfall bins across the park.

Table 4.1: Models were rerun to include only rainfall-linked variation for particular variables. The predicted probability of escape were then compared to the species-specific “standard” escape predictions with linear models. The strength of the effect of different factors varied by species.

Species	Source of Variation	Adj. R²	AIC
<i>C. mopane</i>	Only Frequency Varies	0.872	-78.5913
	Only Growth Varies	0.100	-43.4498
	Only Intensity Varies	-0.04	-61.5176
<i>Combretum</i> sp.	Only Growth Varies	0.863	-64.8287
	Only Frequency Varies	0.489	-20.2012
	Only Intensity Varies	-0.025	3.4805
<i>T. sericea</i>	Only Intensity Varies	0.163	-75.1212
	Only Frequency Varies	0.076	-71.7723
	Only Growth Varies	-0.004	-68.9193

Chapter 5

Summary and concluding remarks

5.1 Overview

It has been established previously that fire has an important role in Southern African savannas. At broad scales, fire affects the structure (Higgins et al., 2007) and composition (Scholtz et al., 2014) of woody species, but this relationship varies based on rainfall (Higgins et al., 2007) and productivity (Smit et al., 2013). Disturbance, particularly fire, is thought to limit woody cover in savannas with mean annual precipitation above 650 mm (Sankaran et al., 2005). As rainfall increases, grass fuel load, and, consequently, fire frequency and intensity, also generally increase (Moustakas et al., 2013; Smit et al., 2013; Govender et al., 2006a). However, despite this, average percent woody cover in savannas *increases* above 650 mm, and continues until this relationship saturates and the biome shifts into a forest. This introduces a key paradox: how does tree cover, thought to be limited by fire, also increase with

increasing fire frequency and intensity?

We investigated this central question through an explicitly spatial framework, using Kruger National Park, South Africa as our model system. We sought to model this relationship using best available data from a wide variety of studies as well as through empirical observations of fire. We measured variation in fire intensity as a function of tree canopies and woody cover, to determine if feedbacks from trees could reduce fire intensity in a meaningful way. Lastly, we empirically verified the role of fireline intensity in driving fire effects and fire severity through two different independent datasets.

5.2 Chapter Summaries

5.2.1 Fire Behavior Summary

We measured fire intensity as a function of grass fuel load and both canopy cover and woody cover. Grass fuel load predicted two of our measurements (*maxTemp*, *sumTemp*, but not *Duration*). For *maxTemp* and *sumTemp*, we found greater explanatory power by including some metric of woody cover with grass fuel load; for *Duration*, results were best predicted by just a metric of woody cover (Table 2.2). Surprisingly, this relationship was positive for all significant variables: in our experiments, fire intensity increased with both woody cover and grass fuel load.

Our results are contrary to our expectations, as well as the hypothesized feedbacks between increasing woody cover and decreasing fire intensity (Sankaran et al., 2004). These feedbacks almost certainly occur in forests (Hoffmann et al., 2012,

2011; Hoffmann and Solbrig, 2003), but within the relatively mesic sites in which we sample (451 - 702 mm yr⁻¹), there are potential facilitative effects of trees on grass (belsky1994influences). Thus, these effects may carryover into increased fire intensity around some woody species, which may overshadow any inhibitory effects of woody species on grass (through either competition or increased fuel moisture) or fire behavior (through increased wind turbulence). Alternatively, whatever soil nutrient or hydrological mechanisms may be increasing woody cover in a neighborhood around our sensors may also be increasing grass fuel loads, and thus fire intensity increases. Both February et al. (2013) and Moustakas et al. (2013) found either a lack of or positive relationships between tree cover and grass productivity in research at similar sites in Kruger National Park. Their results did not identify mechanisms, but do present a supportive evidence for our results from similar *in situ* studies.

5.2.2 Modeling Summary

Our modeling effort provided a number of novel conclusions. We show that topkill probability can vary widely within a given rainfall scenario, due to the interrelationships of collinear but widely varying variation in fire frequency, fireline intensity, and tree growth rates. We note in our literature review the general poverty of tree growth data for savannas, and suggest that this severely limits our ability to effectively model this component.

Our models suggest that probability of topkill varies with tree species, and that this variation varies across the niches in which these species are found. When accounting for variation in species distribution across rainfall gradients, we show that average probability of escape is functionally flat with increases in rainfall (Figure 4.7b). This

is driven by the general increase in tree growth rates at wetter sites, which gives trees advantages over the more frequent and more intense fires found in these sites. This challenges the assumption that is more important at maintaining low tree dominance in wetter savannas than in drier savannas (Sankaran et al., 2005); if that were the case, we would observe lower probability of escape at wetter sites than at drier sites.

These results also support the hypothesis that not all fires are ecological meaningful to all communities. Although any given fire may positively or negatively affect a less fire tolerant organism like an amphibian, a “normal” fires may be unable to effect meaningful ecological change on the many fire adapted woody species in savannas. Thus, higher severity outlier fires, perhaps combined with other ecological stresses like drought, may exhibit greater control on tree / grass dynamics than fires within the normal range of variation.

5.2.3 Fire Severity Summary

Our research into fire severity presented a number of surprising and useful results. We quantitatively linked multiple metrics of fire severity to Byram’s fireline intensity. Although previous work had shown that fireline intensity was important for predicting topkill, we showed that it could be used for predicting a wide range of categorical and continuous descriptions of fire severity (Figure 3.6). These relationships held across the soil, vegetative, and rainfall conditions captured by the Experimental Burn Plots.

Interestingly, we provided evidence that, for the sampled wildfires, the severity of impact on woody cover decreased with increasing woody cover (Figure 3.2a). This provides indirect support that increasing woody cover reduces fire behavior through feedbacks on wind (van Langevelde et al., 2014), fuel moisture and composition (Hoff-

mann et al., 2011), or, potentially, grass species composition relative to flammability. Degree of severity of herbaceous consumption, conversely, increased with mean annual precipitation (Figure 3.2b), which may be linked to increasing grass fuel loads in higher rainfall sites providing more continuous fuels for fire propagation (Govender et al., 2006a).

5.3 Key Conclusions

We questioned the two assumptions underpinning bistability of mesic savannas: 1) trees are suppressed by fire more with increasing rainfall and 2) trees produce feedbacks on woody cover that reduce fire intensity.

5.3.1 Probability of Escape and MAP

Our modeling does not support the contention that fire is more important at controlling tree cover at higher rainfall sites than in lower rainfall sites. Although intraspecific trends suggest the potential for trees to be suppressed by fire at increasingly wetter sites, when accounting for species turnover, this relationship changes: overall, probability of escape remains similar across a precipitation gradient. These results do not support this widely accepted assumption of bistability.

Our modeling results suggest the importance of growth rates relative to fire frequency and fire intensity. Different trees on average grow faster or slower relative to one another, and this variation, when combined with other factors, affects their resistance to fire and their likelihood of escaping the fire trap. Previous work in southern African savannas has emphasized the importance of the fastest growing trees (Wake-

ling et al., 2011), but our knowledge of how this varies within species at different life history stages and between species is poor. Research in Australian eucalypt savannas has shown the importance of understanding this variation with regard to how trees escape fire (Dantas and Pausas, 2013; Werner, 2012; Lawes et al., 2011), but we lack this nuanced understanding for many common species in southern African savannas.

Our results also suggest the importance of quantifying variation in and between fires. Although spatial variation is certainly important, so too are other levels of variation. We showed that fire effects on tree escape probability is generally flat across rainfall gradients, but there are increases in tree cover in wetter sites. This may be explained by uncaptured variation in and between fires. Just as the fastest growing individuals are more likely to escape “average” fires (Wakeling et al., 2011), so too may the most intense fires have an outsized effect on plant and animal communities. Understanding the conditions that create more severe fires, and how these fires affect different biotic communities, may be essential to improving our understanding of how to effectively use fire and which fires to suppress.

5.3.2 Tree feedbacks and fire

Our results suggest a scale dependent relationship between fires and their impact on woody cover. Our individual-based model suggests that increasing MAP does not exhibit increasing control on individual tree escape (Figure 4.7b). However, our analyses of fire severity in Kruger suggest a negative relationship between increasing woody cover (which tracks broadly with MAP, Sankaran et al. (2005)) and impact on woody cover (Figure 3.2a), suggesting feedbacks that may occur to reduce fire behavior in wetter, woodier sites. These effects may not be apparent at the level of the individ-

ual when modeled through relationships between fire frequency, fireline intensity, and growth rate, but could appear through spatially-linked, scaling processes.

However, at a scale, we observed a weak positive relationship between woody cover and fire intensity. We observed no relationship between woody cover or canopy coverage and grass biomass. These results undermine the assumption that trees produce feedbacks that reduce fire intensity around them.

5.4 Conclusion

Savannas are defined by interactions of trees and grass, and fire is certainly an important component of this. We investigated two assumptions for bistability in mesic savannas ($< 650 \text{ mm yr}^{-1}$ MAP), and did not find support for these assumptions within our inference space. Our modeling efforts suggest that fire may not exert as powerful a control on woody cover as previously thought, but our empirical studies still suggest an important interaction between woody cover and fire. Our results do not rule out the potential for bistability at greater MAP, as Staver et al. (2011b); Hoffmann et al. (2012) suggest. Our research opens the door for further investigations of tree growth rates, micro-scale variation in fire behavior, and drivers of fire severity in savannas.

Appendix A

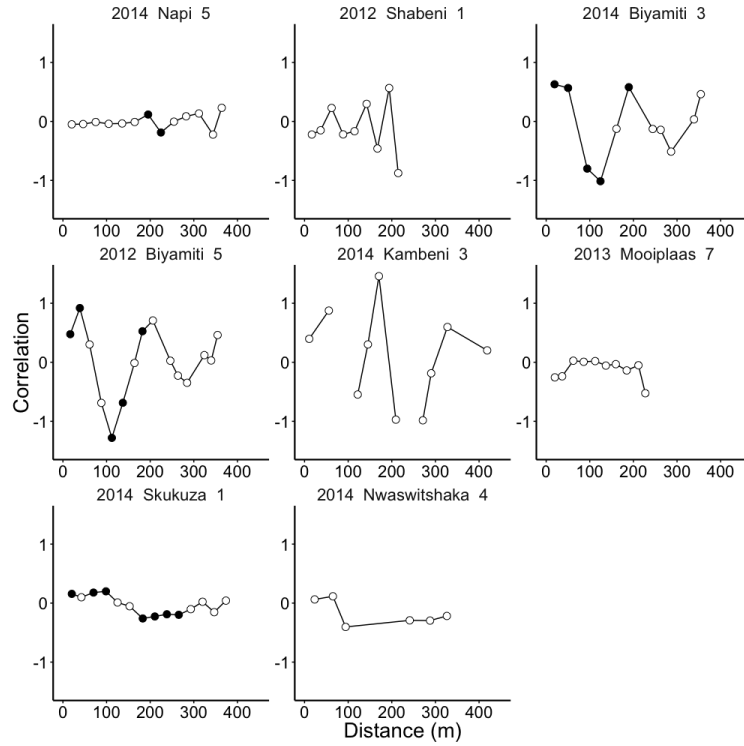


Figure A.1: Correlogram of maximum temperatures recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p \leq 0.05$ lag distances.

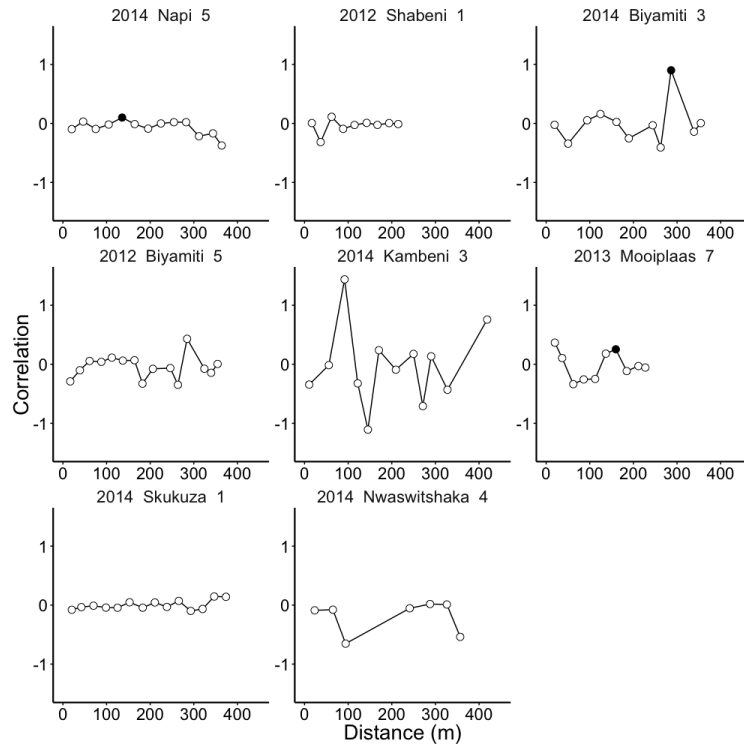


Figure A.2: Correlogram of residuals of models fit to maximum temperatures recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p \leq 0.05$ lag distances.

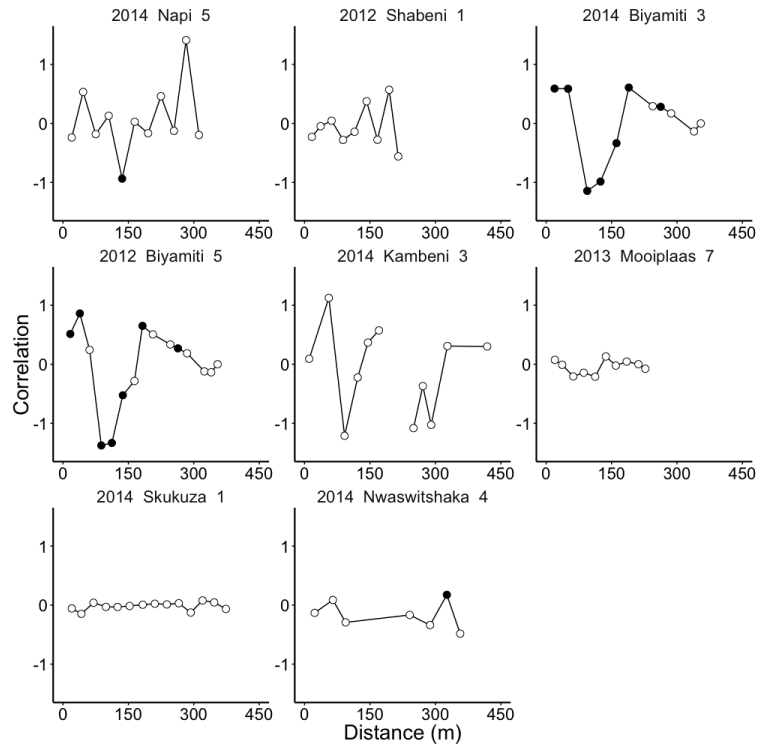


Figure A.3: Correlogram of summed temperatures recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p \leq 0.05$ lag distances.

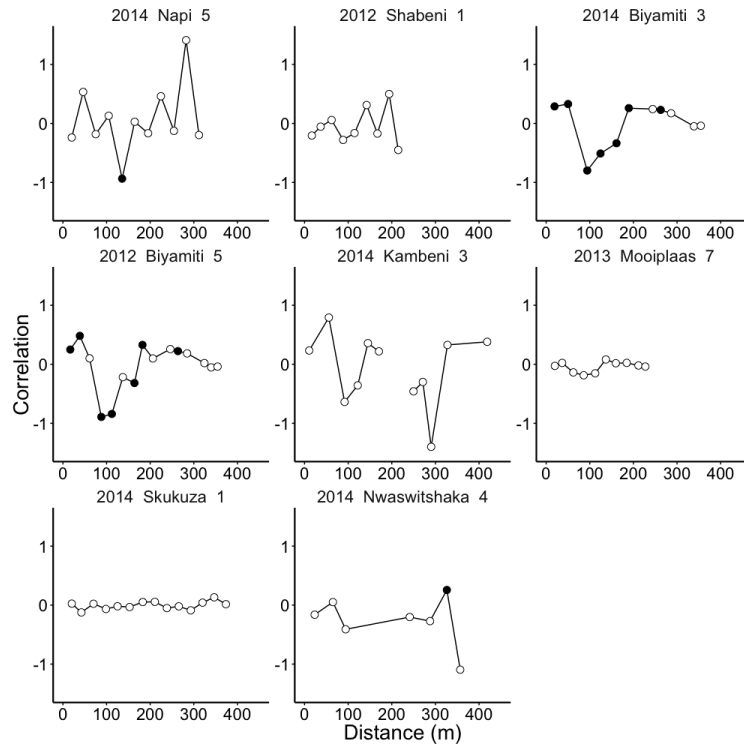


Figure A.4: Correlogram of residuals of models fit to summed temperatures recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p = 0.05$ lag distances.

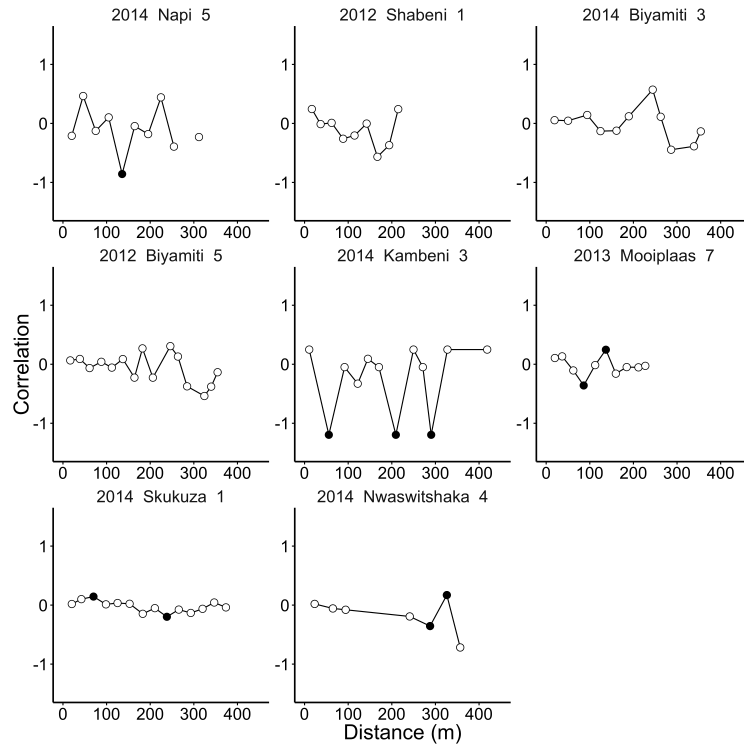


Figure A.5: Correlogram of fire durations recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p \leq 0.05$ lag distances.

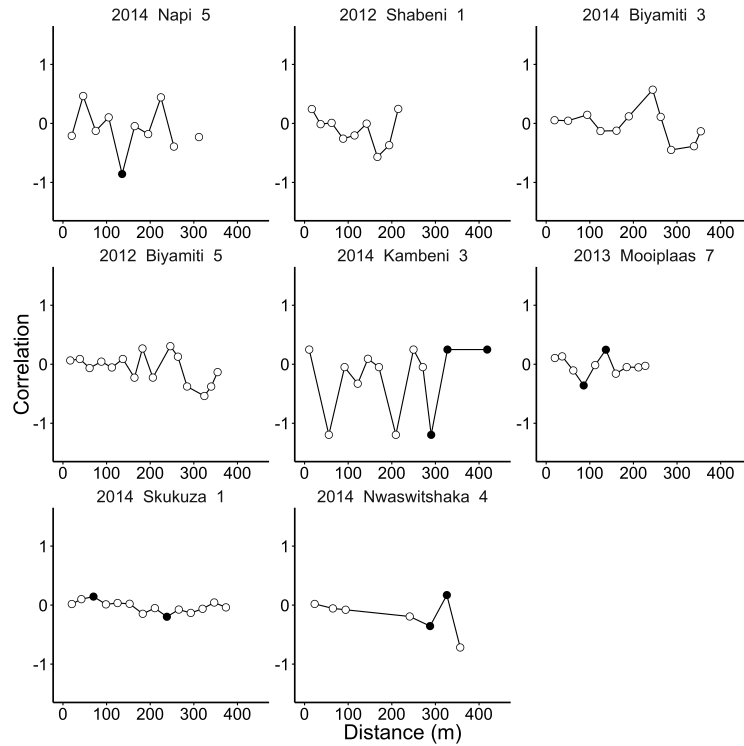


Figure A.6: Correlogram of residuals of models fit to fire durations recorded per plot by experimental burn (Year and Site). Black circles indicate significantly correlated values at $p \leq 0.05$ lag distances.

Appendix B

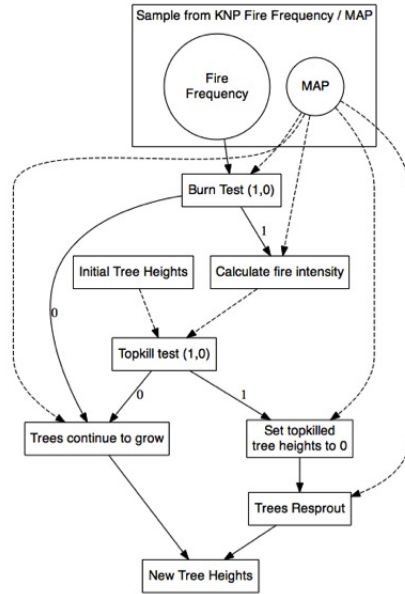


Figure B.1: Model diagram showing how initial paired values of fire frequency and MAP are sampled from the Smit et al. (2012) data set for KNP. Dashed lines show where outputs or values are used as functions in models; Solid lines show model flow.

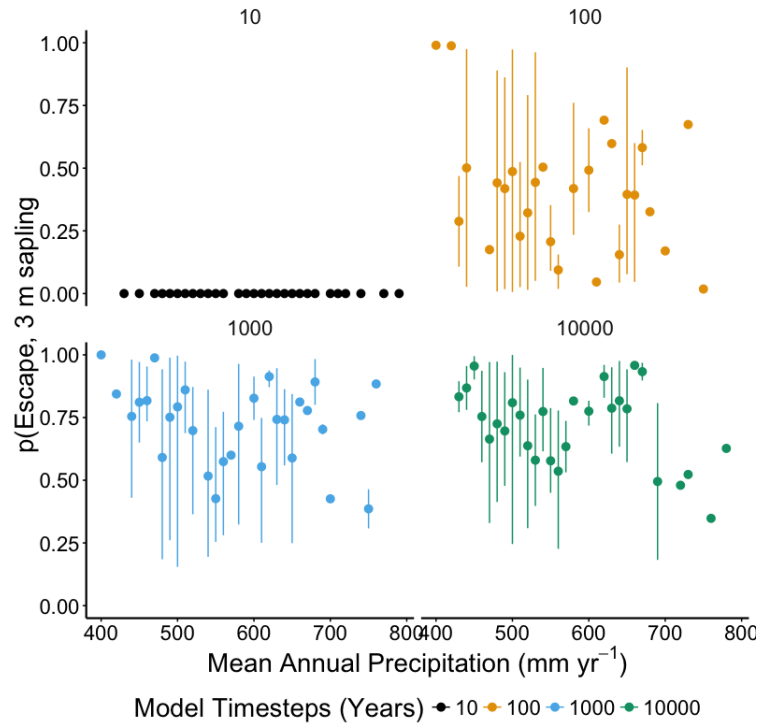


Figure B.2: The default model (*Terminalia sericea*, positive rainfall-linked growth) was run with varying time limits (10, 100, 1,000, 10,000 years) to assess whether this affected the probability of topkill.

Table B.1: Variables and parameters used in the model.

Variable	Description	Value
Trees	The number of trees in each model run.	500
Model Runs	The number of times a model scenario is repeated	10,000
Years	The number of model time steps.	100
β_0 [S]	Error term in intensity model	0
β_1 [S]	Non-specific coefficient for effect of height on probability of topkill	-3.9
β_2 [S]	Non-specific coefficient for effect of intensity on probability of topkill	0.05
β_3 [S]	Non-specific coefficient for effect of season on probability of topkill	1

Table B.2: Annual radial increment measurements, the mean annual rainfall in which the samples were collected, and the studies that collected the data.

Species	Site	MAP (mm)	ADI (cm yr ⁻¹)	Citation	Original Format
<i>C. mopane</i>	Oshikoto, NA	504	0.22	Mushove <i>et al.</i> 1995	Δ Diameter
<i>C. mopane</i>	Chiredzi, ZM	564	0.21	Mushove <i>et al.</i> 1995	Δ Diameter
<i>C. mopane</i>	Kadoma, ZW	593	0.17	Prior and Cutler 1996	Δ Radius
<i>C. mopane</i>	Zambezi Valley, ZM	750	0.18	Mushove <i>et al.</i> 1995	Δ Diameter
<i>C. mopane</i>	Kadoma, ZM	751	0.17	Mushove <i>et al.</i> 1995	Δ Diameter
<i>Combretum</i> sp.	Chiredzi, ZW	564	0.25	Prior and Cutler 1996	Δ Radius
<i>Combretum</i> sp.	Matapos, ZW	593	0.23	Prior and Cutler 1996	Δ Radius
<i>Combretum</i> sp.	Hwange NP, ZW	650	0.21	Holdo 2005	Δ Diameter
<i>Combretum</i> sp.	Zambezi Valley, ZW	750	0.19	Prior and Cutler 1996	Δ Radius
<i>Combretum</i> sp.	Kadoma, ZW	751	0.21	Prior and Cutler 1996	Δ Radius
<i>T. sericea</i>	Forest Hill, ZW	635	0.27	Calvert 1993	Δ Diameter
<i>T. sericea</i>	Hwange NP, ZW	650	0.53	Childes 1984	Δ Circumference
<i>T. sericea</i>	Hwange NP, ZW	650	0.19	Holdo 2005	Δ Diameter
<i>T. sericea</i>	Wits Rural, ZA	665	0.3	Shackleton 2001	Δ Circumference
<i>T. sericea</i>	Tembe, ZA	700	0.28	Gaugris <i>et al.</i> 2008	Δ Circumference

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VITA

Daniel Godwin was born and raised in Tallahassee, FL. He attended the University of Florida for undergraduate, earning a Bachelor of Science in Geography, a Bachelor of Arts in Anthropology, and a Minor in African Studies. He conducted research in Namibia and Botswana on mapping savanna tree communities through satellite imaging. After graduating in 2008, he began working with The Nature Conservancy as a prescribed fire practitioner. In 2011, he began his graduate career at the University of Missouri - Columbia with Dr. Ricardo Holdo.

While pursuing his graduate work, Daniel stayed active in the professional fire management community. He served on the executive board of the Missouri Prescribed Fire Council and organized two meetings. He founded the local chapter of the Student Association for Fire Ecology (SAFE), bringing in over \$20,000 in grants, and went on to serve as the national president of SAFE. He collaborated on a number of Fire Learning Network Prescribed Fire Training Exchanges, and served as the Acting Assistant Engine Captain at Mesa Verde National Park.

Daniel will be starting his new career as a Wildland Fire Analyst with the Center for Environmental Management of Military Lands in Fort Collins, CO, where he will be joining his partner.