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The long-term effects of fire frequency and season on the woody vegetation in the Pretoriuskop Sourveld of The Kruger National Park

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1 INTRODUCTION

Savanna ecosystems can be broadly described as “tropical grasslands with scattered trees” (Bourliere and Hadley 1970). The term savanna, refers to “a suite of tropical and subtropical vegetation types in which fire-adapted, co-dominant, continuous or discontinuous herbaceous [dominated by C_4 grasses] and largely deciduous woody strata experience markedly seasonal growth patterns and processes in relation to the seasonal delivery of precipitation, which occurs during hot summers, followed by cooler, but warm, dry winters” (Shackleton *et al.* 1999). The co-existence of the tree and grass elements as dominant components is a key factor that distinguishes savannas from other ecosystems (Scholes and Walker 1993, Scholes and Archer 1997). Fire is a dominant feature in savannas and is thought to have played a role in the evolution, establishment, and growth of savanna and grassland ecosystems from their woodland and forest origins (Vogl 1974; Bond and Van Wilgen 1995; Higgins *et al.* 2000, Bond *et al.* 2005). Fire is seen as one of the primary biotic factors, along with soil water depth, that mediates the co-existence between the tree and grass components in savanna ecosystems (Walter 1971, Walker and Noy-Meir 1982, Scholes and Walker 1993, Scholes 1997, Scholes and Archer 1997, Higgins *et al.* 2000, Bond *et al.* 2005).

The use of fire in the conservation management of savanna ecosystems has been and still is a controversial issue. This is mainly because fire has traditionally been used as an inexpensive and powerful management tool, instead of being viewed as an ecosystem process. However, this mindset has changed since the mid 1980’s with process based conservation management objectives having gained ground.

The formulation and implementation of a fire management policy in the Kruger National Park (KNP) in the early 1950's was characterised by controversy and disagreement. This controversy highlighted the lack of data and understanding of the role that fire played in this predominantly arid savanna ecosystem. In response to this controversy, a fire experiment was started in 1954, and the aim of the experiment was to provide a scientific basis for fire management policies within the KNP.

The experimental design of the fire experiment was a pseudo-randomised block design in which 12 fire treatments were replicated four times each, in each of four major veld types defined in the KNP by HP Van Der Schijff who was the resident assistant research biologist in Skukuza at the time (Van Der Schijff 1958). The four major veld types were, the sourveld of Pretoriuskop, the *Combretum* veld surrounding Skukuza, the Knob-thorn - Marula veld near Satara, and the Mopane veld between Shingwedzi and Letaba. The twelve treatments were no fire, annual fire in August, and biennial and triennial fires in February, April, August, October, and December.

In the mid 1990’s the Kruger National Park Scientific Services came under pressure to justify the cost and continued existence of the Experimental Burn Plots (EBP) experiment. Efforts were initiated to consolidate existing data and findings in order to finalise the experiment and provide recommendations regarding the future of the experiment and the experimental infrastructure. This MSc forms part of the finalisation of the Experimental Burn Plot experiment in the Pretoriuskop region of the Kruger National Park.

1.1 AIMS AND OBJECTIVES

The aim of this MSc was to investigate the long-term effects of the twelve fire treatments on the density, structure, and species composition of the woody vegetation in the Pretoriuskop sourveld region of the Kruger National Park.

The objectives of this study were to:

1. Conduct a complete survey of the trees and shrubs on the Pretoriuskop EBPs. In 1954, a baseline survey of the woody vegetation on each of the Pretoriuskop EBPs was conducted before the

experiment was started. Resurveying the Pretoriuskop EBPs in 1996 completed a 42-year period over which the long-term application of the fire treatments on the woody vegetation density, structure, and composition were investigated.

2. Capture into a digital format pertinent woody vegetation survey data from surveys that were conducted on the Pretoriuskop EBPs between 1954 and 1996. Since the inception of the EBP experiment, in 1954 a number of surveys had been conducted on the woody vegetation of the Pretoriuskop EBPs. However, none of the datasets from these surveys were available digitally and these required capturing and formatting.
3. Compare the density, structure, and composition of the woody vegetation on the Pretoriuskop EBPs between 1954 and 1996 to determine the effects of the prolonged application of the fire treatments on the woody vegetation. The Pretoriuskop EBP experiment is unique in the length of time that the experiment has been running and the comprehensive nature of the data available from the experiment. This provided a rare opportunity to investigate the effects of fire frequency and timing on the woody vegetation density, structure, and composition of the Pretoriuskop region.
4. Investigate the history of the Kruger National Park Experimental Burn Plots experiment. It is important to understand the historical context of the EBP experiment because it provides a framework within which the scientific value of the experiment can be assessed.

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2 LITERATURE REVIEW

Vegetation fires are a global phenomenon, and although the properties of fire (intensity, type, season, extent, and frequency) vary considerably between ecosystems, the role of fire is often pivotal for ecosystem structure and functioning.

2.1 THE DETERMINANTS OF FIRE

The occurrence of fire in natural vegetation is dependent upon a number of factors (Bond and Van Wilgen 1996; Van Wilgen and Scholes 1997):

- There must be enough suitable fuel to support a fire.
- The climatic and soil conditions must support the growth of a vegetation structure, which provides suitable fuel to support a fire.
- Suitable weather conditions for a fire must be present.
- There must be an ignition source.

These factors vary from ecosystem to ecosystem and contribute to a wide variety of fire regimes globally. The determinants of fire can be broadly categorised into environmental determinants, vegetation determinants, fuel determinants, and fire characteristics (Figure 2-1). Unlike many other disturbance forces, fire is influenced by the biota of an ecosystem and hence the determinants of that ecosystem. Furthermore, each fire event is affected by previous fire events and impacts upon future fire events. This event-system feedback means that the characteristics of each fire event are determinants of the fire regime.

2.1.1 The environmental determinants of fire

Environmental characteristics such as climate, weather, soil, topography, herbivores, and ignition sources are the primary determinants of an ecosystem's fire regime (Figure 2-1). These characteristics determine whether fire will occur in an ecosystem, how regularly, and at what time of the year. Almost all vegetation types will burn if there is sufficient fuel to burn and if the fuel is dry enough to burn (Bond and Van Wilgen 1996; Van Wilgen and Scholes 1997). Therefore, the occurrence of fire is dependant on the soil, topography, and climate, which create an environment in which the primary production of the vegetation is high enough to produce suitable fuel to burn. The primary production of the vegetation must be greater than herbivore consumption and organic decomposition of the vegetation so that there is sufficient fuel accumulation to sustain fire. Furthermore, there must also be adequate dry periods so that the fuel is sufficiently dry to ignite, and finally, there must be ignition sources.

2.1.1.1 Climate and weather

Fires can occur under most climate regimes so long as there are periodic dry spells (Bond and Van Wilgen 1996). Climatic conditions also play an important role in determining when (season) and how often (frequency) fires occur, this is because climatic conditions are primary determinants of vegetation productivity. However, the weather plays an even more significant role in determining the exact occurrence and behaviour of fire. Apart from anthropogenic ignition sources, lightning, which is a weather related phenomenon, is considered the most widespread ignition source of wildfires (Komarek 1968, Komarek 1971). Furthermore, the moisture content of the fuel (living and moribund), which is also weather related, significantly affects the intensity and behaviour of fire (Trollope 1999b).

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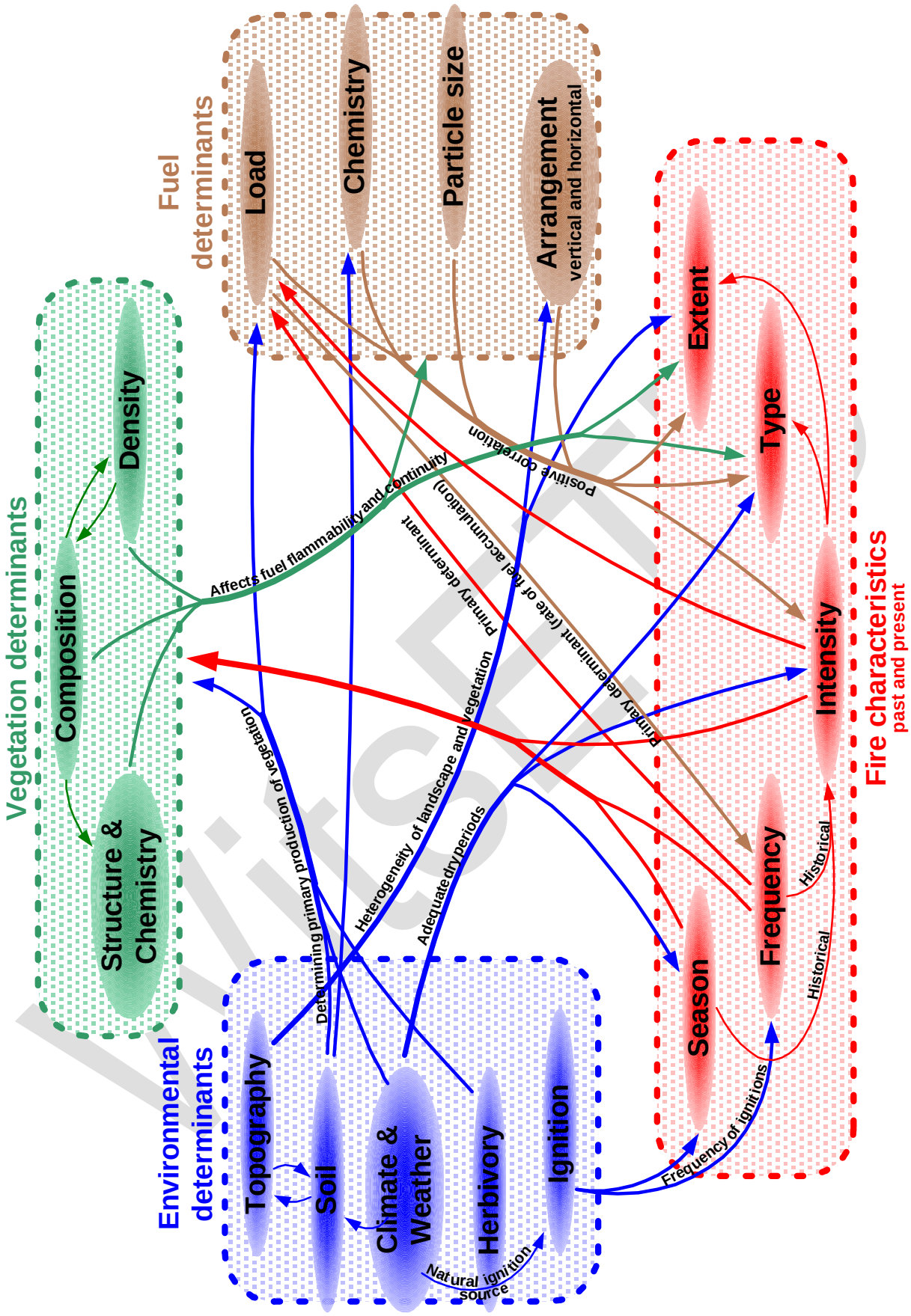

Figure 2-1: Model showing the interdependence of the determinants and characteristics of fire.

2.1.1.2 Soil and Topography

Soil and topography shape an ecosystem's fire regime in various ways. Both soil and topography determine the structure, composition, and density of the vegetation in an ecosystem (Witkowski and O'Connor 1996). For example, climatic conditions being similar, the primary production of vegetation is higher in ecosystems with fertile soils than in ecosystems with nutrient poor soils (Van Wilgen and Scholes 1997). This directly affects the amount of fuel and the fuel continuity within an ecosystem, which determines how a fire spreads through a landscape (Whelan 1995). Furthermore, topographic features such as rock outcrops, or less flammable plant communities can act as natural fire barriers hindering and even preventing the spread of fire within the landscape (Whelan 1995, Stalmans 2002).

2.1.1.3 Herbivory

Herbivores and fire are considered competitors for fuel, and so ecosystems with high levels of herbivory are less likely to burn than ecosystems with lower levels of herbivory (Van Wilgen and Scholes 1997). The converse is also true in that fires may have devastating effects on herbivore populations if they occur when food is scarce. These fire-herbivore interactions are mostly prevalent in grass-dominated ecosystems such as grasslands and savannas.

2.1.1.4 Ignition sources

All else being conducive, fire can only occur when there is an ignition source. The primary source of wildfire ignitions in most regions of the world in the last 10 to 20 thousand years has been anthropogenic (Komarek 1968, Komarek 1971). Lightening is the most general and widespread of the non-anthropogenic sources of ignition for wildfires (Komarek 1968, Komarek 1971). There are also records of less common sources of ignition such as rock falls and volcanic activity (Whelan 1995).

2.1.2 The characteristics of vegetation in fire prone ecosystems

The morphological, chemical, and structural properties of plants and plant communities play a significant role in the seasonal variability of their flammability (Whelan 1995, Bond and Van Wilgen 1996). This is because these characteristics influence the fuel properties of the vegetation, which determine whether, how and when an ecosystem will burn.

2.1.2.1 Structure and chemistry of the vegetation

The structure and chemistry of individual plants determines the structure and chemistry of fuel available to burn. The retention of dead plant parts is an important structural property that affects flammability (Bond and Van Wilgen 1996). The flammability of live plant material is much lower than that of dead plant material since the moisture content can be in excess of 200% greater in live plant material (Bond and Van Wilgen 1996). The physical structure of plants also contributes to their potential to burn. Fine leaves, stems and other plant parts, maximise the fuel surface area to air ratio, which optimises combustion of the fuel.

Furthermore, the chemical composition of plants also affects their flammability. Many plants have high concentrations of flammable oils and turpentines, which are effective herbivore deterrents. However, while protecting the plants from herbivory these chemicals make them highly susceptible to burning, and often at a higher intensity than if the chemicals were not present.

This poses the very interesting and tricky evolutionary question of whether flammability is an adaptive trait. This topic has been argued, with one notable hypothesis standing out, being that of Mutch (1970). Mutch proposed that the evolution of flammability was indeed an adaptive trait, the benefit being the exclusion of fire intolerant species within flammable communities. This hypothesis is fundamentally flawed since natural selection does not occur at the species or community level but rather at the level of the individual.

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Bond and Midgley (1995) rephrase Mutch's hypothesis to argue for the individual benefits of enhanced flammability. The essence of the individual benefits for enhanced flammability are "kill thy neighbour" and in doing so free up space and local resources for a more effective post fire recovery. Furthermore, in freeing up local resources and space the individual provides preferential sites for post fire recruitment into previously unoccupied space. This model predicts that enhanced flammability is most likely to evolve in dense tree populations such as conifer and eucalyptus forests, as opposed to in solitary trees such as in savanna ecosystems.

2.1.2.2 Species composition of the vegetation

The species composition of vegetation communities is critical to their flammability. Communities comprising flammable species, that is species with low moisture content and fine plant parts (leaves and stems), are likely to burn more vigorously than communities with less flammable species (Bond and Van Wilgen 1996).

2.1.2.3 Density of the vegetation

The density of the vegetation also plays a role in the flammability of vegetation since the homogeneity of fuel determines the rate of spread and extent of a fire.

2.1.3 The characteristics of fuel in fire prone ecosystems

Fuel is dead and/or live plant material that will burn. Fuel characteristics are a function of vegetation and environmental characteristics. Besides the quantity of material available to burn, the size, arrangement, and chemistry of the fuel are also important in determining the behaviour of fire within an ecosystem (Bond and Van Wilgen 1996) (Figure 2-1).

2.1.3.1 Fuel load

Fuel load is measured as the total dry weight of fuel per unit of surface area, and this is used as a surrogate measure of the amount of energy stored in the fuel (Whelan 1995). There is a strong positive correlation between fuel load and fire intensity (Whelan 1995). Fuel load is a function of time since the last fire, until the rate of fuel accumulation is balanced by the rate of fuel decomposition (Whelan 1995; Bond and Van Wilgen 1996). Decomposition is like herbivory in that it competes with fire for fuel, and ecosystems with high decomposition rates are less likely to burn than ecosystems with lower decomposition rates (Bond and Van Wilgen 1996). Hence nutrient rich ecosystems, in which the decomposition rates are fast, are less likely to burn than nutrient poor ecosystems, in which decomposition rates are slow.

2.1.3.2 Chemistry of the fuel

The chemical composition of the fuel affects the flammability of the fuel. The presence of oils, fats, waxes, and terpenes in dead and/or live fuel makes them more susceptible to fire (Whelan 1995; Bond and Van Wilgen 1996). These chemicals are volatile and are driven out of the plants at relatively low temperatures and then burn as gasses, this makes the fuel more flammable (Bond and Van Wilgen 1996). Furthermore, oils and waxes have up to two times the combustion heat values of other plant constituents resulting in more intense burning (Bond and Van Wilgen 1996).

2.1.3.3 Particle sizes of the fuel

The size distribution of fuel affects the likelihood of an ignition occurring (Whelan 1995; Bond and Van Wilgen 1996). The fuel size distribution also affects fire intensity because the size distribution affects the fuel surface area to air ratio (Whelan 1995; Bond and Van Wilgen 1996). The more fuel surface area that is in contact with air the more oxygen there is available to promote the combustion reaction. Once a fire has started the size of the fuel particles affects the rate of spread of the fire, the fire intensity, and the local

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persistence of high temperatures. This is because there are three stages when vegetation burns (Trollope 1983; Whelan 1995):

1. Preheating of the fuel just ahead of the fire front, in which the fuel is dried and slightly burnt.
2. Flaming combustion in which flammable hydrocarbon gasses are released and ignited
3. Glowing combustion phase in which the remaining charcoal is consumed leaving ash.

The fine fuels are consumed in the flaming combustion phase and are responsible for the spatial propagation of the fire (Whelan 1995), while the larger fuel particles are burnt more slowly in the glowing combustion phase and are responsible for the temporal longevity of the fire.

2.1.3.4 The vertical and horizontal arrangement of the fuel

The arrangement of the fuel is important in determining how hot a fire will be (intensity) and how extensively the fire will burn (size). Fuel that is packed tightly affects the aeration, and the combustion rate of the fuel (Whelan 1995), while fuel packed loosely affects the propagation of fire. The horizontal arrangement of fuel affects the rate of spread of fire and the fire size, while the vertical distribution of fuel is important in determining the type and intensity of a fire (Whelan 1995).

2.1.4 The characteristics of fire

As with most other recurrent disturbances, fire can be classified by a regime (Sousa 1984). The most important characteristics of a fire regime are type, intensity, timing, frequency, and extent (Figure 2-1).

2.1.4.1 Type of fire

There are three main types of vegetation fire, namely ground fires, surface fires and canopy fires (Trollope 1983, Albini 1993; Whelan 1995, Bond and Van Wilgen 1996). Ground fires occur in subsurface organic fuels, surface fires occur above ground in grass and litter layers, and crown fires spread through the canopy layer in stands of trees (Trollope 1983, Albini 1993; Whelan 1995, Bond and Van Wilgen 1996). The type of fire that occurs in an area depends on the type of vegetation and climate of the area (Whelan 1995). Furthermore, in fire managed areas the ignition procedure, namely point versus perimeter ignition, also determines the type of fire.

2.1.4.2 Timing of fire

The timing is when the fire occurs. This is important because soil moisture, vegetation moisture, humidity, and temperature change both daily and seasonally, and these are key factors in determining the behaviour of the fire and its intensity. The primary determinant of season is climate since this determines the season of natural ignition sources like lightning (Whelan 1995).

2.1.4.3 Frequency of fire

Frequency is how often fire events occur, which is generally a function of two factors: the rate of fuel accumulation since the last fire event and the frequency of ignitions (Whelan 1995).

2.1.4.4 Intensity of fire

Intensity is a measure of how fiercely a fire burns (Bond and Van Wilgen 1996). A number of characteristics are used to measure fire intensity, namely vertical distribution (mean flame height) of the fire, the rate of spread of the fire, the rate of heat release of the fire, and the total heat release (energy) of the fire (Trollope 1983, Whelan 1995). Once a fire has started, a range of factors affect the intensity of the fire like weather, topography (slope and aspect), fuel load, fuel distribution, and fuel chemistry (Whelan 1995; Bond and Van Wilgen 1996). Fire history will also have an affect on intensity (Whelan 1995).

2.1.4.4.1 The effect of fire frequency and fire timing on fire intensity

The intensity of a fire event is affected by the time of the fire event and the period since the last fire event. Fire frequency affects fire intensity because the amount of fuel accumulated before a fire event is related to the time since the previous fire event. This is because after a fire the fuel load increases until the rate of fuel decomposition equals the rate of fuel accumulation. Ecosystems that have high decomposition rates have lower fuel loads and ecosystems with low decomposition rates have higher fuels loads (Whelan 1995; Bond and Van Wilgen 1996). Fuel load determines the maximum energy available to a fire (Whelan 1995). This means that the higher the fuel load the more intense a fire is likely to be. Therefore, the intensity of a fire is related, among other things, to the time since the previous fire event. Fire timing affects fire intensity because soil, air, and fuel moisture are linked to season. These factors affect fire intensity directly and the higher the soil, air and fuel moisture the less intense a fire is likely to be.

2.1.4.5 Extent of fire

The extent of the fire is the size of the fire, or the surface area in space that is burnt by the fire. This is influenced by many of the characteristics that determine an ecosystem's fire regime. Topography and vegetation can create natural barriers to passage of fire in the landscape (Whelan 1995; Bond and Van Wilgen 1996). Fire history also plays a role because an area that has been burnt recently may be less flammable because of the patchy nature of the fuel (Whelan 1995).

The characteristics and determinants of fire are spatially and temporally interdependent on one another (Figure 2-1), and variations in these fire characteristics define the fire regimes for different ecosystems.

Fuel comprises both dead and/or live vegetation. It is quite interesting that the higher the productivity of a system, all-else being conducive, the higher the probability of fire. Plants ultimately contribute to their own conflagration.

2.2 HOW DO PLANTS SURVIVE FIRE EVENTS?

When considering the survival of plants in fire events there are two components to consider: (1) surviving the direct effects of fire, and (2) surviving in the post fire conditions (Whelan 1995).

2.2.1 Surviving the direct effects of fire

The direct effects of fire on plants are the result of raising the temperature of the living tissue. These can range from brief disruption of biochemical pathways to the complete combustion of the tissue resulting in mortality (Whelan 1995). The physical effects of fire on woody plants are burning the bark and killing cambium, leaves, buds, twigs, and branches (West 1969). Plants are made up of repeating units (modules) that make up the entire plant (genet) (Begon *et al.* 1986). Some modules can be damaged or even die without resulting in the death of the genet. This equips plants for a sessile existence in fire prone environments, where part of a plant may be burnt and die but the entire plant does not necessarily die. Some tissues are however critical to the survival of plants. For example damage to or death of meristematic tissue, which is important for new growth, is critical to the post fire persistence of a plant (Whelan 1995). Damage to the vascular tissue found in the cambium, which transports minerals and nutrients throughout the plant body, can result in the mortality of entire modules of a plant through starvation (Whelan 1995). Mortality of seeds, which are one of the mobile phases in a plant's life history, has a large impact on the continued persistence of individual plant genets and even that of the species within a fire prone environment (Mbalo and Witkowski 1997, Garner and Witkowski 1997).

There are two ways plants critical tissues survive fire:

1. The critical tissues can have higher lethal temperatures, which allow the tissues to survive exposure to heat. The lethal temperature of a tissue is affected by a number of factors, for example the state of

metabolic activity of the cells, and the level of hydration of the cells (Whelan 1995; Bond and Van Wilgen 1996). Lethal temperatures of a plant however, do not vary much regardless of the metabolic or hydration state of the plant (Whelan 1995; Bond and Van Wilgen 1996).

2. The critical tissues can be physically protected from fire damage, for example, cambium and meristematic tissues are protected from heat damage by bark (Whelan 1995; Bond and Van Wilgen 1996, Wilson and Witkowski 2003). Critical tissues can also be protected from heat damage by being placed out of harms way, for example, subterranean meristematic tissue and nutrient storage tissues are insulated against heat radiation by overlying soil, or meristematic tissues occur at a height that effectively protects them from being damaged by heat radiation (Whelan 1995). Seeds are protected from heat damage in a variety of ways such as having a protective fruit covering or being buried in the ground (Whelan 1995, Garner and Witkowski 1997).

Protecting critical tissue is not enough to ensure that a plant survives fire. Plants also require adequate non-structural carbohydrate reserves, which are necessary for them to sprout from meristematic tissues (Ligavha *et al.* 1999, Hoffmann *et al.* 2000). These non-structural carbohydrate reserves are replenished between fire events, and the replenishment of carbohydrate reserves following burning or cutting of woody plants may take 1 to 2 years (Miyanishi and Kellman 1986). Many woody fire tolerant savanna species form underground carbohydrate storage organs called ligno-tubers, which provide the necessary non-structural carbohydrates for sprouting after fire damage.

Having protected the critical tissues from the direct effects of fire and stored enough carbohydrate reserves to sprout after a fire, what post fire survival strategies do plants have?

2.2.2 Post fire survival strategies

There are wide varieties of plant responses to fire. These responses can however, be categorised into four plant types (Whelan 1995; Bond and Van Wilgen 1996):

1. Annual and pauciennial plants: The life histories of these plants are not linked to fire because their life spans often occur completely between the fire events.
2. Fire ephemeral plants: These plants depend on fire for regeneration, and usually appear after fire events, have a short life span, and are usually dead before the next fire event.
3. Obligate seeding or non-sprouting plants: These plants usually die after a fire event without sprouting. The persistence of these species in an ecosystem rests solely on the production and germination of seeds. There are two main categories of non-sprouting plants, namely non-fire-recruiting non-sprouters and fire-recruiting non-sprouters.
    a. Non-fire-recruiting non-sprouters are plants that die after fire events and whose reproductive recruitment is not linked to fire events. These plants are not common in fire prone environments, however where the inter-fire periods are long enough they may become dominant, and can even transform the fuel properties of a community (Bond and Van Wilgen 1996).
    b. Fire-recruiting non-sprouters are plants that die after fire events and whose reproductive recruitment is linked to fire events. These plants have discrete populations of even-age cohorts with non-overlapping generations between fire events, and the populations usually decline between fires (Bond and Van Wilgen 1996). The main concern about the persistence of these species is the size of their seed banks. These species can become locally extinct when the inter-fire periods are too short or too long, when in both cases their seed banks become exhausted through seed germination without replacement or seeds losing viability (Bond and Van Wilgen 1996).
4. Sprouters: These plants survive fire events by sprouting from protected meristematic tissue. These plants may also rely on seeds for persistence. There are two main categories of sprouters, namely non-fire-recruiting and fire-recruiting sprouters.

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a. Non-fire-recruiting sprouters are plants that sprout in response to fire events and whose reproductive recruitment is not linked to fire events. Fire sensitive seedlings often die in fire events, and short inter-fire periods often eliminate fire sensitive juveniles. These populations often comprise overlapping generations because seed germination is not linked to discrete fire events. The populations usually increase between fire events (Bond and Van Wilgen 1996).
b. Fire-recruiting sprouters: These plants sprout in response to fire events and their reproductive recruitment is linked to fire events. These species have discrete population growth after fire events and the populations usually decline between fires (Bond and Van Wilgen 1996).

2.2.3 Post fire resilience and inertia

Plant life history phases can be classified as being resilient or inert to disturbance events such as fire (Malanson 1987). Resilient life history phases are those in which disturbance events affect the individuals in some way and the individuals then recover from the disturbance. Inert life history phases are those in which individuals resist the disturbance event in some way, and failure to resist the disturbance event results in mortality.

Sprouting species in fire prone ecosystems go through a number of life history phases such as the seedling phase, the suppressed juvenile phase, and adult phase. Each of these life history phases is different regarding their resilience or inertia to fire events. In the seedling phase, individuals are generally fire intolerant, and the post-fire mortality rate for these individuals is high. The seedling phase of sprouting species is an inertial phase in which individuals that fail to resist the disturbance event die. In the suppressed juvenile phase, individuals are fire tolerant but not sexually mature. Fire resistance and sexual maturity of individuals in the suppressed juvenile phase have been linked to the stem height of the plants and the thickness of the bark on the stems (Trollope 1999a, Higgins *et al.* 2000, Wilson and Witkowski 2003). Plants in the suppressed juvenile phase are often burnt back before their stems reach a height at which their bark is thick enough to protect the underlying cambium tissue. Bond and Van Wilgen (1996) call these suppressed individuals “gullivers” and they may persist in a stunted sexually inactive form in the herbaceous layer for many years constantly being suppressed by fire before escaping to a fire resistant height. Gullivers recover quickly from fire events even when they experience total top kill. The suppressed juvenile phase of sprouting species is a resilient phase in which the individuals are affected by the disturbance but they recover. In adult phase, individuals are fire resistant and sexually mature. Unless a fire event is unusually intense, the adults seldom die because of fire. The adult phase of sprouting species is an inertial phase in which the individuals resist the fire and most often survive. Very intense fire events may result in the mortality of adult sprouters because in the adult phase they seldom sprout after top kill (Whelan 1995).

Non-sprouting species in fire prone ecosystems are fire sensitive in all their life history phases. These individuals have an inertial response to fire throughout their lifetime and inevitably die when the fire events are too intense.

In a fire prone environment, frequent low intensity fires favour inert life history phases where individuals survive and persist after the fire events over resilient life history phases where the individuals must recover after the fire event (Malanson 1987). Very infrequent low intensity fires also favour inert life history phases, and high intensity fires at medium inter-fire periods favour resilient life history phases (Malanson 1987). Intermediate fire regimes comprising high and low intensity fires at a range of return periods favour the coexistence of resilient and inertial life history phases (Malanson 1987). Therefore, diversity is expected to be highest when a mixture of inertial and resilient responding individuals coexists. This occurs under an intermediate fire disturbance regime.

WITHDRAWN

2.2.4 Understanding species responses under different fire regimes

The make up of a woody community determines the effect fire events have on the vegetation density, structure, and composition of the woody vegetation. Post fire survival strategies of woody species describe the main effects fire events have on individuals. Resilience and inertia refine the description concerning the individuals' response to disturbance timing, frequency, intensity, and size. Post fire survival strategies and inertia and resilience responses of life history stages provide a convenient model for predicting community response to fire regimes. For example:

- When inter-fire periods are medium and fire intensities are high, resilient fire responses are expected to dominate over inert fire responses. The higher the intensity of a fire the higher the likelihood a woody plant has of being severely damaged. Inert individuals damaged by high intensity fires may be unable to recover and might die, whereas resilient individuals damaged by high intensity fires are able to recover, given adequate time between fire events.
- When the inter-fire periods are long, obligate seeders that reach sexual maturity between fire events are expected to coexist with sprouters.
- When the inter-fire periods are similar in length of time to the age of sexual maturity then fire-recruiting individuals (obligate seeders and sprouters), are expected to dominate over non-fire-recruiting individuals (obligate seeders and sprouters). This is because the reproductive potential of fire-recruiting individuals is maximised by their recruitment being synchronised with the inter-fire periods, and their potential for reaching fire resistant or fire tolerant heights between fire events is maximised.
- When the inter-fire periods are medium and the fire intensities are high, fire-recruiting sprouters are expected to dominate as fire suppressed juveniles, which are resilient life history phases.

2.3 SAVANNAS AS FIRE PRONE ENVIRONMENTS

Fire is a ubiquitous phenomenon and in comparison with other herbivorous activities can consume up to 80% of above ground primary production in some ecosystems (Bond and Van Wilgen 1996). Many ecosystems have developed with fire playing an integral and often pivotal role within the ecosystem's functioning, structure and composition. There are as many fire regimes as there are vegetation types and climate regimes, and they range from annual fires in grasslands to crown fires occurring every 100 – 1000 years in the North American coniferous forests (Bond and Van Wilgen 1996). The focus of this study is savanna ecosystems, in particular the southern African savannas.

Savannas are characterised by the coexistence of both grasses and trees. The tree-grass mix in savanna ecosystems ranges from woodlands with grass, to grasslands with trees, from near desert arid lands, to near tropical woodlands (Scholes and Walker 1993).

Globally savannas occupy some twenty percent of the earths land surface, and are second to tropical forests in contributing to terrestrial primary production. They occupy more than 40% of the land surface of Africa (Scholes and Walker 1993).

Savannas are difficult to define precisely, however, one common characteristic is that both the grass and woody components affect ecological processes, such as primary production, hydrology and nutrient cycling, above all other vegetation components (Scholes and Walker 1993).

Savannas are found on varied soil types however, soil organic matter content is generally low. They occur in the hot regions of the world that have highly seasonal rainfall and prolonged dry seasons, which permit frequent hot fires (Scholes and Walker 1993).

Fire plays a vital role in savanna ecosystem structure and function. It varies in return period from annual to more than ten years and up to fifty years between fire events. The main season for fire occurrence is the dry

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season. However, fires do occur all year round, with their intensity being lower and their size (extent) being smaller in the wet season (Scholes and Walker 1993; Bond and Van Wilgen 1996).

2.3.1 Determinants of southern African savannas

Four main factors (water supply, nutrient supply, herbivory and fire) determine savanna structure and function (Scholes and Walker 1993). These four factors have been used in trying to understand and model, savanna ecosystem dynamics, especially the seemingly unstable coexistence between trees and grass.

As water is a strong determinant in savanna ecosystems, they are found in areas whose average rainfall ranges from 350 to 1800 mm (Scholes and Walker 1993). The water requirements of savanna plants has been found to be a main determinant of the spatial plant patterns in savannas, which often closely match the pattern of subsurface water supply in space (Scholes and Walker 1993). Water availability also plays an important function because it determines the length of the period during which primary production and nutrient mineralization can occur in savanna ecosystems (Scholes and Walker 1993).

Savannas in Southern Africa have been classified into two main groups based on biotic patterns that coincide primarily with moisture availability (Huntley 1982). These two groups are arid savannas and moist savannas. Arid savannas are those that receive less than 650 mm rainfall annually, and moist savannas receive more than 650 mm rainfall annually (Huntley 1982). Moist savannas tend to be infertile with deeply leached soils, whereas arid savannas tend to be fertile (Scholes and Walker 1993; Van Wilgen and Scholes 1997). This association between savanna ecosystems and water appears to be quite clear. However, at finer scales plant water relationships have been used unsuccessfully in trying to model the tree-grass coexistence in savannas (Bond and Van Wilgen 1996).

2.3.2 The effect of fire on the woody vegetation of savanna ecosystems

The effect of fire on woody vegetation is dependent on the amount of heat energy released by the fire, the rate of spread, and the vertical profile of the heat distribution (Trollope 1984). The post fire survival strategy and resilience or inertia regarding fire of the life history phase of a plant determines the plant's response to fire.

The woody component of savanna ecosystems is dominated by species that sprout in response to fire damage (Scholes and Walker 1993; Bond and Van Wilgen 1996). The resilience or inertia to fire of the life history phases of sprouters determines their response to fire events. Seedlings usually die in fire events, however the mortality rates of suppressed juveniles, and adults are typically low but increase with increasing fire intensity (Higgins *et al.* 2000).

Frequent fire events appear to favour grassland and savanna ecosystems in regions with climates that are capable of supporting woodland and forest ecosystems (Vogl 1974). Fire interrupts the competitive advantage of the woody species and provides for the coexistence of both the woody and grass elements as dominant components (Malanson 1987, Scholes and Walker 1993, Scholes 1997, Higgins *et al.* 2000). Higgins *et al.* (2000) argue that variation in the abundance of trees in savanna ecosystems is dependant on demographic bottlenecks at the seedling recruitment or sapling release stage. Fire frequency regulates these demographic bottlenecks. The more frequent the fires the lower the chance of seedlings and saplings growing to a mature adult in between fire events. Mortality of these seedlings and saplings is not necessarily high and consequently a seedling and sapling "bank" develops. Sporadic favourable conditions (i.e. an unusually long period between successive fires) result in the release of seedlings and saplings, and these individuals grow to mature reproductive adults resulting in the density of adult tree population increasing to form savanna woodlands or forests. Periodically events occur (i.e. very intense fires) in which the mortality of the mature adult trees is high and the savanna woodlands and forests are converted to open savanna grasslands. Generally, the most universal effect of fire frequency on savanna woody plant communities is

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that as the fire interval increases, the density, height, canopy volume and biomass of the woody vegetation tends to increase (Scholes and Walker 1993).

2.3.3 The role of fire in the management of savanna ecosystems

Because the coexistence of trees and grass in savanna ecosystems is perceived to be so unstable, the role of management in maintaining the stasis in conservation areas has been a conscious and often controversial one. In many ecosystems not much can be controlled, however, fire has proved to be a very powerful and cost-effective management tool for both agricultural and conservation purposes. It can be used to prevent uncontrolled fires by reducing the fuel load, or to control parasite populations. However, even more importantly fire can be used to alter the vegetation structure and composition and has frequently been prescribed as a low cost means of opening up woodlands for pastoral purposes or opening up wooded areas that were not previously wooded (Trollope 1980, Sweet 1982).

The use of fire in conservation management has long been a controversial issue. The reason for this is that the role of fire within these ecosystems is not always clearly understood, and it was from these roots of disagreement and uncertainty that the Kruger National Park Experimental Burn Plots experiment was established in 1954.

2.4 ELEVATED CO_2 LEVELS, FIRE AND THE MANAGEMENT OF SAVANNA ECOSYSTEMS

C_4 grass dominated grasslands and savanna ecosystems appeared in the late Miocene period some six to eight million years ago (Cerling *et al.* 1997). The Miocene was a time of warmer global climates than those in the proceeding Oligocene, or the following Pliocene, and atmospheric CO_2 levels dropped below 500ppm during this period (Cerling *et al.* 1997). This drop in CO_2 levels favoured the expansion of C_4 grass dominated ecosystems over C_3 tree dominated ecosystems (Ehleringer *et al.* 1997). The widespread post industrialisation combustion of fossil fuels has resulted in a dramatic increase on the levels of tropospheric CO_2 (Ludewig *et al.* 1998). An increase in the levels of atmospheric CO_2 is expected to affect not only savanna ecosystems but also all vegetation ecosystems globally.

CO_2 is a major source of organic carbon, which is assimilated by plants during photosynthesis (Ludewig *et al.* 1998). Since CO_2 limits the rate of photosynthesis it is expected that vegetation will respond to elevated CO_2 with enhanced rates of photosynthesis and greater production of carbohydrates leading to a significant increase in plant growth and crop yield (Ludewig *et al.* 1998). Excess non-structural carbohydrates are converted to starch and are stored in leaves and roots for future use (Idso *et al*. 2000b). Furthermore, a strong correlation has been found in the size and number of tubers and elevated CO_2 levels, in plants that produce underground starch storage organs (Bhattacharya *et al.* 1985, Ludewig *et al.* 1998, Miglietta *at al.* 1998, Idso *et al*. 2000a). Some plants respond to elevated CO_2 conditions by reducing their stomatal apertures because the inward diffusion of CO_2 for photosynthesis is adequate at smaller apertures (Idso *et al*. 2002a). The net result is that plants are able to assimilate enough CO_2 while reducing their loss of water via transpiration effectively increasing their water use efficiency (Idso *et al*. 2000b). Bond *et al.* (2002 and 2003) suggest that the increased water use efficiency of C_3 plants under elevated CO_2 conditions in savanna ecosystems effectively creates moister conditions for the plants. For example, 500mm of rainfall experienced at CO_2 levels of 370 ppm would be equivalent to about 300mm of rainfall at CO_2 levels of 180 ppm (Bond *et al.* 2002). As the CO_2 levels in the earths atmosphere increase and plants loose less water and produce more biomass it is expected that perennial woody species will become more dominant relative to annual herbaceous plants (Idso *et al*. 2003). Furthermore, these perennial woody species are expected to expand their ranges more than non-woody species with future increases in the levels of CO_2 (Idso *et al*. 2003).

Many woody savanna species respond to fire damage by sprouting from undamaged meristematic tissue, which requires non-structural carbohydrate reserves. Elevated CO_2 levels result in an increase in the storage of non-structural carbohydrates in many C_3 plants, and it is proposed that this will enhance the post-fire

recovery of some savanna trees (Bond and Midgley 2000, Hoffman *et al.* 2000). Simulations using Sheffield Dynamic Global Vegetation Model (DGVM) with fire predict that trees would be eliminated from mesic savannas at low CO_2 levels (180 ppm) (Bond *et al.* 2003). This is because the post-fire recovery rate of the trees is slow (15 years) in comparison with the potential fire return period (2 years) (Bond *et al.* 2003). Further simulations predict that the density of trees should increase in mesic savannas at current CO_2 levels (360 ppm) (Bond *et al.* 2003).

This creates a fascinating management dilemma for the conservation management of mesic savannas. Does one allow mesic savannas to become more wooded as the global CO_2 levels increase, or does one actively intervene in the management of the system, using fire for example to manipulate the vegetation and create desired vegetation state.

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3 STUDY AREA

3.1 THE EXPERIMENTAL BURN PLOT EXPERIMENT LAYOUT AND DESIGN

The Experimental Burn Plot (EBP) experiment was set-up in a pseudo-randomised block design. Four replicates of treatments were placed in each of four major plant communities that had been defined by Van Der Schijff (1958) at the time (Figure 3-1), namely the *Terminalia- Dichrostachys* sourveld with long grass of Pretoriuskop, the *Combretum* veld between Skukuza and Pretoriuskop, the Knob-thorn – Marula veld near Satara, and the Mopane veld between Shingwedzi and Letaba. In 1954, each replicate comprised seven plots to which seven fire treatments had been randomly assigned (Annual report 1954, Van Der Schijff 1958). These treatments were no burning at all, annual fire in August, and biennial fire in August, October, December, February, and April (Table 3-1). In 1956 the experiment was expanded, and a further five treatments were added and randomly assigned to each of the replicates. The treatments were triennial burns in August, October, December, February, and April (Table 3-1) (Annual report 1955, Annual report 1956, Van Der Schijff 1958). In total the EBP experiment comprised twelve fire treatments, replicated four times each in each of the four major vegetation zones (Figure 3-1 and Table 3-1) making a total of 192 plots covering 12km^2 in the KNP. Biggs *et al*. (2003) concluded that, since the treatments had not been allocated to the replicates completely randomly, the EBP experiment was not a true randomised block design and could only be considered pseudo-randomised.

A detailed description of the layout and application of the experiment is presented in the Results chapter in "A critical analysis of the history of the Kruger National Park Experimental Burn Plots experiment" (p. 43).

Table 3-1: The twelve treatments applied to the plots on four replicates (blocks) within each of the four major plant communities defined at the time by Van Der Schijff (1958). The table also shows the year in which the treatments were started, and the treatment code by which the treatments are referred to throughout this document in tables and figures.

Year started	Return period	Timing	Description	Treatment code
1954	None	None	No Burn (Control)	Con0
	Annual	August	Annual burn in mid-winter	Aug1
	Biennial	August	Biennial burn in mid-winter	Aug2
	Biennial	October	Biennial burn after the first rains	Oct2
	Biennial	December	Biennial burn in mid-summer	Dec2
	Biennial	February	Biennial burn in late summer	Feb2
	Biennial	April	Biennial burn in Autumn	Apr2
1956	Triennial	August	Triennial burn in mid-winter	Aug3
	Triennial	October	Triennial burn after the first rains	Oct3
	Triennial	December	Triennial burn in mid-summer	Dec3
	Triennial	February	Triennial burn in late summer	Feb3
	Triennial	April	Triennial burn in Autumn	Apr3

This project deals with that part of the EBP experiment that was laid out in the Pretoriuskop sourveld.

3.2 THE PRETORIUSKOP LANDSCAPE

The Pretoriuskop sourveld is a moist infertile or mesic savanna, and is located in the south west of the Kruger National Park (KNP) (31°10'E, 25°10'S) (Figure 3-2) (Acocks 1953, Van Wilgen and Scholes 1997, Scholes 1997). As with many mesic savanna ecosystems, it is characterised by the predominance of broad-leaved thorn-less trees, relatively high annual rainfall, and nutrient poor soils.

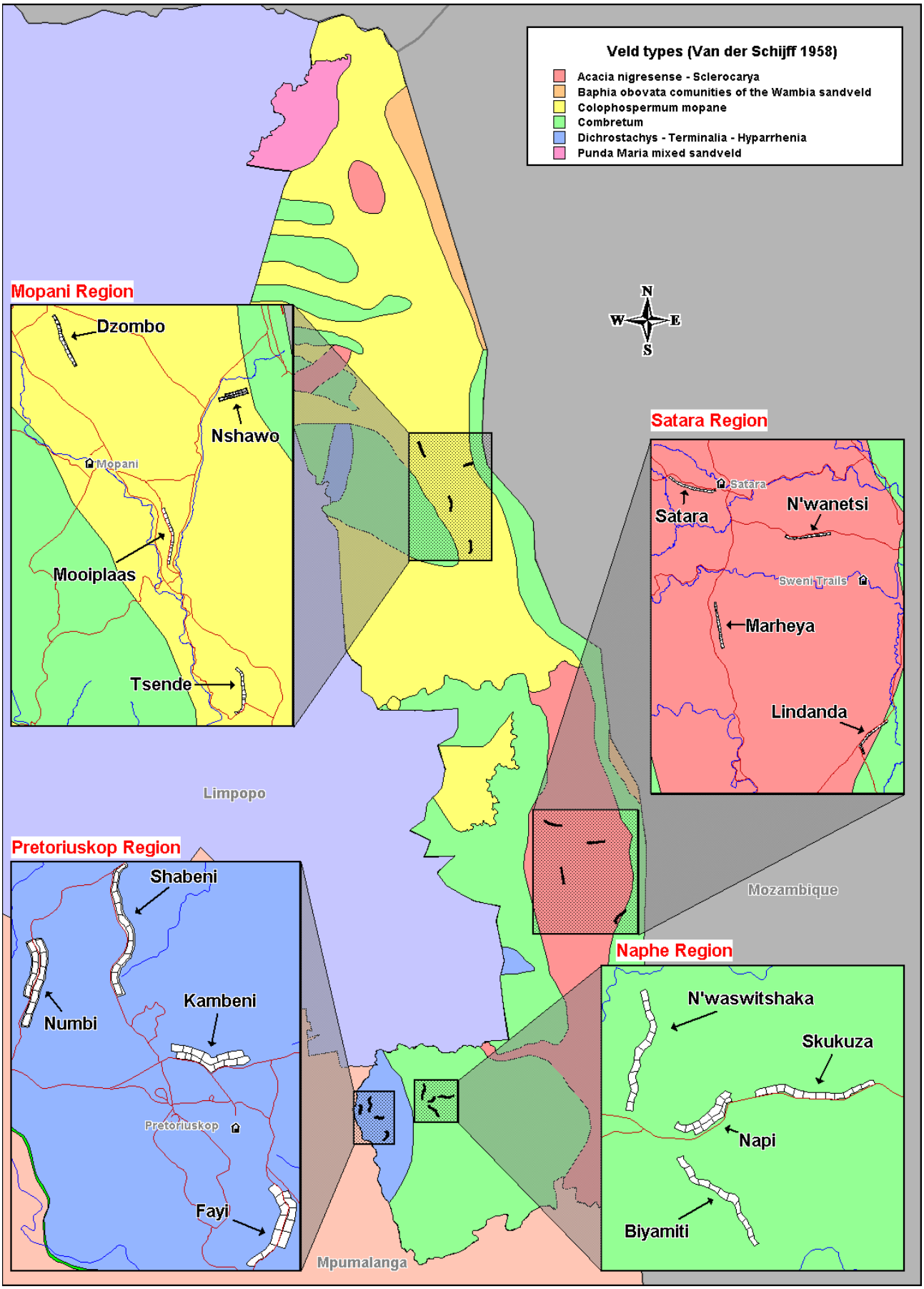

Figure 3-1: The layout of the Experimental Burn Plot experiment in the four broad vegetation communities defined by Van Der Schijff (1958) in the Kruger National Park.

3.2.1 Environmental features of the Pretoriuskop region

Pretoriuskop has a warm subtropical climate, with annual temperatures that range from 4-39 °C (Gertenbach 1983). The average summer (December – February) temperatures in the Pretoriuskop region vary from 18-30 °C, and the average winter (June- August) temperatures vary from 10-25 °C (Gertenbach 1983).Annual rainfall in the Pretoriuskop region ranges from 600-1000mm with an average of about 744mm, which is higher than for the rest of the KNP (Gertenbach 1980a, Venter and Gertenbach 1986). The wet season is during summer with 85% of total annual rainfall occurring between October and March (Munnick *et al*. 1990).

The terrain is moderately undulating, with isolated steep rocky outcrops and a dendritic drainage pattern (Munnick *et al.* 1990). The soils on the watersheds vary from sandy to loam, and are deeply leached. In the drainage lines, the soils are well developed with an accumulation of clays and minerals (Gertenbach 1983).

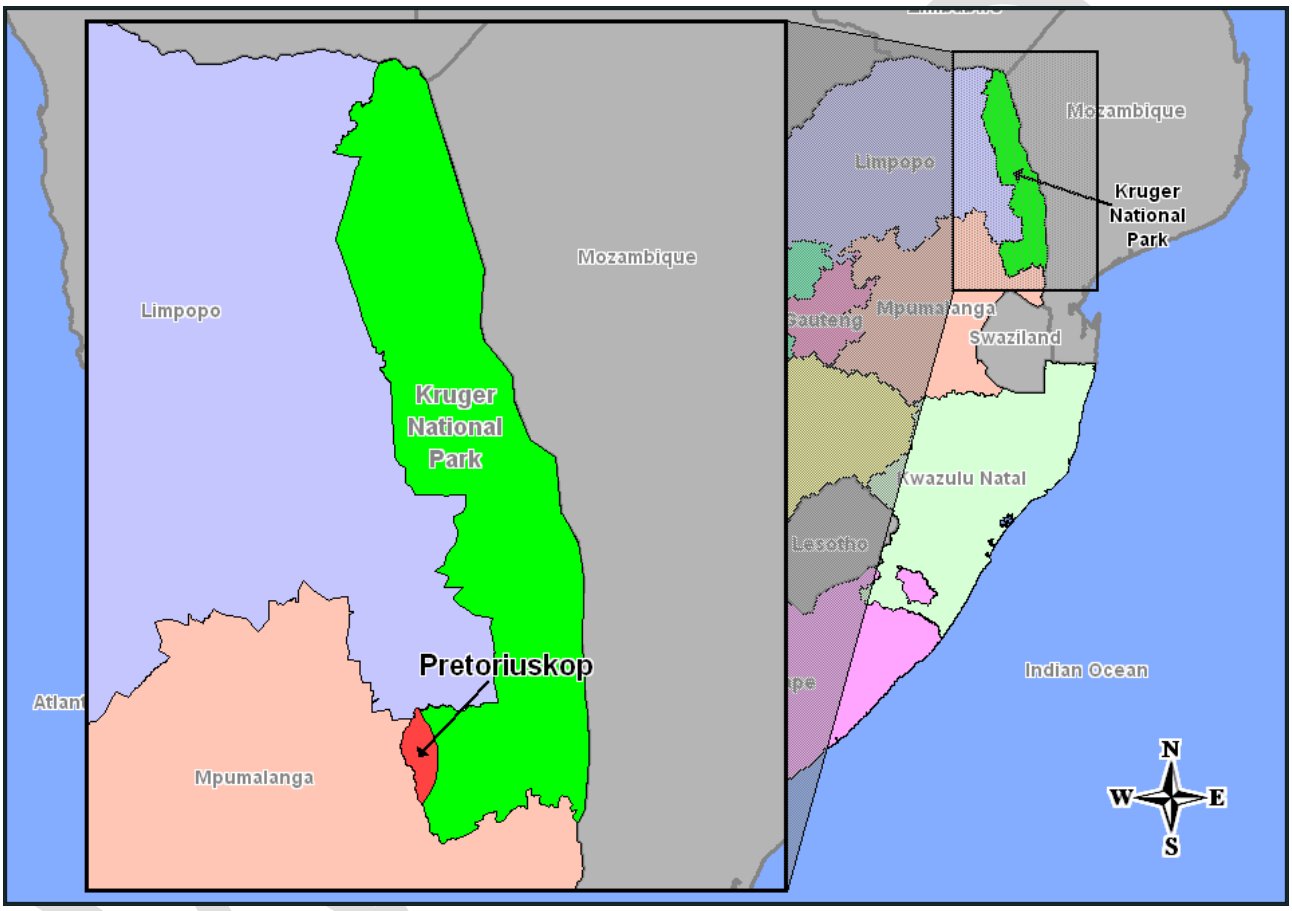

Figure 3-2: Pretoriuskop is located in the south west of the Kruger National Park.

3.2.2 Vegetation description of the Pretoriuskop region

Acocks (1953) describes the vegetation of this area as the Lowveld Sour Bushveld. It has also been described as broad-leaved deciduous woodland with tall grass (Van Der Schijff 1958). The vegetation on the watersheds is predominantly open woodland, while the low-lying areas and drainage lines are more densely covered with trees and shrubby vegetation (Gertenbach 1983). The dominant tree species in this area are *Terminalia sericea* and *Dichrostachys cinerea* subsp. *Nyassana*, and the dominant grass species is *Hyperthelia dissoluta* (Van Der Schijff 1958, Gertenbach 1983). Post fire recovery of the grass and herbaceous vegetation in the Pretoriuskop region tends to be quicker than in other areas of the KNP, because the Pretoriuskop region is a mesic savanna in comparison with other areas of the KNP, which are arid savannas (Van Wilgen and Scholes 1997).

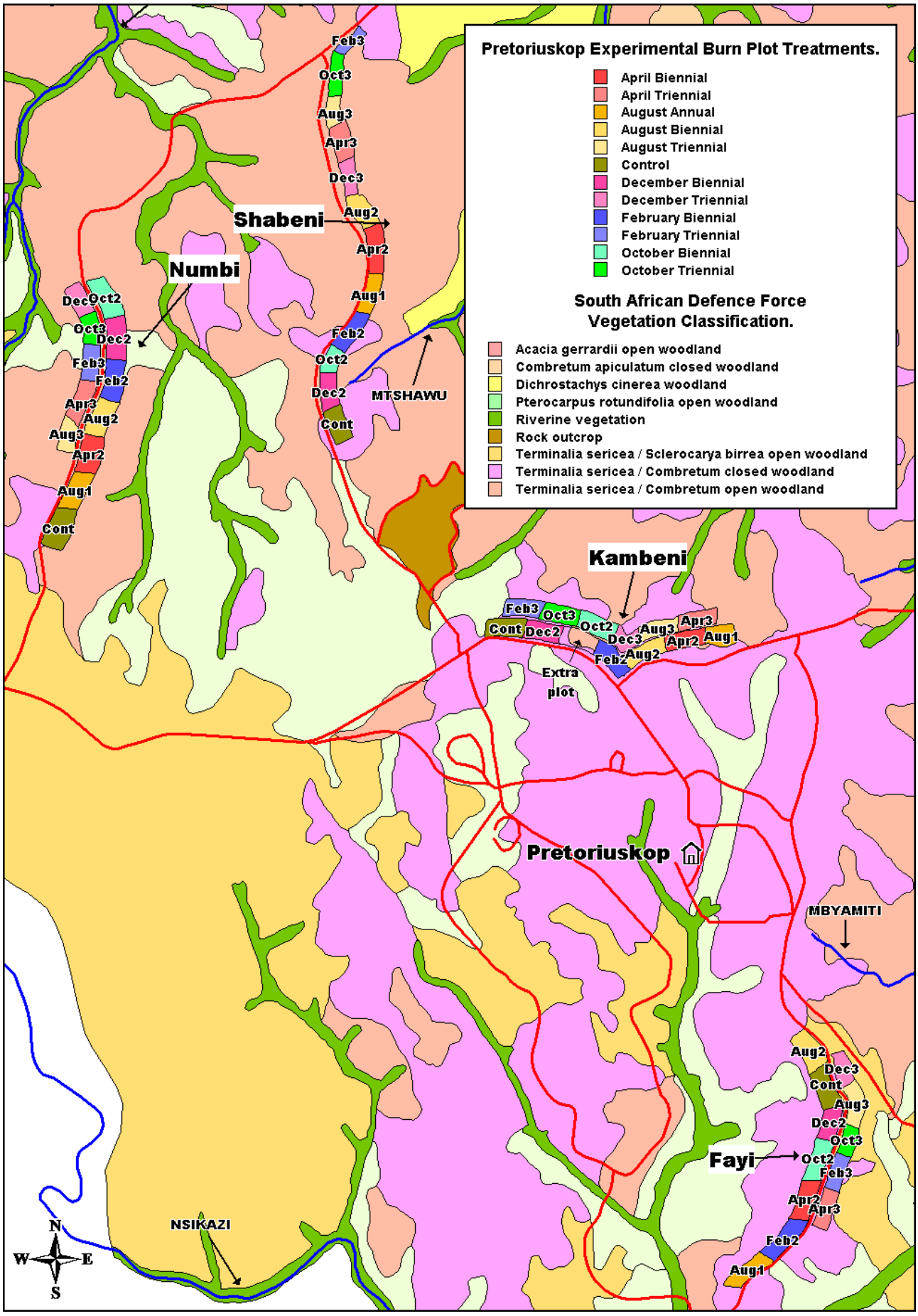

Figure 3-3: Layout of the Experimental Burn Plots in the Pretoriuskop landscape, showing the placement of the four replicates and the treatments that were applied to each burn plot.

3.3 THE LAYOUT OF THE EXPERIMENTAL BURN PLOTS IN THE PRETORIUSKOP REGION

Four replicates of twelve plots each were laid out in the Pretoriuskop sourveld. The four replicates, named after nearby landmarks, were Numbi, Shabeni, Kambeni, and Fayi (Figure 3-3). The Numbi and Shabeni replicates are located in predominantly *Terminalia sericea* - *Combretum* open woodlands of Pretoriuskop and the Kambeni and Fayi replicates are located in predominantly *Terminalia sericea* - *Combretum* closed woodlands of Pretoriuskop (Figure 3-3).

The twelve treatments were assigned in a pseudo-random manner to the plots within each replicate, and these treatments have been applied since 1954. There is an extra plot in the Kambeni replicate (coloured white in Figure 3-3). This is because soil from this plot was used to construct the road between Numbi gate and Pretoriuskop rest camp in 1954 (Annual report 1955). The affected treatment was the October biennial treatment, which was relocated to the second row of the Kambeni replicate in 1956.

3.3.1 The fire characteristics of the Experimental Burn Plots experiment in the Pretoriuskop region

Fires in the Pretoriuskop region are typically surface fires in the grass and herbaceous layer. Fires typically occur during the dry winter months in the Pretoriuskop region, they have intensities that range from 100-6000 kJ/s/m and return periods that range 1-6 years (Van Wilgen and Scholes 1997). In the Pretoriuskop region fire intensity (kJ/s/m) is approximately 3000 kJ/s/m and is significantly correlated with flame height ($r = 0.5883$, $DF = 78$, $p < 0.01$) and with rate of spread ($r = 0.8768$, $DF = 80$, $p < 0.01$) (Trollope and Potgieter 1983, Trollope and Potgieter 1985).

3.3.1.1 The extent or size of the fires on the Pretoriuskop EBP treatments

The extent (size) of the treatment fires and the types of treatment fires in the EBP experiment are constant. The extent of the fires in the experiment is controlled by the size of the experimental plots, which are approximately six and a half hectares in size (Figure 3-4). The grass and herbaceous layer does not burn completely during treatments applied in the wet season months (February, April, and December) and there are often islands of un-burnt grass (Van Wyk 1971). Treatments applied during the dry months often result in the complete combustion of the grass and herbaceous layer (Van Wyk 1971).

3.3.1.2 The type of fires on the Pretoriuskop EBP treatments

The fire types of the treatment fires applied to the plots are surface fires that move through the grass and herbaceous layer (Figure 3-4). Even though the canopies of some trees burn, the surface fire front in the grass layer sustains the flame front and this determines the type of fire.

3.3.1.3 The intensity of fires on the Pretoriuskop EBP treatments

Fire intensity is not controlled on the EBP experiment. However, the fire intensity is affected by the frequency and timing of fire events. Fire frequency affects fire intensity because the amount of fuel accumulated before a fire event is related to the time since the previous fire event. Fire intensity is affected by the fire timing because soil, air and fuel moisture are linked to the timing of the fire, and these factors affect fire intensity.

The fire intensity of the EBP treatments have been quantified a number of times since the inception of the experiment in 1954. In 1969, the temperatures of the fires on each EBP treatment in the Pretoriuskop region were measured at four heights above the ground, namely 0.5m, 0.9m, 1.8m, and 3.7m (Van Wyk 1971). Van Wyk (1971) found that fires during August and October were very hot (Table 3-2). Fires in December and February were cooler and burnt slower than fires in August and October even though high temperatures were sometimes recorded at 0.5m above ground (Table 3-2). The April treatments burnt slowly and

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unevenly, and did not generate much heat (Table 3-2). Generally, the grass and herbaceous layers were burnt completely on treatments that were applied during the dry season (i.e. August and October), and smaller trees and shrubs were burnt back to the ground, and larger trees were scorched. During wet season treatments (i.e. December, February, and April), the grass did not completely burnt and islands of un-burnt grass and grass stalks remained.

In 1982, the fire behaviour on the Pretoriuskop EBP treatments was characterised by Winston Trollope and Andre Potgieter (Trollope and Potgieter 1983). The fire intensities (kJ/s/m) on the Fayi (1940), Kambeni (4059), Numbi (3438), and Shabeni (3120) replicates did not differ significantly (Table 3-3) (Trollope and Potgieter 1983). The Kambeni replicate had the highest average fire intensity and the Fayi replicate had the lowest average fire intensity. The mean fuel moisture content was significantly higher in April than in August and December ($p < 0.01$), and the fire intensity on the April Triennial treatments (1787) was significantly lower than on the August and October Triennial treatments (5155 and 2854 respectively) ($p < 0.05$) (Table 3-4) (Trollope and Potgieter 1983). The fire intensity was higher on the August Triennial treatment (5155) than on the August Biennial treatment (3518), and the fire intensity was higher on the August biennial treatment (3518) than on the August Annual treatment (2567) (Trollope and Potgieter 1983).

Table 3-2: The average length of time (in minutes) taken for a treatment to burn, and the average temperature (°C) of the treatments at different heights. The data was collected in 1969 at the same time as the quadrate middle-point surveys of the EBPs were done (Van Wyk 1971). The data was not presented in Van Wyk (1971) though, and was found in the archive material for the EBPs.

Treatment	Burn time (minutes)	0.5m (°C)	0.9m (°C)	1.8m (°C)	3.7m (°C)	Average temperature (°C)
Apr2	36	121	93	< 93	< 93	65
Apr3	34	149	121	< 93	< 93	93
Aug1	24	232	232	149	93	176
Aug2	16	399	260	232	177	266
Aug3	25	316	232	204	177	232
Dec2	30	232	149	121	< 93	141
Dec3	26	288	177	121	< 93	162
Feb2	29	149	93	< 93	< 93	72
Feb3	38	93	121	< 93	< 93	79
Oct2	21	343	260	204	149	239
Oct3	15	316	232	177	149	218

Table 3-3: The average fire intensity for the Fayi, Kambeni, Numbi, and Shabeni EBP replicates on the Pretoriuskop region, based on the data that was collected on the five treatments in Table 3-4 in 1983 (Trollope and Potgieter 1983).

Replicate	Intensity (kJ/s/m)
Fayi	1940
Kambeni	4059
Numbi	3438
Shabeni	3120

In 1992, the fire behaviour on two of the Pretoriuskop EBP treatments (August and October biennial treatments) was characterised as part of the ground component projects of the SAFARI 92 (South African Fire-Atmosphere Research Initiative conducted in 1992) project (Trollope *et al*. 1994). The Fayi replicate had the lowest fire intensity (kJ/s/m) in both the Aug2 (93) and Oct2 (474) treatments (Table 3-5). The Shabeni replicate had the highest fire intensity in the Aug2 treatment (1703), and the Kambeni replicate had the highest fire intensity in the Oct2 treatment (3644). The average fire intensity on the October Biennial treatment (1988) was more than double the average fire intensity on the August Biennial treatment (930) in the Pretoriuskop region.

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Table 3-4: The average fire intensity for five of the Pretoriuskop EBP treatments. The data was collected in 1982 (Trollope and Potgieter 1983).

Treatment	Intensity (kJ/s/m)
Aug1	2567
Aug2	3518
Aug3	5155
Oct3	2854
Apr3	1787

Fires in the KNP have been classified into five categories based on fire intensity, namely very cool fire, cool fire, moderately hot fire, hot fire, and extremely hot fire (Table 3-6) (Trollope and Potgieter 1983, Trollope and Potgieter 1985). These categories provide a convenient framework to rank the EBP treatments in the Pretoriuskop region from very cool fire to extremely hot fire (Table 3-7). The ranking of the treatments uses the data collected on the Pretoriuskop EBPs regarding the intensity of the different fire treatments presented above, and conventional thought regarding the relationship between fire intensity and fire timing and frequency.

Table 3-5: The fire intensity for the August and October Biennial treatments of the Pretoriuskop EBPs. The data was collected in 1992 as part of the ground component projects in SAFARI 92 (Trollope *et al*. 1994)

Treatment	Replicate	Fire intensity (kJ/s/m)	Treatment	Replicate	Fire intensity (kJ/s/m)
August Biennial	Fayi	93	**October Biennial**	Fayi	474
	Kambeni	1182		Kambeni	3644
	Numbi	742			
	Shabeni	1703		Shabeni	1846
	Average	**930**		**Average**	**1988**

Regarding the fire frequency of the EBP treatments, an annual fire is less intense than a biennial fire at the same time of the year because more fuel accumulates over two years than over one year. Furthermore, a triennial fire is more intense than a biennial fire at the same time of the year because more fuel accumulates over three years than over two years. Regarding the timing of the EBP treatments, an August fire is more intense than an October fire because the soil, air, and fuel moisture levels are lower in August at the end of the dry season than in October, which is at the beginning of the wet season. An October fire at the beginning of the wet season is more intense than an April fire, which is at the beginning of the dry season. An April fire at the beginning of the dry season is more intense than a February fire, which is toward the end of the wet season. A February fire toward the end of the wet season is more intense than a December fire, which is in the middle of the wet season.

Table 3-6: Five fire categories based on fire intensity (Trollope and Potgieter 1983, Trollope and Potgieter 1985)

Fire Intensity (kJ/s/m)	Description
> 3001	Extremely hot fire
2001-3000	Hot fire
1001-2000	Moderately hot fire
501-1000	Cool fire
< 500	Very cool fire

The frequency of the treatments was ranked from low intensity fires being Annual (1), medium intensity fires being Biennial (2), and high intensity fires being Triennial (3) (Table 3-7). The timing of the treatments was

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ranked from low intensity fires occurring in December (1), medium-low intensity fires occurring in February (2), medium intensity fires occurring in April (3), medium-high intensity fires occurring in October (4), and high intensity fires occurring in August (5) (Table 3-7). Using the data presented above, a rank correction factor was then applied to account for any perceived timing and frequency rank inconsistencies (Table 3-6 and Table 3-7). For example, one rank point was subtracted from the Aug3 treatment because it was believed that the Aug3, Oct3, and Aug2 treatments were similar in intensity, and one rank point was added to the Dec3 treatment because it was believed to be hotter than the Feb2 treatment (Table 3-7). The timing intensity rank, frequency intensity rank, and intensity rank correction for each treatment were then summed to give a treatment intensity rank which was used to rank the EBP treatments from most intense treatment (Aug3) to the least intense treatment (Dec2) (Table 3-7). The treatments were then assigned to one of the five fire intensity categories described by Trollope and Potgieter (1983 and 1985), based on the fire intensity rank of the treatment (Table 3-7).

Table 3-7: Fire treatments of the Experimental Burn Plots ranked from most intense fire treatment to least intense fire treatment based on the timing and frequency of the treatment.

Treatment	Timing intensity rank	Frequency intensity rank	Intensity Rank Correction	Treatment intensity rank (Time + Freq + Correction)	Type of fire
Aug3	5	3	-1	7	Extremely hot fire
Oct3	4	3	0	7	Extremely hot fire
Aug2	5	2	0	7	Extremely hot fire
Oct2	4	2	0	6	Hot fire
Apr3	3	3	0	6	Hot fire
Aug1	5	1	0	6	Hot fire
Apr2	3	2	0	5	Moderately hot fire
Feb3	2	3	0	5	Moderately hot fire
Dec3	1	3	1	5	Moderately hot fire
Feb2	2	2	0	4	Cool Fire
Dec2	1	2	0	3	Very cool fire
Con0	0	0	0	0	No fire

3.3.1.4 The timing of the fires on the Pretoriuskop EBP treatments

Fire timing on EBP treatments is manipulated. Fire treatments are applied at five different times of the year, namely February, April, August, October, and December (Figure 3-4).

The February treatments are less intense than the April, August, and October treatments and more intense than the December treatments. The February treatments tend to burn slowly, and the grass and herbaceous layer burns patchily with tall grass stalks of *Hyparrhenia dissoluta* and *Trachypogon capense* remaining un-burnt. Top kill of shrub forms is low in February fires but leaves are often severely singed. The *Panicum maximum* (Buffalo grass) growing under large trees is green at this time of the year and so the large trees and under-canopy seedlings are protected from the fire in February. Regeneration and recovery of the vegetation is relatively quick if rains continue into autumn however, if the rains end early in the wet season the plots are grazed, browsed, and trampled heavily through out the winter and only recover in the following wet season.

The April treatments are less intense than the August, and October treatments, and more intense than the February and December treatments. The April treatments tend to burn slowly. Conditions are dryer than in February, and the grass and herbaceous layer burns less patchily than in February. Top kill of shrub forms is low in April fires but higher than in February. The *Panicum maximum* growing under large trees is still green at this time of the year protecting the large trees and under-canopy seedlings from fire. The conditions are dryer in April than February and regeneration and recovery of the vegetation is slower. The plots are grazed, browsed, and trampled heavily through out the winter generally only recovering in the following wet season.

The August treatments tend to be very intense, and the grass and herbaceous layer is burnt completely in August. *Panicum maximum*, which is occurs under large trees, is dry in August and these fires tend to scorch

the trunks and lower branches of large trees. Top kill of shrub forms on these treatments is very high. Many trees and shrubs are less susceptible to fire damage in August because August is a time of dormancy and low resource utilisation for these species. However, grazing, browsing, and trampling of both grass and basal tree and shrub shoots is high after August fires. Post fire recovery of the vegetation after August fires in the Pretoriuskop region is slow because the first rains usually occur in October.

The October treatments tend to be very intense fires in which the grass and herbaceous layer is burnt completely. *Panicum maximum*, which is occurs under large trees, is often still dry in October and these fires tend to scorch the trunks and lower branches of large trees. Top kill of shrub forms in these treatments is very high. West (1965) postulated that many trees and shrubs would be susceptible to fire damage in October because their carbohydrate reserves would be deleted by new spring growth. However, Trollope, Potgieter and Zambatis (1990) found that post fire tree-shrub mortality was low in the Kruger National Park (1.3%), regardless of the season in which the fire was applied. They concluded that the tree-shrub component of the vegetation did not appear to be sensitive to burning at the end of the dry season when they were in the spring flush. Post fire grazing, browsing, and trampling of both grass and basal tree and shrub shoots is low after October fires in comparison with after August fires. Game do not concentrate much in areas burnt in October because the surrounding vegetation is in spring flush providing alternative graze and browse material. As the first rains in the Pretoriuskop region usually occur in October, regeneration and recovery of vegetation after October fires is relatively quick.

The December treatments are less intense than the February, April, August, and October treatments. The December treatments tend to burn slowly, and the grass and herbaceous layer burns patchily with tall grass stalks of *Hyparrhenia dissoluta* and *Trachypogon capense* remaining un-burnt. Top kill of shrub forms is very low in December fires. The *Panicum maximum* growing under large trees is green at this time of the year and so the large trees and under-canopy seedlings are protected from the fire in December. Regeneration and recovery of the vegetation is relatively quick because fires occurring in December are in the middle of the wet season. Post fire grazing, browsing, and trampling of both grass and basal tree and shrub shoots is low as game does not concentrate in areas burnt during December.

3.3.1.5 The frequency of the fires on the Pretoriuskop EBP treatments

Fire frequency on the EBP treatments is manipulated. Fire treatments are applied at three frequencies, namely Annual, Biennial, and Triennial (Figure 3-4). The Annual treatment is applied only in August, and the Biennial and Triennial treatments are applied at all five times of the year. There is also a Control treatment in where fire is excluded from the plots.

The Annual treatments are less intense than the Biennial and Triennial treatments at the same time of the year. Annual treatments tend to burn more slowly than Biennial and Triennial treatments at the same time of the year because the fuel accumulation on the Annual treatments is low in comparison with the Biennial and Triennial treatments. Trees and shrubs tend not to recover completely between fires on the Annual treatments, there is a bottleneck effect in which seedlings, and saplings are stunted by repetitive burning and prevented from becoming mature adult trees.

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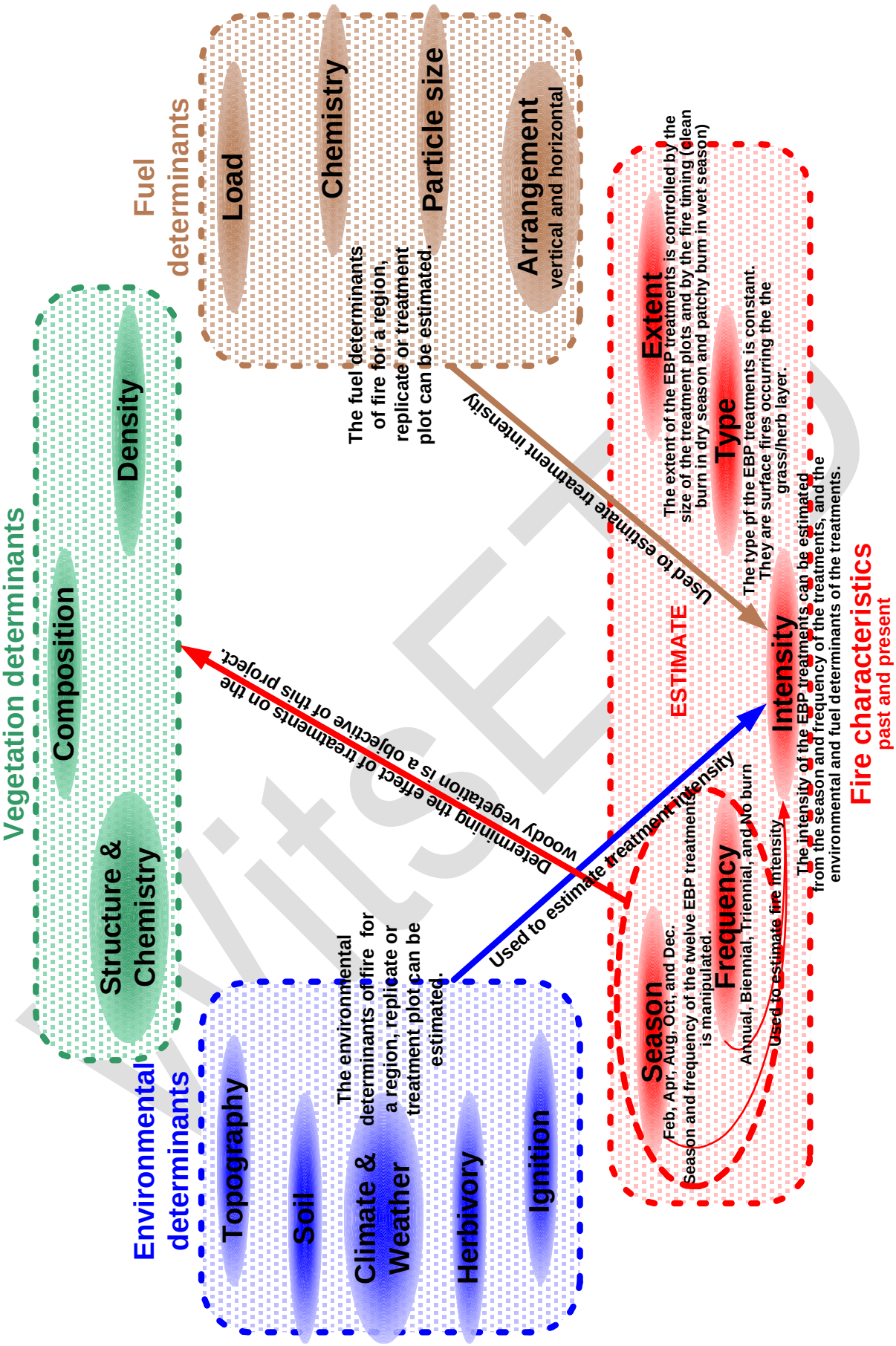

Figure 3-4: The fire characteristics of the Experimental Burn Plots (EBPs) based on the model showing the interdependence between the determinants and characteristics of fire shown in Figure 2-1 (p. 4).

4 RESEARCH HYPOTHESES

A diachronic (longitudinal) research approach was used in this project, in which the effects of fire on woody vegetation were investigated over time within the structure of a long-term controlled experiment (Trabaud and Lepart 1981). Data collected at the start of the experiment in 1954 was used as a baseline against which data collected in 1996, 42 years later, was compared. Differences between the treatment plots in 1954 and 1996 were used to determine the effects of the prolonged application of the fire treatments on the woody vegetation in the Pretoriuskop region.

The hypotheses stated have been deliberately constructed as broad statements regarding a particular problem domain to avoid being bogged down in the detail of the methods and analyses used to investigate the problem domain.

4.1 CHANGE IN THE WOODY VEGETATION DENSITY, STRUCTURE AND COMPOSITION ON THE PRETORIUSKOP EXPERIMENTAL BURN PLOTS BETWEEN 1954 AND 1996

Using the Sheffield Dynamic Global Vegetation Model (DGVM), Bond *et al.* (2003) predict that the density of trees in mesic savannas will have increased as the atmospheric CO_2 levels have increased from pre-industrial levels (270 ppm) to current levels (360 ppm) over the last 150 years. Over the past half a century, rangers and researchers have made anecdotal observations that the vegetation in the Pretoriuskop region appears to be gradually becoming more wooded (Annual Report 1951, Van Der Schijff 1958, Brynard 1964). It is assumed that broad trends in woody vegetation change occurring in the Pretoriuskop region between 1954 and 1996 has also occurred on the Pretoriuskop Experimental Burn plots over the same period. The basis for this assumption is that the layout of the EBP replicates in the Pretoriuskop region is considered representative of the landscape, and the experimental treatments applied to the EBPs between 1954 and 1996 cover the same range of fire frequencies and timing that have occurred in the Pretoriuskop landscape for the same period.

Using the data collected on the Pretoriuskop EBP experiment in 1954 and 1996, the anecdotal observations that have been made regarding the woody vegetation in the Pretoriuskop region can be tested.

Hypothesis 1: Savanna ecosystems are not static state ecosystems and the density, structure, and composition of the woody vegetation in these systems changes in time and space. The global increase in atmospheric CO_2 is expected to drive change in mesic savannas like Pretoriuskop. The first hypothesis is that the density of the woody vegetation on the Pretoriuskop EBPs increased between the inception of the experiment in 1954 and 1996.

4.2 DIFFERENCES IN THE WOODY VEGETATION DENSITY, STRUCTURE AND COMPOSITION BETWEEN THE PRETORIUSKOP EXPERIMENTAL BURN PLOT REPLICATES

The EBP replicates were placed in four representative locations within each of four landscapes within the KNP. Many factors such as soil, catenal position, grazing pressure, and the structure and composition of the vegetation vary between the replicates. The magnitudes of these non-experimental differences between the replicates are in some cases large and are cause for concern when analysing the treatment effects on the woody vegetation density, structure, and composition (Van Der Schijff, 1958, Van Wyk 1975, Trollope *et al.* 1998).

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Using the data collected in the 1954 and 1996 surveys, differences in the density, structure, and composition of the woody vegetation between the replicates can be tested.

Hypothesis 2: True replication in uncontrolled heterogeneous ecological ecosystems is difficult. This often leaves ecologists with non-experimental variation, which can confound true pattern. The second hypothesis is that there was no difference in the density, structure, and composition of the woody vegetation between the four Pretoriuskop EBP replicates in 1954 or in 1996.

4.3 THE EFFECTS OF FIRE FREQUENCY AND TIMING ON THE DENSITY, STRUCTURE, AND COMPOSITION OF THE WOODY VEGETATION ON THE PRETORIUSKOP EXPERIMENTAL BURN PLOTS

In savanna ecosystems, frequent fire events appear to favour grassland over woodland in regions with climates that are capable of supporting woodland and forest ecosystems (Vogl 1974). Most woody plants in savanna ecosystems are fire resistant to some degree, and fire does not so much kill fire resistant woody species as reduce the above ground woody biomass through scorching and top kill. Furthermore, the intensity of a fire event is related to the time since the previous fire event because the amount of fuel accumulated is related to the time since the previous fire event. Some woody species are more susceptible to top kill or total mortality after high intensity fire events than less intense fire events. This affects the structure, composition, and density of the woody vegetation.

Using the data collected in the 1954 and 1996 surveys, differences in the density, structure, and composition of the woody vegetation on the Pretoriuskop Experimental Burn Plots burnt at different frequencies can be tested.

Hypothesis 3: In savanna ecosystems, frequent fire kills fire intolerant woody species, and suppresses fire tolerant woody species preventing them from reaching fire resistant heights. The third hypothesis is that the woody vegetation on plots burnt less frequently or not at all will be denser, comprise taller less shrubby trees, and have more fire intolerant species than plots burnt more frequently.

The season of burning in relation to the phenology of plant non-structural carbohydrate reserves determines the degree of damage caused by fire to the plant (West 1965, Bond and Van Wilgen 1996). Fire directly after a non-structural carbohydrate resource depleting phenological phase (i.e. after the spring flush of leaves or flower blooming) is more detrimental to the persistence of a woody plant than fire during or directly after a resource-accumulating phenological phase (i.e. during or at the end of the rainy season) (West 1965, Bond 1997). Furthermore, soil, air, and fuel moisture is linked to the timing of a fire and these factors affect the intensity of a fire. Some woody species are more susceptible to top kill or total mortality after high intensity fire events than less intense fire events. This affects the structure, composition, and density of the woody vegetation. Season has been found to be one of the most important aspects of a fire regime affecting plant species diversity (Malanson 1982). Regarding the fire timing of the EBPs the most intense treatments are those occurring during and at the end of winter (August and October). The October treatments occur at a time when plants are phenologically most sensitive in comparison with the treatments that occur in August, which is a time of dormancy (December and February). The relationship between the frequency, timing, and the intensity of the EBP treatments is discussed in more detail in “The fire characteristics of the Experimental Burn Plots experiment in the Pretoriuskop region” p. 19.

Using the data collected in the 1954 and 1996 surveys, differences in the density, structure, and composition of the woody vegetation on the Pretoriuskop Experimental Burn Plots burnt at different times of the year can be tested.

Hypothesis 4: In savanna ecosystems, fire occurring during different phenological phases of woody plants impacts upon the post-fire persistence of the woody plants differentially. The fourth hypothesis is that the woody vegetation on the plots burnt during and at the end of winter will be less dense, comprise shorter more shrubby trees, and have less fire intolerant species than plots burnt during and at the end of summer or not burnt at all.

4.4 THE EFFECT OF NOT BURNING ON THE DENSITY, STRUCTURE AND COMPOSITION OF THE WOODY VEGETATION ON THE PRETORIUSKOP EXPERIMENTAL BURN PLOTS

In general, when fire is excluded from Southern African savanna ecosystems, the woody plant biomass increases (Scholes 1997). In mesic savannas such as Pretoriuskop, the long-term exclusion of fire can also result in species change with fire intolerant species becoming more prominent (Scholes 1997).

Using the data collected in the 1954, 1959, and 1996 surveys, differences in the density, structure, and composition of the woody vegetation on the Pretoriuskop Experimental Burn Plots excluded from fire for different lengths of time can be tested.

Hypothesis 5: In savanna ecosystems, in the absence of fire, the woody biomass increases because suppressed woody plants are able to escape the fire zone and fire intolerant species are able to establish themselves. The fifth hypothesis is that the woody vegetation on the control (no burn) plots will be denser, comprise taller less shrubby trees, and have more fire intolerant species as the time since the inception of the experiment in 1954 increases.

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5 MATERIALS AND METHODS

5.1 METHODS OF HISTORICAL ANALYSIS

An understanding of the historical background of the Experimental Burn Plots (EBP) experiment provides a context within which the worth of the experiment can be assessed.

Management philosophy in the KNP has changed over the last half century since the inception of the EBP experiment in 1954. During the early 1950's the romanticised notion of man's subservience to "Mother Nature" was replaced by scientific rationality and administrative dominance (Carruthers 1995). Teams of scientists studying all elements within the ecological landscape replaced the solitary game warden and custodian (Carruthers 1995). Maintaining the physical state of the ecosystem became the main management focus. In the mid 1990's, management by intervention gave way to a wilderness approach in which management intervention was limited. This approach prescribed an understanding of ecosystem processes and the scale at which these processes occur. Ecosystem processes have come to be considered as important to the conservation management of an ecosystem as maintaining the physical state. It is important to understand how changing attitudes and motives of scientists and management have influenced the KNP EBP experiment over time.

The aim of this historical analysis was to investigate how and why the EBP experiment was started. Furthermore, how the EBP experiment was maintained and how it persisted between its inception in 1954 and the mid 1990's. Finally, what attitudes prevailed concerning the experiment, and how these affected the credibility and integrity of the experiment?

To answer these questions archive materials from both the Kruger National Park and South African National Parks head offices were collated and analysed. Most of the archive material was recorded in Afrikaans and required translation. The archive material included Annual Reports (from 1951 to 1990), Minutes of Meetings, Unpublished Reports, and miscellaneous notes. The collation of archived material took eight months from May 1996 to December 1996.

These data were used in conjunction with published material to construct a historical analysis of the EBP experiment, which is presented in the Results chapter in "A critical analysis of the history of the Kruger National Park Experimental Burn Plots experiment" (p. 43).

5.2 FIELD METHODS

The main criterion in choosing a method to survey the woody vegetation in 1996 was that the data collected was comparable to the baseline (1954) data. A number of survey methods were assessed including those previously used to survey the EBPs, like the quadrate middle-point and step-point methods and the half-hectare plots. The belt transect method used in the baseline (1954) survey was selected as being most suitable.

The different survey methods used to survey the woody vegetation on the EBPs between 1954 and 1996 are discussed in more detail in "A critical analysis of the history of the Kruger National Park Experimental Burn Plots experiment" (p. 43) in the Results chapter.

The survey methodology used in 1996 differed slightly from that used in the baseline (1954) survey. The differences were in the size of the sampling transects which was a result of the imperial unit measure system (inches and feet) being used in 1954 and the metric unit measure system (centimetres and meters) used in 1996.

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Two transects, each 2m wide by 300m in length, were laid along the diagonals of each experimental plot (Figure 5-1). Each transect was subdivided into six 50 m sample units (segments), and the woody vegetation in each segment within each belt transect was surveyed (Figure 5-1).

The following woody vegetation data were recorded:

- Every woody plant within each sample unit was recorded and identified.
- The height of the living part of the woody plant in meters was measured.
- The height of the dead part of the woody plant in meters was measured. This was recorded if the woody plant was dead or if one of the main stems of the woody plant was dead.
- Whether the plant had a single stem or many stems at the base was recorded.
- Stem diameter in centimetres for single-stem individuals was measured.
- Basal diameter in centimetres (coppice diameter) for multi-stem individuals was measured.
- Whether the individuals were live or dead was recorded.
- The magnitude and type of damage other than fire (i.e. animal or wind) to the plant, where evident, was recorded.

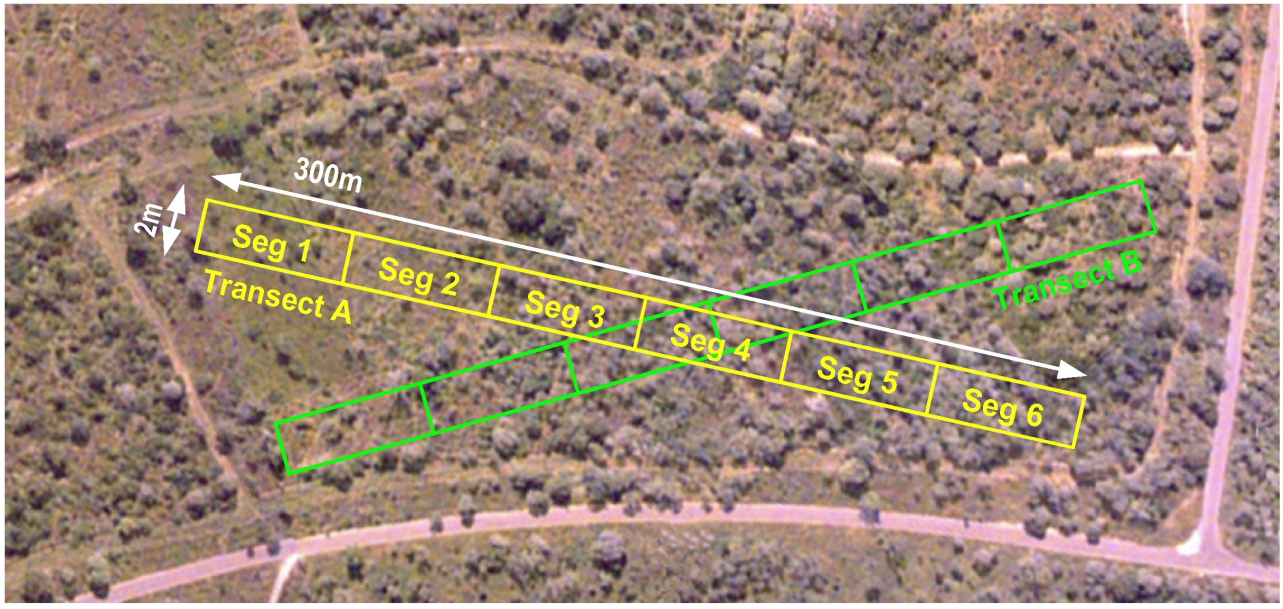

Figure 5-1: Showing the placement of the two transects along the diagonals of a treatment plot in the 1996 woody vegetation survey of the Pretoriuskop EBPs. The belt transects were divided into six segments each.

The resurvey of the woody vegetation on the Pretoriuskop EBPs took seventeen months from May 1996 to September 1997. This survey concluded a 42-year period, between 1954 and 1996, over which the effects of the fire treatments were investigated.

5.3 CAPTURING AND COLLATING HISTORICAL SURVEY DATA

Four complete surveys of the woody vegetation on the EBPs in the Pretoriuskop region were conducted from the inception of the experiment in 1954 to 1996. These were the baseline survey (1954), the quadrate middle-point survey (1967-1968), the step point survey (1970), and the half-hectare monitor plots (1971-1973). In 1959 a belt transect survey was also conducted on the control plots of the Pretoriuskop and Naphe regions of the EBP experiment. None of the data from these surveys was available in digital format.

The data from two surveys, in 1954 and 1959 belt transect surveys, were selected to meet the third objective of this study, namely to "…compare the density, structure, and composition of the woody vegetation on the Pretoriuskop EBPs between 1954 and 1996…" (Aims and Objectives p. 1)

The data from the three other surveys were not selected for the following reasons:

- The quadrate middle-point survey (1967-1968), because the data collected during this survey was not directly comparable with the data collected using the belt-transect method in 1954 and 1959.
- The step point survey (1970), because the distance from the point to the nearest individual was not recorded, and density calculations are not possible.
- The half-hectare plot survey (1971-1973), because the control plots of the Pretoriuskop region were not surveyed.

The data from the 1954 and 1959 surveys took five months to capture from January 1997 to May 1997. The data collected during the 1996 survey took eight months to capture from July 1997 to February 1998.

5.3.1 Cross-referencing species

Between 1954 and 1996 the taxonomic classification of some of the woody species occurring on the Pretoriuskop Experimental Burn Plots changed. A number of species names changed and other species were reclassified as new species or as sub-species. The survey data collected in each of the surveys (1954, 1959, and 1996) was cross-referenced to standardise the species identification and naming.

The species designations in Palgrave (1991) were used as a reference for the standardisation of the species found in each survey. Refer to Appendix 1 (p. 210) for a complete list of species identified in the surveys conducted in 1954, 1959 and 1996.

5.4 ESTIMATING HEIGHT FOR THE 1954 AND 1959 DATA

The heights of the plants were not measured in the 1954 and 1959 surveys. Plant height is a useful measurement of dominance or importance of an individual. It is also useful for quantifying the effect of fire on the physical structure of the vegetation. Plant heights for the 1954 and 1959 survey data were estimated using the plant diameter and height measurements collected in the 1996 survey.

5.4.1 Estimating height class

1. Each individual in the 1996 survey was classified into one of the eight single-stem or multi-stem basal diameter classes used in the 1954 and 1959 surveys. These classes are displayed in Table 5-1.

Table 5-1: The single-stem and multi-stem diameter classes used to classify individuals during the 1954 baseline survey (Van Der Schijff 1958).

Basal stem class	Diameter class (cm)	Diameter class code
Multi	0.00 – 30.48	**S01**
	30.48 – 91.44	**S13**
	> 91.44	**S3**
Single	0.00 – 2.54	**T01**
	2.54 – 7.62	**T13**
	7.62 – 12.7	**T35**
	12.7 – 17.78	**T57**
	> 17.78	**T7**

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2. Each individual in the 1996 survey was also classified into one of four height classes shown in Table 5-2.

Table 5-2: The height classes used to classify individuals in the 1996 survey.

Height class (m)	Height class code
0 – 1	**H01**
1 – 3	**H13**
3 – 5	**H35**
> 5	**H5**

3. The species height classes for the 1954 and the 1959 data were estimated using one of two methods:

   a. The procedure used for species common to the 1954, 1959 and 1996 surveys:
   The species-height-class ratios (the relative number of individuals per height class) were calculated for each diameter class from the 1996 data. These ratios were used to estimate the number of individuals in each height class within each diameter class for each species in the 1954 and 1959 data.

   b. The procedure used for species present in the 1954 and 1959 surveys but not present in 1996:
   The height class ratios for each diameter class were calculated for the entire 1996 dataset. These ratios were used to estimate the number of individuals in each height class within each diameter class for those species present in the 1954 and 1959 surveys and not in the 1996 survey.

5.4.2 Estimating height

The mean height for each of the four height classes (0-1 m, 1-3 m, 3-5 m and >5 m) was calculated using the 1996 data. These mean heights were used to estimate the height of each individual in the 1954 and 1959 surveys based on the individuals estimated height class.

5.4.3 Assumptions made in estimating height classes for the 1954 data

- The height class ratio at the species level for a given diameter class remains constant over time i.e. the relative number of individuals in each height class for each diameter class for each species in 1954 and 1959 were the same as those in 1996.
- In the absence of species level height ratios, the average height class ratios for the entire data set are good approximations of the species level height class ratios for a given diameter class.

5.5 DATA ANALYSIS

The data collected during the three surveys conducted in 1954, 1959 and 1996 was used to investigate the long-term effects of the fire treatments on the woody vegetation of the Experimental Burn Plots (EBPs) in the Pretoriuskop region. This data comprised records on more than 45 000 individuals from 97 woody species.

5.5.1 Indices calculated to summarise key vegetation structure and composition characteristics

Twelve vegetation indices were used to summarise the data collected in the 1954, 1959, and 1996 surveys. These indices were calculated for each treatment plot at each survey and were then used to compare the woody vegetation density, structure, and composition between the plots.

5.5.1.1 Woody plant density

The density of woody individuals per hectare was calculated per treatment plot.

$$d_j = \frac{n_j \times 10000}{a_j}$$ **Equation 1: Woody plant density per hectare.**

Where d_j is density (*n*/*ha*), n_j is the number of individuals, 10000 is the number of square meters per hectare, and a_j is the survey area (m^2) for treatment plot *j*. The survey area of each of the survey transects in the 1954, 1959, and 1996 surveys are presented in Appendix 3, Table 11-1 (p. 215).

5.5.1.2 Mean woody plant height

The arithmetic mean height of woody individuals was calculated per treatment plot. Mean height was used to quantify the woody plant height structure on each treatment plot as a single value.

$$\bar{h}_j = \frac{\sum h_i}{n_j}$$ **Equation 2: Mean woody plant height.**

Where $\bar{h}_j$ is the mean height (m), h_i is the height of individual trees or shrubs (m), and n_j is the number of individuals for treatment plot *j*.

5.5.1.3 Number of tree equivalents

The tree equivalents index is a composite measure of the number of individuals in a collection and the height structure of that collection. The index expresses the total height of a collection of individuals as the potential number of tree equivalents (trees that are 1.5 m tall) within the collection (Trollope *et al*. 1990).

$$te_j = \frac{(\frac{\sum h_i}{1.5}) \times 10000}{a_j}$$ **Equation 3: Number of tree equivalents.**

Where te_j is the number of tree equivalents per hectare, h_i is the height of individual trees or shrubs (m), 1.5 is the height (m) of an equivalent tree, 10000 is the number of square meters per hectare, and a_j is the survey area (m^2) for treatment plot *j*.

This index is useful because it combines the height structure and density of a collection of individuals into a single quantity. Tree equivalents are an estimate of the phytomass (plant mass) of the woody vegetation, measured as the equivalent number of 1.5 m tall trees (Trollope *et al*. 1990).

5.5.1.4 Single-stem to multi-stem index

Many woody plants respond to fire damage by sprouting at the base of the plant. This often results in the plants having more than one stem. The single-stem to multi-stem index is used to quantify the physical structure of the woody vegetation with respect to the basal sprouting response of individuals to fire damage.

The single-stem to multi-stem index is calculated as the proportion of single-stem individuals relative to the total number of individuals. The ratio ranges from zero to one, where zero indicates the absence of single-stem individuals and one indicates the absence of multi-stem individuals.

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$$sm_j = \frac{ds_j}{n_j}$$ **Equation 4: Single-stem to multi-stem index.**

Where sm_j is the single-stem to multi-stem index, ds_j is the density of single-stem individuals, and n_j is the density of woody individuals on treatment plot *j*.

5.5.1.5 Diversity

Diversity is a measure of the variability of composition (Pielou 1975). Composition can comprise any categorization or grouping used to classify a collection of individuals. Diversity has two distinct components: 1) the number of different groups in a collection, and 2) the relative amount in each group in a collection (Huston 1994).

Many indices have been developed to estimate the separate and combined components of diversity. For the sake of clarity, indices that quantify the first component of diversity are referred to as "count" or "richness" indices, and indices that quantify the second component of diversity are referred to as "evenness" indices, while indices that quantify the first and second components of diversity combined are referred to as "diversity" indices.

Two aspects of woody vegetation diversity were investigated, namely species diversity and structural diversity.

5.5.1.5.1 Species diversity

Palgrave's "Trees of Southern Africa" (Palgrave 1991) taxonomic nomenclature was used as the naming convention of woody species in the Pretoriuskop region. A complete list of woody species identified in the 1954, 1959, and 1996 surveys is presented in Appendix 1, Table 9-1 (p. 210).

5.5.1.5.2 Structural diversity

The structural diversity of the woody vegetation was investigated using a structural classification comprising 32 structural groups. The structural groups included three aspects of woody vegetation structure, namely number of basal stems (single-stem or multi-stem), basal diameter (5 single-stem classes and 3 multi-stem classes Table 5-1), and height (4 classes Table 5-2). The 32 structural groups are shown in Table 5-3.

5.5.1.5.3 Indices of diversity

The diversity of the woody vegetation on the Pretoriuskop EBPs was measured for each plot using four indices that quantify the different components of diversity. The indices calculated were number of groups, Menhinick's richness index, Shannon's diversity index, and Shannon's evenness index.

5.5.1.5.3.1 Number of species or structure groups

The number of groups (s_j) is a count of the number of species or structural groups on plot *j*. This index is used to quantify the first component of diversity.

5.5.1.5.3.2 Menhinick's species or structural richness

Menhinick's index of richness (sm_j) calculates the number of species or structural groups (s_j) relative to the square root of the number of individuals (n_j) on a plot *j* (Brower and Zar 1977).

$$sm_j = \frac{s_j}{\sqrt{n_j}}$$ **Equation 5: Menhinick's richness index.**

This index quantifies the first component of diversity relative to the sample size, and consequently standardises the estimation for different collection sizes.

Table 5-3: The structural classification used to group the woody plants surveyed in the 1954, 1959, and 1996 surveys. The height and diameter class codes are defined in Table 5-1 and Table 5-2.

Basal stem class	Height class code	Diameter class code	Structure class code
Multi-stem classes	**H01**	**S01**	H01_S01
		S13	H01_S13
		S3	H01_S3
	H13	**S01**	H13_S01
		S13	H13_S13
		S3	H13_S3
	H35	**S01**	H35_S01
		S13	H35_S13
		S3	H35_S3
	H5	**S01**	H5_S01
		S13	H5_S13
		S3	H5_S3
Single-stem classes	**H01**	**T01**	H01_T01
		T13	H01_T13
		T35	H01_T35
		T57	H01_T57
		T7	H01_T7
	H13	**T01**	H13_T01
		T13	H13_T13
		T35	H13_T35
		T57	H13_T57
		T7	H13_T7
	H35	**T01**	H35_T01
		T13	H35_T13
		T35	H35_T35
		T57	H35_T57
		T7	H35_T7
	H5	**T01**	H5_T01
		T13	H5_T13
		T35	H5_T35
		T57	H5_T57
		T7	H5_T7

5.5.1.5.3.3 Shannon's species or structural diversity index

Shannon's index of diversity was used to quantify the species and structural diversity on the treatment plots. This index is a measure of the uncertainty of predicting the identity (class) of an individual chosen randomly from a population (Brower and Zar 1977). It quantifies the combined components of diversity, namely the number of groups and relative abundance of each group in a collection of individuals.

Regarding species diversity, Shannon's index is a measure of α-diversity on the plots, where α-diversity is defined as diversity of species within a community (Southwood and Henderson, 2000).

This index was chosen over Simpson's index of diversity because it is unaffected by absolute species abundances as long as the relative abundances remain the same.

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$H'_j = -\sum p_i \ln p_i$ **Equation 6: Shannon's diversity index.**

Where H'_j is Shannon's diversity, and p_i is calculated as $p_i = \frac{n_i}{n_j}$, where n_i is the number of individuals in species or structural group *i* and n_j is the number of individuals on plot *j*.

5.5.1.5.3.4 Shannon's species or structural evenness index

Shannon's evenness is also known as Pielou's J index (Huston 1994). This index is a measure of the nearness of the calculated diversity index to the maximum possible diversity, where maximum diversity occurs when all species are evenly proportioned (Brower and Zar 1977). Pielou's *J'* quantifies the evenness of the relative abundance of species.

$J'_j = \frac{H'_j}{H\max'_j}$ **Equation 7: Shannon's evenness index.**

Where J'_j is Shannon's evenness and H'_j is Shannon's diversity. $H\max'_j$ is calculated as $H\max'_j = \ln s_j$, where s_j is the number of species or structural groups on plot *j*.

5.5.2 Quantifying the data distributions and testing the vegetation indices calculated per plot for normality

The distribution of each of the twelve vegetation indices calculated for each plot was quantified using skewness and kurtosis statistics. Deviation from normality by each of these distributions was tested using Kolmogorov-Smirnov one-sample tests (KS) for normality.

5.5.2.1 Skewness and Kurtosis

Skewness quantifies the deviation of the data distribution from symmetry and is a measure of the distribution of the data around the arithmetic mean (Cangelosi *et al.* 1983, Systat 1998, StatSoft 1999). A positive skewness value indicates a long right tail and a negative skewness value indicates a long left tail. Skewness shows how the data conforms to a symmetrical bell shaped curve.

Kurtosis measures the peakedness of a distribution near its central mode (Cangelosi *et al.* 1983, StatSoft 1999). It is a measure of the magnitude of the peak and the spread around the arithmetic mean (Systat 1998). A value greater than zero indicates that the distribution is more peaky than a normal distribution and a value less than zero indicates that the distribution is flatter than a normal distribution. Kurtosis indicates how the data conforms to the requirements of the standard normal curve.

Skewness and kurtosis values were calculated for the distributions of the twelve vegetation indices that were estimated from the 1954 and 1996 survey data, and were used to describe the distribution of the vegetation indices. The skewness and kurtosis values were also used in conjunction with Kolmogorov-Smirnov analyses to determine whether the vegetation index distributions differed from normality and in what way they differed from normality. The skewness and kurtosis values were also used to compare the data distributions between the 1954 and 1996 surveys to give an indication to the kind of change that had occurred in the woody vegetation over time.

5.5.2.2 Kolmogorov-Smirnov one-sample tests for normality

The Kolmogorov-Smirnov one-sample test for normality is based on the maximum difference between a samples' cumulative distribution (frequency distribution) and the hypothesized cumulative distribution (standard normal distribution) (Systat 1998, StatSoft 1999).

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Kolmogorov-Smirnov tests for normality were performed on the data from the twelve vegetation indices calculated for the 1954 and 1996 survey data. These analyses were done to determine whether the indices might require transformation in order to use parametric analyses, or whether non-parametric analyses would be required to analyse the data.

5.5.3 Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA)

One-way ANOVA and ANCOVA analyses were performed on the twelve vegetation indices calculated per plot in 1954 and 1996. The analyses were done on the 1954 data to test for baseline uniformity of the woody vegetation density, structure, and composition against which the 1996 data was compared. The analyses were done on the 1996 data to test for the effects of the fire treatments on the density, structure, and composition of the woody vegetation. Analyses were also done on the 1954 and 1996 data to test for change over time in the density, structure, and composition of the woody vegetation. The twelve vegetation indices calculated, namely: density, mean height, tree equivalents, single-stem to multi-stem index, number of species, number of structure groups, Menhinick's species richness, Menhinick's structural richness, Shannon's species diversity, Shannon's structural diversity, Shannon's species evenness and Shannon's structural evenness were used in the analyses.

5.5.3.1 The size of the tests

The size (α) of the ANOVA, ANCOVA, and Tukey tests was set at 0.10. That is the probability of rejecting a null hypothesis was set at 0.10.

Conventionally the size of the test α is set at 0.05 or less, however, this decision is arbitrary and is a function of the trade-off between falsely rejecting (Type I error) or falsely accepting (Type II error) a null hypothesis (Cangelosi *et al.* 1983, Rosenthal and Rosnow 1991, Scheiner 2001). The heterogeneous nature of the experimental environment, the scale of the experimental layout, and the small number of replicates, amongst other confounding factors, resulted in a high variance in the data collected on the EBPs that is not correlated to the applied treatments (Biggs *et al.* 2003). Because of this, it was decided that the probability of Type I errors would be high and a higher test level (α) was set (α = 0.10) to decrease the probability of Type I errors.

5.5.3.2 The data groupings used in the ANOVA and ANCOVA analyses

The twelve vegetation indices calculated for each plot were grouped in the ANOVA and ANCOVA analyses in a number of ways to test for differences in the woody vegetation density, structure, and composition over time, between replicates, and between treatments. Table 5-4 (p. 38) lists the data groups used in the different analyses and a short description of each grouping is presented below.

5.5.3.2.1 Testing for differences in the woody vegetation on the Pretoriuskop EBPs between 1954 and 1996

The aim of these analyses was to test for differences in the twelve vegetation indices on all the plots between 1954 and 1996 (Hypothesis 1 p. 25). The data grouping in the analyses was the year in which the data was collected, namely 1954 or 1996 (the "Over time" column in Table 5-4).

5.5.3.2.2 Testing for differences in the woody vegetation between Pretoriuskop EBPs found on the four replicates, Fayi, Kambeni, Numbi and Shabeni

Essentially these analyses were used to test the homogeneity of the EBP experimental replicates in the Pretoriuskop region (Hypothesis 2 p. 26). The aim was to establish which, if any, of the replicates stood out as being different regarding their woody vegetation density, structure, and composition. The data grouping in the analyses was the replicate or block on which the data was collected, namely Fayi, Kambeni, Numbi, and Shabeni (the "Block/Replicate" column in Table 5-4).

5.5.3.2.3 Testing for differences in the woody vegetation between Pretoriuskop EBPs burnt at different frequencies (Annual, Biennial, Triennial and no burn)

The aim of these analyses was to test for differences in the twelve vegetation indices between the Pretoriuskop EBPs that were burnt at different frequencies between 1954 and 1996 (Hypothesis 3 p. 26). The EBP treatment factors, fire frequency and timing, are not completely crossed. For example, an annual fire frequency is applied in August only while the biennial and triennial fire frequencies are applied at five different times of the year, namely February, April, August, October, and December. Because of this, the annual treatment is not directly comparable to the biennial and triennial treatments without introducing timing effects into the frequency analyses. Two data groupings were used to ensure that the treatments were fully crossed preventing timing effects confounding ANOVA and ANCOVA analyses on the effect of fire frequency on the woody vegetation. The first data grouping comprised the Biennial and Triennial treatments. The annual August treatment was excluded from this analysis because there were no annual treatments at any other time of the year (the "Frequency - No August Annual" column in Table 5-4). This grouping will be referred to as the No-August-Annual grouping here after. The second data grouping comprised the Annual, Biennial and Triennial August treatments and the Control treatment, all other treatments were excluded from the analyses (the "Frequency - August & No Burn" column in Table 5-4). This grouping will be referred to as the August-Control grouping hereafter

5.5.3.2.4 Testing for differences in the woody vegetation between the Pretoriuskop EBPs burnt at different times of the year (February, April, August, October, and December)

The aim of these analyses was to test for differences in the twelve vegetation indices between the Pretoriuskop EBPs that were burnt at different times of the year between 1954 and 1996 (Hypothesis 4 p. 27). The EBP treatment factors, fire frequency and timing, are not completely crossed. Because the August treatments represent annual, biennial, and triennial treatments while the February, April, October and December treatments represent only biennial and triennial treatment they are not directly comparable. The No-August-Annual data grouping described above was used to prevent frequency effects confounding ANOVA and ANCOVA analyses on the effect of fire timing on the woody vegetation. The data grouping in these analyses was the treatment timing, namely February, April, August, October, and December (the "Timing - No August Annual" column in Table 5-4).

5.5.3.2.5 Testing for differences in the woody vegetation between the Pretoriuskop EBPs burnt at different frequencies and at different times of the year (i.e. between the EBP treatments)

The aim of these analyses was to test for differences in the twelve vegetation indices between the twelve treatments that were applied to the Pretoriuskop EBPs between 1954 and 1996 (Hypothesis 3 (p. 26) and Hypothesis 4 (p. 27)). The data grouping in these was the twelve fire treatments, namely No Burn, Annually in August, Biennially in February, April, August, October, and December, and Triennially in February, April, August, October, and December (the "Treatment – Timing & Frequency" column in Table 5-4).

5.5.3.2.6 Testing for differences in the woody vegetation on the Pretoriuskop EBP Control (no burn) plots between 1954, 1959 and 1996

The aim of these analyses was to test for differences in the twelve vegetation indices on the Control (no burn plots) between 1954, 1959, and 1996 (Hypothesis 5 p. 27). The data grouping in these analyses was the year the survey data being used was collected, namely 1954, 1959, and 1996 (the "No Burn" column in Table 5-4).

5.5.3.3 The covariates for the Analysis of Covariance

Analyses of covariance were performed on the 1996 data using the 1954 data as covariates. These analyses were done to test the effects of the fire treatments on the density, structure, and composition of the woody vegetation taking into account the woody vegetation density, structure, and composition at the beginning of the experiment.

Table 5-4: Plot groupings used in the Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA).

Over time	Block/Replicate	Frequency No August Annual	Frequency August & No Burn	Timing (season) No August Annual	Treatment (Timing & Frequency)	No Burn
1954	Fayi	No burn	No burn	February	No burn	1954
1996	Kambeni	Biennial	Annual	April	August Annual	1959
	Numbi	Triennial	Biennial	August	February Biennial	1996
	Shabeni		Triennial	October	April Biennial	
				December	August Biennial	
					October Biennial	
					December Biennial	
					February Triennial	
					April Triennial	
					August Triennial	
					December Triennial	
					October Triennial	

5.5.3.4 Post hoc analyses on the significant results from the ANOVA and ANCOVA analyses

Student's t-tests can be used to test whether or not two means are significantly different from each other if they represent the only two samples taken. Post-hoc analyses techniques on the other hand, specifically take into account the fact that more than two samples have been taken. The Tukey Student's t statistic was used for *post hoc* comparisons to determine which pairs of means differ significantly in the ANOVA and ANCOVA analyses. The Tukey test like the Bonferroni test uses a Studentized range statistic to make pair-wise comparisons between groups, and sets the error rate to the error rate for the collection for all comparisons (Systat 1998).

5.5.3.5 Graphs showing the least squares means and standard errors of the vegetation indices from the ANOVA and ANCOVA analyses

Graphs showing the least squares means and standard errors of the vegetation indices from the ANOVA and ANCOVA analyses were created for each of the ANOVA and ANCOVA analyses performed. In one-way ANOVA designs the least squares means are the same as the arithmetic means of the subpopulations (StatSoft 1999). In ANCOVA analyses, the least squared means are the adjusted subpopulation means after removing all differences that can be accounted for by the covariates.

5.5.4 Horn's index of community similarity

Horn's index of community similarity was calculated using the species by plot data and the structure by plot data from 1954 and 1996. Horn's index was used to compare the similarity of the woody vegetation species diversity and structural diversity between the Pretoriuskop EBPs.

Horn's index of community similarity is based on Shannon's diversity index (Equation 6 p. 35). The similarity of two communities is calculated by comparing their combined diversity, with their potential maximum and minimum diversity. Horn's index is zero, when the two communities have no species in common and one when the species composition and relative abundances are identical (Brower and Zar 1977).

Horn's index is computationally complex, and is a measure of the group overlap between two communities. This index measures the binary co-occurrence of groups between two communities, and measures the relative abundance of the groups. Horn's index was chosen over other measures of community similarity such as Jaccard's, Sorensen-Dice, and Ochiai's coefficients, which measure the binary co-occurrence of groups of between communities only. Furthermore, Horn's index is unaffected by the absolute abundance of species, as long as the relative abundances remain the same. Finally, Horn's index does not include

negative matches (i.e. species that do not occur in either location), which tend to inflate the influence of rare species in other indices.

Horn's index was used as a measure of the similarity in species composition or structural composition between the treatment plots in the Pretoriuskop region.

5.5.4.1 Calculating Horn's index

1. Calculate Shannon's diversity (H') for each community:

$$H_A' = -\sum \frac{x_i}{N_A} \ln \frac{x_i}{N_A}$$ **Equation 8: Shannon's diversity - Community A.**

$$H_B' = -\sum \frac{y_i}{N_B} \ln \frac{y_i}{N_B}$$ **Equation 9: Shannon's diversity - Community B.**

2. Calculate the diversity for the two communities combined:

$$H_{AB}' = -\sum \left(\frac{x_i + y_i}{N_A + N_B} \ln \frac{x_i + y_i}{N_A + N_B}\right)$$ **Equation 10: Combined Shannon's diversity.**

Where H_{AB}' is the diversity of community A and B combined. The value of H_{AB}' is lowest when the two communities are similar, and highest when they are dissimilar.

3. Calculate the maximum diversity obtainable between the communities. This is calculated by treating each species or structural group abundance (x_i and y_i) as though they were different (Brower and Zar 1977).

$$H_{\max}' = -\sum \left(\frac{x_i}{N_A + N_B} \ln \frac{x_i}{N_A + N_B}\right) - \sum \left(\frac{y_i}{N_A + N_B} \ln \frac{y_i}{N_A + N_B}\right)$$

Equation 11: Maximum Shannon's diversity.

Where $H_{\max}'$ is the maximum possible diversity between the two communities A and B.

4. Calculate the minimum diversity obtainable between the communities (i.e. with maximum over lap of x_i and y_i).

$$H_{\min}' = \frac{(N_A H_A' + N_B H_B')}{N}$$ **Equation 12: Minimum Shannon's diversity.**

Where $H_{\min}'$ is the minimum possible diversity between communities A and B, and N is calculated as $N = N_A + N_B$.

5. Horn's index of community overlap:

$$R_o = \frac{H_{\max}' - H_{AB}'}{H_{\max}' - H_{\min}'}$$ **Equation 13: Horn's index.**

Where R_o is horn's index of community overlap.

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A plot-by-plot similarity matrix was constructed using the Horn's similarity indices between each Pretoriuskop EBP.

5.5.4.2 Cluster analyses of Horn's similarity indices

Pearson's distance cluster analyses with Ward's linking method (Pearson-Ward cluster analysis) were performed on a similarity matrix of Horn's similarity indices to detect natural groupings in the Pretoriuskop EBPs. The Pearson's distance measure is one minus the Pearson product-moment correlation coefficient for each pair, and is used for non-ordinal data. Ward's method of cluster linking attempts to minimize the sum of squares of any two hypothetical clusters that can be formed at each step (Ward, 1963). Ward's method of cluster linking is considered very efficient, however it does tend to create small clusters (StatSoft 1999).

Pearson-Ward cluster analysis produces hierarchical clusters that can be displayed in a tree. Firstly, each entity, in this case each plot, is placed into separate clusters. The cluster algorithm begins by joining the two most similar plots in terms of their species composition or structural composition into a cluster. The algorithm continues in a stepwise manner joining one cluster with another, forming larger clusters and creating a hierarchical cluster tree.

Two distances were subjectively chosen to group the plots in the cluster analyses. The first distance was chosen so that ten to twelve clusters could be identified, and the second distance was chosen so that four clusters could be identified.

5.5.4.2.1 Maps of the layout of the Pretoriuskop EBPs with the plots colour coded to the clusters at the second distance (four clusters)

Maps of the Pretoriuskop EBPs were created showing the plot location and the surrounding vegetation based on the South African Defence Force (SADF) vegetation classification of the Pretoriuskop region. The SADF vegetation classification was done in the early 1980's by the South African Defence Force in the Kruger National Park. The classification was based on Braun-Blanquet vegetation surveys, which were then translated onto 1:25000 vegetation maps. The accuracy of these maps is not known, and the precision is thought to be coarse. The Pretoriuskop EBPs were colour coded on these maps to show the plot clustering at distance 2 from the Pearson-Ward cluster analysis. This was done to identify any spatial pattern in the distance 2 clusters of the Pretoriuskop EBPs.

5.5.5 Correspondence Analyses (CA)

Correspondence analyses (CA) were performed on the species density by plot and the structure density by plot data. Correspondence analysis is an indirect gradient analysis (IGA) technique in which a two-way table, like species density per plot or structure group density per plot, is decomposed into primary gradients, reducing the dimensionality of the data. IGA techniques reduce data to primary axes of variation, these axes are mathematical functions of the variation in the data and do not correspond to environmental gradients.

Correspondence analyses were done on the species and structure by plot data in 1954 to examine baseline patterns between the species and structures and the treatment plots. CA's were performed on the 1996 species and structure by plot data to determine the effect of the prolonged application of the fire treatments on the woody vegetation species and structure composition on the Pretoriuskop EBPs. CA's were also performed on the 1996 species and structure by plot data in which the first 8 axes of the CA's done on the 1954 species and structure by plot data were used as covariates. This was done to account for pre-experiment variation in 1954 in the 1996 data.

The species, structure, and plot weighted eigenvector values are approximate values of transformed species, structure, or plot abundance (Ter Braak 1988). These transformed abundances are along unconstrained gradients of variation or axes (eigenvectors). Each axis represents the variation of either species or structure occurrence between plots or the plot (location) variation between species or structures.

Groupings along these axes are used to group species, structures, or plots in multidimensional hypothetical space based on co-variation.

5.5.5.1 Bi-plots of the first two weighted eigenvectors of the species, structure, and plot scores

Bi-plots of the species, structure, and plot scores from the first two weighted eigenvectors were plotted against one another in two dimensional scatter plots. The first weighted eigenvector was plotted along the x-axis and the second weighted eigenvector was plotted along the y-axis. The co-variation between species and plots, and structures and plots was visually assessed by looking for groupings in the species, structures, and plots on the bi-plots. Groups of plots, structures, and species were identified and marked on the bi-plots. The graph points on the bi-plots were colour coded to the cluster group of the plots, structures and species from the step-wise Ward-Gamma cluster analysis on the first four weighted eigenvectors. This was done for comparative purposes between the visual assessment of the species, structure, and plot groupings along the first two eigenvectors and the step-wise Gamma-Ward cluster analysis of the first four eigenvectors.

5.5.5.2 Cluster analyses of the first four weighted eigenvectors of the species, structure, and plot scores from the Correspondence Analyses

Cluster analyses are effective methods of identifying groupings in data. Gamma-Ward cluster analyses were used to identify groupings in the first four axes of the Correspondence analyses on the species and structure by plot data in 1954 and 1996.

In CA's the axis order is important, this is because the first axis explains proportionately more variation than the second axis and the second axis explains proportionally more variation than the third axis and so on. Therefore, groupings along the first axis of variation are important when interpreting groupings along the second axis of variation, and groupings along the first and second axes of variation are important when interpreting groupings along the third axis of variation. To account for the relative importance of the axes of variation a stepwise cluster analysis approach was used to maintain the groupings from the first axis of variation, to the second axis of variation, and from the first and second axis of variation to the third axis of variation and so on to the fourth axis of variation.

Gamma distance cluster analyses with Ward's linking method (Gamma-Ward cluster analysis) were performed on each CA axis pair from axes 1 to 4 (i.e. Axis 1 and 2, Axis 1 and 3, Axis 1 and 4, Axis 2 and 3, Axis 2 and 4, and Axis 3 and 4). The Gamma distance is calculated as one minus the Goodman-Kruskal gamma correlation and is generally used for rank order and ordinal scales (Systat 1998, StatSoft 1999). Correspondence Analyses axes scores are not ordinal. However, the Gamma distance has the unique property of creating only two clusters when there are only two factors. A Gamma-Ward cluster analysis was performed on each axis pair from the first four axes of each Correspondence analysis.

5.5.5.2.1 The stepwise Gamma-Ward cluster method

1. A Gamma-Ward cluster analysis was performed on each pair of axes scores from the first four axes of a Correspondence analysis. This resulted in six Gamma-Ward cluster trees, one for each axis pair (i.e. Axis 1 and 2, Axis 1 and 3, Axis 1 and 4, Axis 2 and 3, Axis 2 and 4, and Axis 3 and 4).
2. When there are only two factors (i.e. axis 1 and axis 2) the Gamma-Ward cluster analysis creates only two clusters, so each species, structure, or plot was identified as belonging to either cluster 1 or cluster 2 for the Gamma-Ward cluster analyses on each axis pair (Table 5-5).
3. The cluster analyses were ranked according to the sum of the variation that each pair of axes accounted for in the Correspondence analysis (Table 5-5).
4. The cluster that each species, structure or plot belonged to for each axis pair was then used in the axes pair rank order to create a cluster identifier (Table 5-5).
5. The cluster identifier comprised 6 consecutive numbers (arbitrarily chosen as ones and twos), and each number represented a level in the classification of the species, structures or plots which was

then used to create a hierarchical classification representing the grouping of entities based on the first 4 axes of the correspondence analyses. Figure 5-2 shows an example of the resulting cluster tree from the hierarchical classification.

Table 5-5: Example of how species, structures, and plots were classified by a stepwise Gamma-Ward cluster analysis of the first four ordination axes from the Correspondence Analyses.

Axis pair rank	1	2	3	4	5	6	
Structure	Axis 1 & 2 clusters	Axis 1 & 3 clusters	Axis 1 & 4 clusters	Axis 2 & 3 clusters	Axis 2 & 4 clusters	Axis 3 & 4 clusters	Cluster Identifier
H13_S01	1	1	1	1	1	1	111111
H13_S13	1	1	1	2	1	1	111211
H13_S3	1	2	1	2	2	1	121221
H01_T01	2	2	1	2	2	1	221221
H01_T13	2	2	2	2	2	1	222221
H01_T35	2	2	2	2	2	2	222222

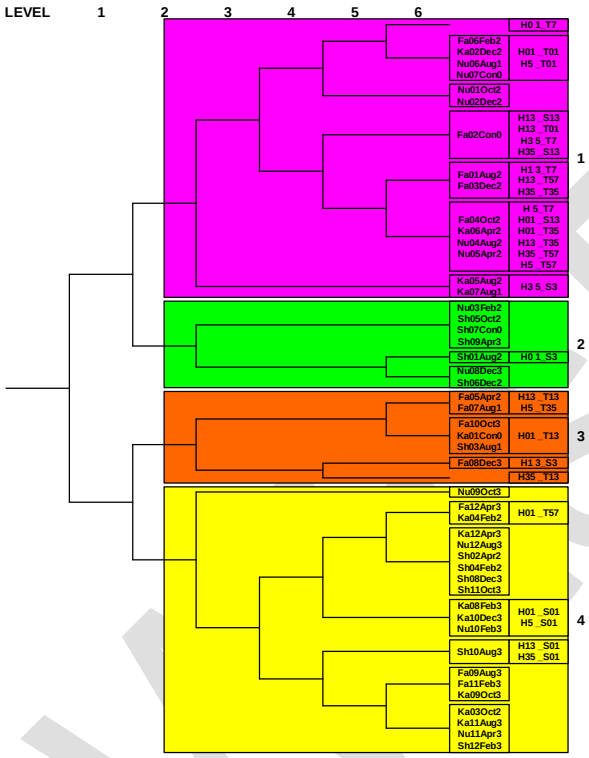

Figure 5-2: Example of the tree cluster diagram showing the structure plot classification from the stepwise Gamma-Ward cluster analysis of the first four ordination axes from the Correspondence Analyses on the 1954 structure by plot data.

The graph points on the bi plots were colour coded to show the clusters at level 2 from the stepwise Gamma-Ward cluster analyses.

5.5.5.2.2 Maps of the layout of the Pretoriuskop EBPs with the plots colour coded to the level 2 clustering of the plots

Maps of the Pretoriuskop EBPs were created showing the plot location and the surrounding vegetation based on the South African Defence Force (SADF) vegetation classification. The Pretoriuskop EBPs were colour coded on these maps to show the plot clustering at level 2 from the stepwise Gamma-Ward cluster analyses. This was done to identify any spatial pattern in the level 2 clusters of the Pretoriuskop EBPs.

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