EFFECT OF SEASON AND TYPE OF FIRE ON *Colophospermum mopane* WOODLAND IN THE SOUTH-EASTERN LOWVELD OF ZIMBABWE

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Declaration

I hereby declare that the contents of this dissertation comprises my own original work, except where otherwise acknowledged or stated. This work has not been submitted for degree purposes to any other university.

....
Michael J Walters

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"Trust in the Lord with all your heart, and never believe what you think you know."
Proverbs 3:5. Thank you Lord for all that you have given me.

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Abstract

The majority of the vegetation types occurring on Malilangwe Estate, in the south-eastern lowveld of Zimbabwe, are dominated by *Colophospermum mopane* (mopane). Over the past 30-50 years the stand density of these mopane vegetation types has increased, and an investigation was undertaken to determine the effect of season of burning and type of fire on mopane woodlands. From this study the following was ascertained:

1) A single predictive equation cannot be used over all seasons to estimate standing crop (fuel load) using the standard disc pasture meter procedure. The calibration equations developed using this procedure accounted for between 39 and 72% of the variation in standing crop, illustrating the high variation in basal cover of the grass sward, as well as the variation between months. Although the revised procedure, developed for areas with low basal cover, accounts for a lot more of the variation in standing crop, this procedure was not used to estimate standing crop over the study period because the calibration equation covered a number of vegetation types, and was not specific to the mopane woodlands.

2) Standing crop tracks effective rainfall (monthly rainfall divided by monthly pan evaporation) closely, with a lag period of less than one month. Standing crop can be estimated using a predictive equation that utilizes effective rainfall from the previous month. There is a positive relationship between peak standing crop and rainfall. A predictive equation was developed to estimate peak standing crop, using annual rainfall. Standing crop declines through the dry season as effective rainfall decreases, and this 'decrease function' allows for the estimation of the standing crop for a particular month, after peak standing crop is reached.

3) Two leaf quantification equations were developed for mopane trees in the south-eastern lowveld of Zimbabwe, one for coppicing and for non-coppicing individuals. These allow for the estimation of leaf dry mass from measured canopy volume.

4) There was no significant difference between the fire intensities attained for the three seasons of burning. Over all seasons, head fires were significantly more intense than back fires.

5) Percentage topkill after late dry season burns was significantly higher than topkill after early dry season burns. There was no significant difference between mid and late dry season burns, and head fires led to significantly more topkill than back fires. Plants <150 cm experienced significantly more topkill (80%) than did individuals >150 cm (44%).

6) Fire *per se* led to an increase in stand density over all seasons and types of fire, but this change was not significant. Fire did not influence the nett recruitment of new individuals. Height class one (0-50 cm) and three (151-350 cm) were impacted most by fire. This reflects a change in tree structure, with an increase in the amount of leaf material in height class three, and a subsequent decrease in the amount of material in height class one.

7) The effect of season of burning on the change in tree height was significant, whereas the effect of type of fire was not significant. All treatments, except early dry season back fires, led to a reduction in tree height, whereas trees in the no burn areas increased in height.

8) Burning in any season, and implementing either type of fire, led to an increase in the number of stems. Mid dry season burns led to the highest increase in number of stems. However, the more intense the fire the smaller the increase in number of stems.

9) All three seasons of burning (head and back fires) led to a significant decrease in maximum canopy diameter per tree, while the maximum canopy diameter of trees in the no burn areas increased. Mid dry season burns resulted in the greatest decrease in canopy diameter.

10) The effect of burning on the change in leaf dry mass per tree was highly significant. All three seasons of burning led to a decrease in leaf dry mass, while there was no difference between head and back fires. Leaf dry mass in the control areas increased however. High fire intensities led to the greatest decrease in leaf dry mass, late dry season head fires having the greatest decrease.

This study suggests that mopane plants face a constraint due to fire and/or browsing, and a tradeoff occurs between canopy volume, canopy diameter, canopy area; and number of stems. Fire leads to an increase in the number of stems through coppicing, while canopy volume and leaf dry mass decreases. This decrease is either (i) a tradeoff in response to increasing stem number, or (ii) a reduction in canopy because additional leaves on the new stems contribute to photosynthesis.

The most important response to season of burning is the altered phenophase (phenological stage) of the plant. Early dry season burns cause the trees to be leafless during the early dry season (when unburnt trees are carrying full leaf), and then to be in leaf at the end of the dry season (when unburnt trees are leafless). It would appear that fire disturbance initiates leaf senescence after burning, and then leaf expansion earlier than normal *i.e* the whole leaf senescence/growth process is brought forward. Trees in late dry season burn areas remain leafless at the start of the rains, while trees in unburnt areas are carrying leaf. Being leafless these trees do not photosynthesize during this time, and it is proposed that the grass sward is advantaged by the reduced competition from the tree component. The consequences of these two changes in phenophase could not be addressed in this study, but are pertinent questions that must be answered if mopane woodland dynamics are to be more fully understood.

Management recommendations for (1) the removal of unacceptable moribund grass material, or (2) the reduction of encroachment by woody species on Malilangwe Estate are also given. In an attempt to combat the increase in stand density of mopane it is recommended that high intensity head fires be implemented, when standing crop (fuel load) is sufficient and climatic conditions are conducive to maintaining high intensity fires. These should be carried out at the end of the dry season, before the onset of the rains.

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Chapter 1

Introduction

The mopane vegetation of the south-eastern lowveld of Zimbabwe occurs as shrubland or woodland, and forms part of the arid, fertile, mesophyllous savanna community of southern Africa (Figure 1.1). Savannas occupy 54% of southern Africa and 60% of sub-Saharan Africa (Scholes and Walker 1993).

The main control on the recruitment of savanna trees is the interactive effects of fire, herbivory and competition with the grass layer (Frost 1985). In this study the effect of fire (season and type) was examined. It was hypothesized that trees in different phenological stages (seasons) would respond differently to fire, and that head fires would cause more damage than back fires because of their higher fire intensity and flame height. Small trees in the sward grow above the grass layer following a simultaneous release from competition, fire and herbivory. Mopane, being a sprouter/coppicing species, is persistent and is able to coppice from the cambium of the stem if the terminal buds have been damaged or, if the stem has also been killed, from the root collar (Rutherford 1981). This persistence, in the face of burning, varies greatly among different height classes because of the vertical release of heat energy during burning. Unlike other disturbances, fire alone, or in combination with other forces, regularly kills mature plants. It is therefore an important agent in structuring communities, since the new openings created provide the potential for vegetation change (Bond and van Wilgen 1996).

Fire is an important phenomenon in the semi-arid savanna areas of southern Africa. Rainfall occurs in the warmer summer months with a dry period of two to eight months duration during which fire is a typical phenomenon at intervals of one to fifty years (Huntley 1982). Succession advances towards an open woodland or shrub savanna climax, but under disturbed conditions (fire, browsing or edaphic) a dense thicket may develop.

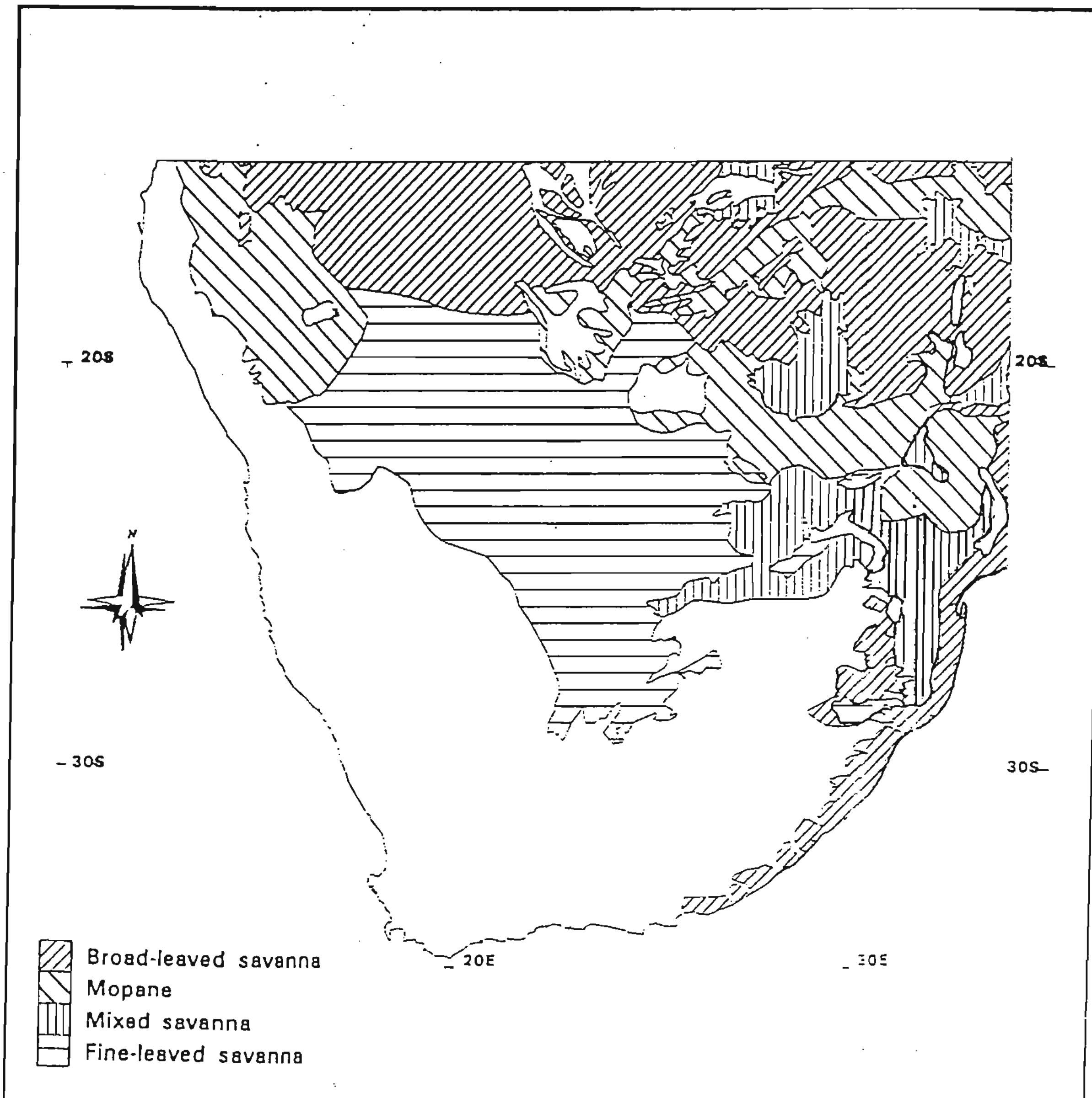

Figure 1.1 The distribution of broad classes of savanna in southern Africa (from Scholes 1997).

The nutritive value of semi-arid savannas is high and, in contrast to the moist savanna areas, can be viewed as sweetveld *ie.* veld which remains palatable and nutritious when mature, and provides forage for a full 12 months (Scott 1947).

Historically the semi-arid savanna areas supported large concentrations of indigenous ungulates (Huntley 1982). Because of the year-round palatability of the savanna grass component, the utilization of these areas for extensive cattle ranching has been widespread. This was the case in the south-eastern lowveld of Zimbabwe, and together with the introduction of large numbers of cattle, the removal of indigenous ungulates and elephants, was the suppression of fire. This simultaneous release of trees from competition, fire and herbivory resulted in the widespread increase in tree density of opportunistic early successional species.

Motivation and objective

It is widely accepted that fire is an essential determinant of savanna structure (Walker 1985), and is an effective method of succession management that has been used by man for centuries (Trollope 1982, Wright and Bailey 1982, Dublin *et al.* 1990, Menaut *et al.* 1990, Silva *et al.* 1991). It has been shown that the exclusion of fire allows for successional development of open savanna to a forest/thicket state (Trapnell 1959, Smith and Goodman 1987), and conversely that fire *per se* can maintain or reduce woody encroachment (West 1971, Trollope 1980, Trollope 1999).

It was with this knowledge of rangeland succession in mind that the previous Director of Malilangwe Conservation Trust, Dr Jeremy Anderson, motivated for a research project to study the effects of fire on mopane (*Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard) woodland. It was perceived that previously open grasslands and savanna areas had been encroached by mopane, and the objective of this study was to gain an understanding of the effects of different seasons of burning and types of fire on mopane woodland. During a cursory visit, and a subsequent data collection period, it was found that mopane encroachment was not as widespread as perceived. Even-aged cohorts of mopane occur on the peripheries of mesic grasslands, while soil physical, chemical and hydrological properties limit the establishment and survival of mopane trees within the mesic grassland areas. Instead, it appears as if mopane stand density has increased within existing stands in the last 30 to 40 years, and encroachment is by microphyllous species such as *Acacia borleae* Burtt Davy and *Dichrostachys cinerea* (L.) Wight Arn.

Chapter 2

Literature review: The major determinants of mopane woodland dynamics in the south-eastern lowveld of Zimbabwe

This chapter deals with the conceptual backdrop to this thesis: Effect of season and type of fire on *Colophospermum mopane* woodland in the south-eastern lowveld of Zimbabwe. A comprehensive synthesis of the global literature pertaining to the following is presented:

1) a review of mopane (*Colophospermum mopane*) physiology and ecology,
2) the major determinants of mopane woodland structure and functioning,
3) fire in semi-arid savanna areas, and
4) the components of the fire regime and how they effect mopane woodland dynamics.

Introduction

"I put this to those studying burning; we are challenged by a most involved process, a series of complex reactions. We must therefore be humble in attempting to apply the interpretations derived from observations and experimentation, even when aided in future by the right feeding in of the right material to the computer." (Phillips 1971). It is with this warning in mind that this literature review is undertaken.

The determinants of the structure and functioning of mopane vegetation are numerous and highly complex, the major factors being climatic and edaphic conditions. Other determinants are human impact, frost, fire, elephants and other browsers, invertebrates, lightning, drought and competition with the herbaceous layer for limited resources. It is widely accepted that fire is a secondary determinant of savanna structure (Walker 1985), and an effective method of succession management that has been used by man for centuries (Trollope 1982, Wright and Bailey 1982, Dublin *et al.* 1990, Menaut *et al.* 1990, Silva *et al.* 1991). It has been shown that the exclusion of fire allows for successional development of open savanna to a forest/thicket state depending on climate and soil factors (Trapnell 1959, Smith and Goodman 1987), and conversely that fire *per* *se* can maintain or reduce woody encroachment (Spinage and Guinness 1971, West 1971, Trollope 1980, Pellew 1983, Bell and Jachmann 1984, Tainton 1999). However, the principles and trends found to be relevant to other savanna tree species may not be relevant to mopane, owing to physiological and ecological factors that make it highly resistant to the effects of fire, very competitive with the grass layer and extremely persistent in semi-arid savanna areas.

The effects of fire regime on mopane vegetation dynamics is still an unknown quantity, and the hypotheses formulated for other semi-arid savanna species still have to be tested specifically for mopane.

Mopane: a review

Introduction

Colophospermum mopane is a widespread and important tree species in sub-tropical southern Africa, occurring between just south of the Tropic of Capricorn and 10° south (Timberlake 1995). It can become locally dominant forming an almost monospecific woodland, in other circumstances it can occur as a component of a more open savanna with numerous other species, or it can occur as an isolated population. Over its whole range it is economically important as fuel and charcoal, for fencing and building material, as the host of a protein-rich human food source (mopane worms), and as valuable browse for domestic and wild animals. Timberlake (1995) stresses the need for an endeavour to understand the ecology of this species, as it is of great importance, especially in the northern areas of southern Africa.

Phytology

Description

It is a shrub or small to large-sized deciduous tree (5-20 m), with an erect narrow crown (van Wyk and van Wyk 1997). It occurs in almost pure stands in hot, low-lying areas, often on alluvial or lime-rich soils and basalt-derived lowlands (Timberlake 1995). Stem diameter is variable, normally 5-80 cm, but can attain 150 cm.

The bark is dark grey or brown, rough, with longitudinal fissures. Leaflets are stalkless, resembling two butterfly wings, with a minute protuberance between the pair, hairless and smell strongly of turpentine when crushed (van Wyk and van Wyk 1997). The root system is generally shallow, 30-120 cm (Thompson 1960). Lateral roots are well developed and a taproot may be present when young but dies back as the tree gets larger (Henning 1976). Fine roots are endomycorrhizal (Hogberg and Piearce 1986).

Inflorescences are greenish-white; wind pollinated, and appear from December to March. The seed pods are light to dark brown, compressed, and have numerous scattered resin glands on the surface (Timberlake 1995).

Life cycle and phenology

Mopane is irregularly deciduous, the leaves turning yellow to red-brown at the start of the dry season. Trees are normally leafless for two to three months at the end of the dry season (September to November). The flush of new leaves coincides with the onset of the rains, or directly thereafter. In most environments this flush of new leaves takes place later than other savanna tree species. Regrowth of leaves is possible if the young leaves are removed soon after the start of the growing season (Guy *et al.* 1979).

Physiology

Mopane is physiologically adapted to xeric and low soil nitrogen and potassium conditions. Stress adaptations differ between areas and appear to be genetically heritable (Prior 1991). It is able to grow at a matric water potential below -15.2 bar (Henning and White 1974) and is also capable of internal osmotic adjustment, involving osmotically active nitrogen compounds in the cell sap. Mopane performance (the product of mean stem diameter by density over all height classes) was found to be correlated with soil nitrogen and phosphorous, exchangeable magnesium and per cent subsoil moisture over a range of soils from southern Africa (Henning 1976).

Seed germination takes place under a wide range of conditions, best being at a water stress of -1.4 bars (Choinski and Tuohy 1991). Seedling growth has been found to lead to a reduction in soil pH due to selective uptake of cations (Smith 1972). Seedlings require freedom from competition, especially from grasses (Sharma *et al.* 1989). Under natural conditions germination is very good, and many seedlings can be found after the first rains. Due to competition and large herbivore selectivity (especially elephants), few survive the first dry season to become saplings (Timberlake 1995). Prior (1991) reports that mopane seedlings are more stress tolerant than those of *Acacia*.

Pests and diseases

Seedlings are prone to damping, and one species of leaf-spot fungus has been reported on mopane in southern Zimbabwe (Piearce 1986).

The mopane worm is the edible larva of the moth *Gonimbrasia belina*, which can cause severe defoliation of trees in some years, but recovery is rapid (van Voorthuizen 1976). Another lepidopteran defoliator is the 'green slug', *Latoia vivida*, which in some years causes large-scale reduction in leaf matter. *Arytaina mopane*, the mopane psyllid, produces an excretory product (lerp) which is reputed to make the leaves more palatable to browsing animals (van Wyk 1972).

Ecology

Distribution

Mopane is a xeric species of the savanna woodland zone of south tropical Africa. It is found mostly on heavier-textured soils in the wide, flat valley bottoms such as the Limpopo, Zambezi, Okavango and Luangwa (Cole 1986). It is indigenous to the semi-arid savanna areas of the south-eastern lowveld of Zimbabwe, with an area of 101 500 km^2 (18.5% of total mopane area) under mopane-dominated vegetation in Zimbabwe (Timberlake 1995).

Altitudinal distribution is from <100 m (Mozambique) to 1200 m (Zimbabwe), and in the Zimbabwe lowveld from 300 to 600 m (Figure 2.1). Within its distribution the annual rainfall ranges from 100-800 mm, with the majority of the population range being found in the 400-700 mm annual rainfall zone. It is intolerant of severe frosts, being restricted by the 5°C mean daily isotherm for July (Henning 1976).

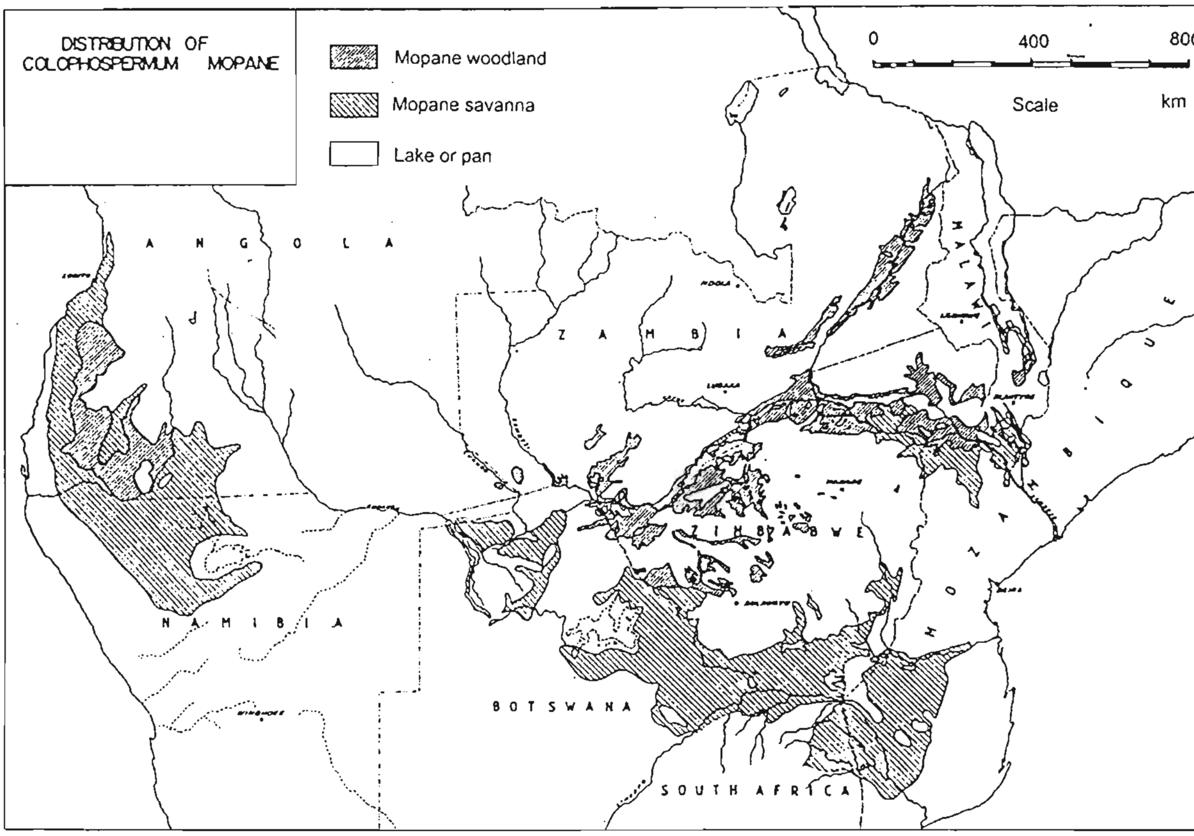

Figure 2.1 Distribution of *Colophospermum mopane* in southern Africa (from Mapaure 1994).

Mopane vegetation distribution is determined by different ecological factors in different areas, with frost incidence, minimum temperatures, rainfall minima/maxima and altitude all contributing. In the south-eastern lowveld of Zimbabwe the land rises from the Mozambique coastal plain to the central plateau, and increased rainfall (soil moisture availability) allows other tree species and vegetation types to dominate (Timberlake 1995). On basalt-derived soils in southern Zimbabwe the mopane vegetation is an early deciduous shrub savanna, whilst on the more alluvial soils it is a dry deciduous tree savanna. The "cathedral mopane" (tall single-stemmed trees) of the northern and western areas of its distribution do not occur in the lowveld.

Mopane-dominated savanna areas are noted for their low alpha-diversity (few associated species). Also, there are a low number of similar associated species (low beta-diversity). Grass cover is generally poor, and often dominated by annuals.

Soils

Mopane generally occurs on clay-rich soils, or soils with a clay layer immediately below the surface. It also establishes on duplex soils and sodic sites, usually as a small tree or shrub, where it endures and expands its range as soil erosion and surface capping increases (Dye 1977). The shallow root system coincides with the zone of maximum moisture retention (Thompson 1960), and mopane is excluded from better soils by deeper-rooted *Acacia* species (Cole 1986). Mopane is thus a strong competitor with the grass layer, as well as with other tree species, where the available soil moisture is retained near the surface. Thompson (1960) notes that factors reducing grass growth will favour mopane on suitable sites, including:

1) low and erratic rainfall in combination with sandy surface soils of low water-retaining capacity,
2) competition for available moisture by massed mopane surface roots, and
3) the occurrence of shallow sandy soils over relatively impervious sodic subsoils.

Short tree and shrub forms are found on the alkaline black clays of the south-eastern lowveld of Zimbabwe (Cole 1986). The tree form is found on more permeable soils. As rainfall increases edaphic factors become more important in its distribution and mopane is confined to physiologically drier sites (Thompson 1965).

Biomass production and tree density

Standing biomass figures vary in response to stand density, soil factors and climatic conditions. For the south-eastern lowveld of Zimbabwe, Kelly and Walker (1976) found that standing above-ground biomass and annual production varied with level of utilisation (Table 2.1).

Table 2.1 Annual production (A) and mean standing above-ground biomass estimates (B) of mopane woodland in the south-eastern lowveld of Zimbabwe (from Kelly and Walker 1976)

	$t.ha^{-1}$	Component	Utilisation
A.	1.18	FW	mean
	1.58	*, FW	no
	1.49	*, FW	light
	1.66	*, FW	moderate
	1.22	*, FW	high
B.	15.0	FW	no
	15.7	FW	light
	28.1	FW	medium
	15.9	FW	high

* tree+shrub, FW field weight (before drying)

Mopane generally comprises >90% of the total biomass of mopane savanna vegetation (Guy 1981), which is probably a higher proportion than most other individual species contribute to the woodland types in which they are found (Timberlake 1995). Only 3.7% of total mopane biomass is browse (leaf + twig), the rest being mainly wood (Martin 1974).

Equations for the prediction of biomass of mopane from individual stem diameter or crown measurements were developed by Kelly and Walker (1976) for the semi-arid south-eastern lowveld of Zimbabwe, and of leaf dry mass and leaf volume for the Soutpansberg in South Africa by Smit (1994), (Table 2.2).

Table 2.2 Predictive equations for mopane field weight (FW, before drying) biomass (Kelly and Walker 1976), leaf dry mass and leaf volume, (Smit 1994)

Equation
Trees - standing biomass
mass (kg Fw.ha^{-1}) = -2934.8 + 219.1(canopy area, m^2 x dbh, cm)
Shrubs - standing biomass
mass (kg FW.ha^{-1}) = -481.4 + 425.6(canopy volume, m^3)
mass (kg FW.ha^{-1}) = 882.3(canopy volume, m^3) [shrubs<1.5 m]
Annual production - trees, shrubs
production (kg FW.ha^{-1}.yr^{-1}) = -2505.4 + 993.1(height, m) [leaves+twigs]
production (kg FW.ha^{-1}.yr^{-1}) = 175.1 + 71.4(canopy volume, m^3) [leaves+twigs]
Leaf dry mass
leaf dry mass (g) = 0.025 x EXP(0.702 x Ln spatial volume, cm^3) [non-coppicing]
leaf dry mass (g) = 0.174 x EXP(0.558 x Ln spatial volume, cm^3) [coppicing]

Density of trees and/or stems is determined by soil properties, soil depth and the successional status of the stand *ie*. a mature woodland versus a coppicing shrubland. Within mopane shrubland, self-thinning of stems and trees occurs (Scholes 1990), therefore size and density affect survival and size-class dynamics. Mature tree densities, shrublands and coppice densities are given in Table 2.3.

Table 2.3 Mean densities of mopane woodland in the south-eastern lowveld of Zimbabwe (Kelly and Walker 1976)

stems.ha^{-1}	utilisation
956	none
984	light
1 717	medium
850	high

Conclusions

Mopane vegetation is generally a species-poor vegetation type that appears to hold no endemics or threatened species. However, it is a key species in a wide range of landscapes not only as an important wildlife habitat, but also as an economically important renewable resource (Timberlake 1995).

It is a resilient and persistent species occurring over a wide range of ecological conditions, but mainly on heavier eutrophic soils, and lighter soils in low rainfall areas (Timberlake 1995). The following points must be noted with regard to mopane dynamics:

1) it is a shallow-rooted tree species (and therefore competes directly with the grass layer for limited resources such as light, water and nutrients);
2) it can utilise water at a lower matric potential than grass species (it therefore has a competitive advantage);
3) over time it can come to dominate a site, forming extensive mono-specific stands, leading to reduced grass growth, and
4) once established is difficult to remove, having to be manually thinned or intensively controlled with arboricide.

In light of these points, and with an understanding of mopane physiology and ecology, a review of the literature pertaining to the determinants of mopane woodland structure and functioning, and in particular the effects of fire on mopane population dynamics, is now undertaken.

Factors determining mopane woodland structure and functioning

Introduction

The factors determining the structure and functioning of mopane woodland are numerous, and the interactions between them are dynamic and highly complex in most instances. In the available literature there are very few instances of work relating to mopane woodland dynamics specifically.

Because of the stochastic nature of semi-arid savannas, it is intuitive that mopane woodlands are dynamic (albeit less than other savanna types because of their more homogenous nature) and that the species composition, tree density, canopy volume and successional status vary both spatially and temporally. Changes may be brought about by the community itself (autogenic factors), or from other external determinants (allogenic factors).

Autogenic factors

Self-thinning

Self-thinning is a form of density-dependent population regulation. It is not reasonable to assume that population growth, survival and fecundity vary only with time and are independent of population density. The manner in which self-thinning occurs has been labelled the -3/2 self-thinning rule, which predicts that plants which are small or occur at low densities grow without thinning until they reach the -3/2 slope of log(plant weight) versus log(plant density), when size increases at the expense of density (Yoda *et al.* 1963). Schlesinger and Gill (1978) studied most of the aspects of density-dependent thinning in a chaparral shrub *Ceanothus megacarpus*, and found a slope of -1.23. Walter (1971) reported that *Acacia mellifera* thickets became moribund and reverted to open savanna after 50 years of protection from fire in Namibia, although this could not be attributed to density-dependent factors. Other researchers found density-dependent mortality due to intraspecific competition (Riggan et al. 1988, Kenkel 1988). Scholes (1990), studying the regrowth of mopane following clearing, found evidence for self-thinning. However, this phenomenon has not been adequately described for mopane woodlands.

Competition, succession and the Gulliver effect

"Ever since Darwin, competition has been considered to be one of the major forces shaping the morphology and life history of plants and the structure and dynamics of plant communities" (Grace and Tilman 1990).

Competition can be the major factor in determining the changes in plant communities over time, over spatial gradients, and can alter species diversity (Bond and van Wilgen 1996). Vegetation changes over time, and Clements (1916) described succession as an orderly and predictable approach towards a dynamic equilibrium. In response to a cleared area, plants colonise the space released, with pioneer species facilitating the invasion of later species by ameliorating the environment, or being superseded by species with a greater competitive ability. An equilibrium is eventually reached (climax) where, if undisturbed, only top competitors persist. The climax was assumed to be self-sustaining and persistent (Bond and van Wilgen 1996).

The relay floristic model of succession, *ie*. the predictable sequence of species replacement, has greatly influenced ecological thinking. By this approach, predictions of community dynamics are based on competition as the central process. Given the strong competitive abilities of mopane, and its persistence over long periods of time, it is proposed that mopane is a late successional species with great competitive ability. Walker (1980) defined three concepts central to system dynamics, *viz*. stability, resilience and a system's domain of attraction. A stable system is one that changes little in composition and production, in response to perturbation or stress. A resilient system may or may not be stable, but remains attracted towards the equilibrium. A domain of attraction is that region of a system's state-space within which the system is attracted towards an equilibrium. Using these definitions, mopane woodland can be described as a stable, resilient system with a large domain of attraction (a large state-space region within which attraction towards equilibrium takes place). The degree of stability and resilience of mopane vegetation needs to be quantified, as well as further investigation into competition-dependent effects in mopane woodland specifically.

In the savanna systems of southern Africa the dynamics of woody plants are affected by interactions with the grass sward. Grasses are effective at suppressing regeneration of other growth forms because of their rapid growth rates (D'Antonio and Vitousek 1992), production of large quantities of seed and competitive advantage in the soil surface layers. Grasses form highly flammable fuels, but recover quickly after burning. Their meristematic regions are near or below the soil surface, and protected from fire. In the event of fire, standing biomass is removed (much of which is dry and dead).

They are thus important in the regeneration phase - producing what Bond and van Wilgen (1996) termed the 'Gulliver effect' (after Swift's sailor bound helpless by hordes of tiny Lilliputians). Gulliver plants are those which dominate communities as adults, but struggle to emerge from the herbaceous layer as juveniles. The grass layer suppresses Gulliver recruitment by competing with seedlings, slowing the growth of established plants, and by fuelling frequent fires that kill or stunt the survivors so that they fail to escape the danger zone (Bond and van Wilgen 1996). Release from this state takes place when the grass layer is removed - normally by grazing or burning, or if fires are suppressed. When released from this state the Gullivers flourish, they escape the danger zone as they grow, and in turn suppress grass growth as they gain a competitive advantage. This process of increasing tree density accelerates as the density of the grass component is subjected to increasing competition from the tree layer. This can be compounded by the pressure placed on the grass sward by grazing ungulates, especially at high grazer stocking densities (Tainton 1999). It is this scenario that may have taken place in the south-eastern lowveld of Zimbabwe, with the exclusion of fire; removal of indigenous ungulates; and the introduction of large numbers of cattle on extensive cattle ranches. This situation released Gulliver-type tree species that have come to dominate certain vegetation types and encroach into others. Mopane, whose distribution is determined by soil type and condition, has generally increased in density within historical ranges rather than encroaching into previously grassland areas.

Allogenic factors

The allogenic factors determining mopane woodland dynamics fall into three categories:

1) climatic,
2) edaphic, and
3) environmental.

The individual factors within these categories contribute, to various degrees, to the structure and functioning of a particular woodland at any one time.

Climatic factors

The climate under which savanna vegetation occurs is widespread all around the world, in a broad belt north and south of the Tropics. Semi-arid savannas are those in which the annual rainfall is between 300 and 750 mm. The south-eastern lowveld of Zimbabwe has a warm climate, with a mean annual rainfall of approximately 500 mm, concentrated in the summer rainy season

(December to March). Owing to the low and erratic rainfall, and the fact that annual potential evaporation is usually twice rainfall, the growth of savanna trees is restricted by the amount and periodicity of rainfall events. Of all the determinants of vegetation production in the semi-arid savanna areas, water is the most limiting (Snyman 1987). The growth and success of both trees and grasses are thus determined by the amount of water each component can obtain and utilise. A simple, general explanation for the coexistence of trees and grasses over 20% of the Earth is based on the apparent niche differences in tree/grass rooting systems (Walter 1971). The two components are able to coexist because they have different strategies for obtaining moisture. Trees tap deeper subsoil sources of water than grasses, but grasses are more competitive in the soil surface layers. Trees should dominate deep, sandy soils because their deep tap roots would benefit from the deeper infiltration of water, and grasses dominate on shallow soils where they would outcompete trees for surface soil moisture. Owing to its shallow root system, this model may not apply as rigorously to mopane however, as it competes strongly with the grass sward in the surface soil layers. Alternatively tree-grass coexistence may be mediated by disturbance factors such as fire, elephants and drought that prevent tree communities from attaining their full growth potential.

Severe droughts have been recorded in the Zimbabwean lowveld, and these occur approximately every nine to ten years. Tree mortality is widespread, and impacts the vegetation of the more mesic sites dramatically (Timberlake 1995, Tafangenyasha 1997). Walker (1996) points out that high inter-annual variation in rainfall keeps the amount of trees lower than the amount that the average rainfall can sustain. This is because dieback of trees is rapid in a drought, but recovery during wet periods is much slower, limited by both demographic and physiological processes. The amount of trees is therefore determined by the periodicity of dry years.

Tafangenyasha (1997) states that loss rates of trees in the Gona-re-Zhou National Park were probably exacerbated by dry spells between 1977 and 1983 during which a severe drought was experienced. He also notes that the impact of drought on woody species was found to be significantly different between burnt and unburnt sites, with unburnt sites displaying higher levels of damage, but the reasons for this are not clear. This supports Wing and Buss (1970) and Field (1971) who suggest that there is a decrease in browsing pressure by elephants with an increase in rainfall (as increased grass intake takes up higher proportions of the diet), and an increase in tree mortality during drought years.

Edaphic factors

Not only the underlying geology, but also the soils they form, are important determinants of plant production potential and consequently the carrying capacity of savannas (Fritz and Duncan 1994). The edaphic factors relating to mopane are covered earlier in this chapter.

Environmental factors

I have included the vertebrate and invertebrate animals that effect mopane woodlands, as the environmental factors. Man, being part of the environment, is also a factor that determines the dynamics of mopane vegetation. However, this paper does not deal with the widespread impacts of man in mopane-dominated vegetation types. Suffice it to say that in the south-eastern lowveld of Zimbabwe, where extensive cattle and game ranching is practised, there is no threat to any of the mopane-dominated vegetation types. However, over-utilization of mopane woodlands for fuel, charcoal production and building materials does threaten some woodlands in communal areas (Kelly and Walker 1976).

Vertebrates

The vertebrate animals that impact mopane are mainly the browsing ungulates such as kudu (*Tragelaphus strepsiceros* Pallas), eland (*Taurotragus oryx* Pallas), black rhino (*Diceros bicornis* Linnaeus) and African elephant (*Loxodonta africana* Blumenbach). Other vertebrates such as the porcupine (*Hystrix africaeaustralis* Peters) and buffalo (*Syncerus caffer* Sparrman) damage trees, and in so doing create sites for further fire damage. However, of all of these, the elephant has the greatest impact, and will be dealt with.

The African elephant is confined to privately owned wildlife ranches, and the Gona-re-Zhou National Park, in the south-eastern lowveld of Zimbabwe. On privately owned land their numbers are low, with densities of less than 1 elephant every 4 km^2. In the Gona-re-Zhou National Park the density is approximately 1 elephant per km^2. Pienaar *et al.* (1966) concluded that in the Kruger

National Park, 6 000 elephants (1 every 1.9 km^2) was the highest number of elephants that could be carried "if the total destruction of the vulnerable areas near water is not to result". This is because elephants have an impact on savanna ecosystems, and if the population is allowed to exceed a certain density, then these affects may lead to an undesirable change in species and structural diversity.

Trollope *et al.* (1996), compared mopane-dominated landscapes that had been excluded from elephant utilisation, with those that had. They showed that neither fire, nor elephants and fire, had any effect on the density of the woody vegetation. However the interaction of elephants and fire caused a significantly marked reduction in the phytomass of bush in areas with clay soils, irrespective of rainfall. It is suggested that the changes in the woody vegetation indicate a change in structural diversity rather than species diversity. This is in agreement with other researchers, who concluded likewise (van Wyk 1971, Pellew 1983 and Dublin 1995).

The kinds and proportions of forage consumed by elephants varies seasonally, with grasses and herbs being selected in the rainy season, and woody plants in the dry season (Field 1971). Browsing involves breaking off branches, uprooting trees, stripping bark and selective removal of leaves. Where fire has removed the grass component, elephants may push over trees to utilise the remaining leaves. In such areas the recruitment of mopane seedlings may be severely curtailed by the effects of the interaction of fire and browsing. The impact of elephant on post-burn coppice material may also lead to structural change, both in the basal and aerial strata. With low elephant densities the effect on a landscape level will be diffused over a wide area. However, Bell and Jachmann (1984) showed that the distribution of elephants is influenced by burning. Elephant use of woodland burnt early in the dry season is lower than the use of areas burnt later, or not at all. The dry season is the time at which most browsing occurs, and early burning reduces the browsing pressure to a significant extent and reduces the impact of elephants on woodlands. Conversely, unburnt areas will experience increased browsing pressure, leading to an impact on the tree layer.

The combined effects of elephants and fire can lead to a reduction in woody phytomass and the creation of more open habitats. If the objective is to achieve this, then the combined effects of fire and elephants may lead to such a situation.

Fire in semi-arid savanna ecosystems

Introduction

Fire is an important phenomenon in the semi-arid savanna areas. Rainfall occurs in the warmer summer months with a dry period of two to eight months duration, during which fire is a typical phenomenon at intervals of one to fifty years (Huntley 1982). In the south-eastern lowveld of Zimbabwe fire has been suppressed during the last 50 years because of the rationale that the burning of grass is a waste of a valuable fodder source for cattle.

Fire history of semi-arid savanna ecosystems

Evidence of ancient fires is available in the Palaeozoic, Mesozoic and Tertiary Periods (West 1965). Modern evidence shows that southern African savanna areas have been subjected to burning at one time or another, but the frequency with which this took place differs greatly over the sub-region. In the south-eastern lowveld of Zimbabwe, extensive areas of the Gona-re-Zhou National Park have been burnt almost annually by runaway fires from within Zimbabwe and Mozambique. The extent of fire in the past is presumed to have been higher than today, as fire protection controls and the removal of communities out of National Parks has reduced the occurrence and extent of man-induced fires. The savanna biome is adapted to regular and frequent burning, and has many plant species whose evolutionary development accords with community behavioural responses to fire (Bews 1925; Bean 1962).

Natural fires

It has been documented that fires can be started by physical means such as falling boulders (Wicht 1945). Other possible causes of physical induction include earthquakes and earth tremors. There is little evidence of the frequency with which boulders and earth tremors cause fires. It appears that these instances are restricted to mountainous areas where there is abundant flammable plant material.

Lightning is generally considered to be the most significant of the natural causes (excluding man) of veld fires in southern Africa (Scott 1970). Lightning is widely accepted as an ignition source, but the literature shows differing opinions as to the frequency and importance of lightning induced fires in natural ecosystems. Ground lightning flash densities from over 300 lightning counters, were recorded between 1975 and 1978 by the Council for Scientific and Industrial Research (CSIR) in South Africa. Highest densities were found mainly at altitudes over 1 000 m in Lesotho and Natal, and lowest in the southern Afro-montane forest and fynbos. Annual reports for the Kruger National Park testify to the incidence of lightning induced fires during electrical storms. In the lowveld of Zimbabwe, the occurrence of intense electrical storms, such as those experienced in the Kruger and Pilansberg National Parks, are infrequent. It is held therefore that lightning induced fires within the south-eastern lowveld of Zimbabwe are very infrequent (Mr Ray Sparrow, previous owner of Lonestar Ranche, P. Bag 7085, Chiredzi, Zimbabwe). Most lightning induced fires cover relatively small areas under present-day conditions (2.43 km^2 per fire average), although there are modern instances of fires having burnt large areas eg. 780 km^2 of savanna in the Kruger National Park (Pienaar 1968) and 200 km^2 in the Mkwasine area of the Zimbabwe lowveld (Gavin Campbell-Young, Estate Manager, ME, P. Bag 7085, Chiredzi, Zimbabwe). It is assumed however that in pre-colonial times with low human population densities, lightning induced fires could have burnt extensive tracts of country, especially when they occurred under conditions favourable for veld fires.

Fire parameters of semi-arid savanna ecosystems

Productivity is a functional parameter of the semi-arid savanna ecosystem and refers to the rate of production of above ground biomass. The structural parameter of the vegetation (herbaceous and woody components) is the above-ground physiognomy of the community. These two parameters together determine the potential natural fuels of savanna areas and communities (Edwards 1984). Thus, the quantity and quality of fuels available for fires varies widely in relation to climate, last rainfall, season and degree of use by man and animals. Herbaceous layer production of the semi-arid savanna areas is related to the density of the woody tree and shrub layers and to rainfall. Rainfall in the northern regions is almost exclusively a summer phenomenon, while winter precipitation increases southwards. The herbaceous layer is more flammable than the woody layer and dense woody vegetation with a low herbaceous biomass is less prone to fire than a mixed grass-woody vegetation (Edwards 1984). In a savanna area of average rainfall (*ca* 500 $mm.yr^{-1}$) herbaceous layer growth is approximately 1 000 $kg.ha^{-1}.yr^{-1}$ or more (Rutherford 1979). The potential fuel loads are lower in the more arid areas.

Despite the high total biomass, fires in the semi-arid savanna areas are mainly close to the ground, though fires impacting the crown sometimes occur in woody vegetation above 3 to 4 m. This may be attributed to the open distribution and lower flammability of the woody plant material and to low herbaceous biomass and its discontinuous distribution.

Savanna communities are characterised by the lateral discontinuity of the herbaceous layer, Edwards (1984) found, for example: from 640 $kg.ha^{-1}$ under shrubs, to 970 $kg.ha^{-1}$ under trees, and 1 230 $kg.ha^{-1}$ between trees and shrubs. It must be noted, however, that the biomass production of the herbaceous and woody components is dependent on a suite of interacting factors. The combined environmental, species-specific and management factors determine the available natural fuels and fuel load for a specific area.

Factors influencing fire behaviour

The findings presented in this section are taken from Trollope's (1983) work on the control of bush encroachment with fire, unless otherwise stated. The three factors influencing fire behaviour are fuel factors, and atmospheric and physiographic conditions. Fuel load is the most significant factor affecting topkill up to 3 m.

Fuel load

Fine fuels (<6 mm diameter) and heavy fuels (>6 mm diameter) can be distinguished. Combustion is rapid and often complete with fine fuels, whereas usually incomplete in heavy fuels. This fuel is distributed vertically *ie*. ground, surface and aerial fuels. Surface fuels support intense surface fires whose intensity is proportional to the biomass per unit area. Fuel compaction relates to the placement of the individual fuel pieces. Fire intensity is optimised when the fuel is loose enough to allow oxygen to reach the flame front.

Fire intensity is directly proportional to the amount of fuel available for combustion at any given rate of spread of the fire front (Brown and Davis 1973). In semi-arid savanna systems such as the south-eastern lowveld of Zimbabwe, rainfall largely determines the available fuel load at any one time, and the frequency of fires would have been determined by the accumulation of high fuel loads after very wet seasons.

Fuel moisture

The most critical factor regarding fuel load, with respect to fire intensity, is fuel moisture. This is expressed on a dry matter basis, and is critical in determining the intensity of a fire as it affects the ease of ignition, quantity of fuel consumed, combustion rate, rate of spread and flame height. However, Trollope (1983) found that fuel moisture per se only had a significant effect on fire intensity when this value exceeded 45%.

Atmospheric and physiographic conditions

Air temperature

Air temperature has a direct effect on fire intensity. High air temperatures raise the temperature of the fuel, and therefore the lower the amount of heat energy required for ignition. The indirect effects of air temperature are on relative humidity and evaporation. Fire intensity of surface fires increases with higher air temperatures, *ceteris paribus*.

Relative humidity

Relative humidity influences the moisture content, and has a negative effect on fire intensity. High fire intensities have been recorded when humidity is below 30% (Trollope 1983).

Wind

Wind is important because it determines the amount of oxygen available for combustion. Rate of energy release is positively related to the wind speed. Also, wind influences the frequency and extent of spotting (fire-brands landing ahead of the flame front) and pre-heating of the unburnt fuel load.

Slope

Slope changes the flame angle, especially when greater than 15-20°. However, due to the flat topography of most of the semi-arid savanna areas, slope is not a critical consideration.

The effect of fire regime on mopane woodland dynamics

Introduction

Fire is a disturbance factor in semi-arid savanna vegetation. A disturbance has been defined as "any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species" (Begon *et al.* 1990). Fire is a discrete event that opens up space at various scales, at various intervals, depending on the nature of the fuels and the occurrence of conditions conducive to fire (Bond and van Wilgen 1996).

The effect of fire on vegetation depends upon the combined effects of the different components of the fire regime:

1) the type and intensity of the fire, and
2) the season and frequency of burning.

The fire regime experienced by a particular system can strongly influence its vegetation composition and dynamics (Collins and Gibson 1990, Glitzenstein *et al.* 1995).

The effect of type of fire

Savanna trees are sensitive to various types of fire because of the differences in the vertical distribution of the release of heat energy. The most common types of fire in savanna areas are surface fires burning either as head (with the wind) or back (against the wind) fires. Crown fires occur under extreme fire conditions (high fuel load, high temperature, low relative humidity and strong winds), and are rare in semi-arid mopane woodlands. Observations in the Kruger National Park and the Eastern Cape indicate that crown and surface head fires cause the highest topkill of stems and branches, as compared with back fires (Trollope *et al.* 1996). This is because the heat energy is released above the soil surface at levels closer to the terminal buds of the aerial portions of the tree (Trollope 1993). However, there is only limited quantitative data to support these observations. A burning trial at the University of Fort Hare (arid savanna) showed that the phytomass of bush was reduced by 75% in the area burnt as a head fire, in comparison to 42% in the area burnt as a back fire (Trollope 1980).

Head fires are recommended because they cause the least damage to the grass sward, but maximum damage to the woody vegetation (Stocks and Trollope 1993). Conversely, back fires have a slow and low release of heat energy. This may have the potential to kill seeds and seedlings, and impact over the long term, as these fires limit or exclude recruitment of tree species (even those that are fire-resistant as adults).

Trollope *et al.* (1996) state that the repeated application of intense head fires (caused by the ignition procedure, applied in the Kruger National Park, whereby burning blocks were ignited around the perimeter, and the subsequent development of a fire convection column) prevented the recruitment of large trees. Also, by repeating the type of fire applied, a more homogenous response (even-structured stands) was observed.

The effect of fire intensity

If the grass component is drastically altered and reduced, then the attainable fuel load is reduced. A reversal to a pioneer stage may have a marked effect on fuel load (van Wilgen *et al.* 1990). Alternatively, an increase in woody density, accompanied by reduced grass production, could have the same effect on fuel load. Trollope (1983) shows that the effects of fuel load, fuel moisture, relative humidity and wind speed were the most significant factors in determining fire intensity. Observations in the Kruger National Park (Trollope *et al.* 1996) indicate that bush is very resistant to fire alone (mopane even more so than other species). The average mortality for 14 of the most common bush species subjected to 43 fires (ranging in fire intensity from 110 to 6 704 $kJ.s^{-1}.m^{-1}$) was only 1.3%. Generally, the main effect of fire on the woody component in semi-arid savannas is to cause a topkill of stems and branches forcing the plants to coppice from the collar region of the stem. The impact is therefore on vegetation structure rather than on tree mortality.

The effect of fire intensity on the topkill of bush was investigated in the savanna areas of the Kruger National Park (Trollope *et al.* 1995), and it was found that the woody vegetation is not significantly affected by fire alone when the trees and shrubs are taller than 3 m (Figures 2.2 and 2.3).

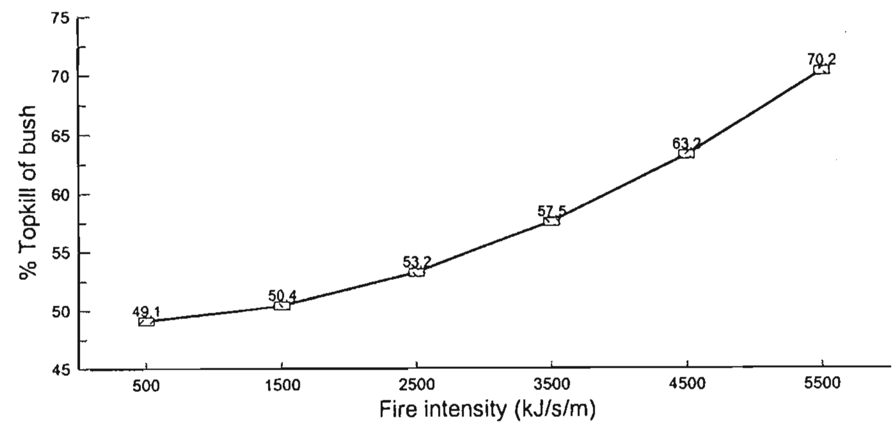

Figure 2.2 Effect of fire intensity on the topkill of bush two metres high in the Kruger National Park, South Africa

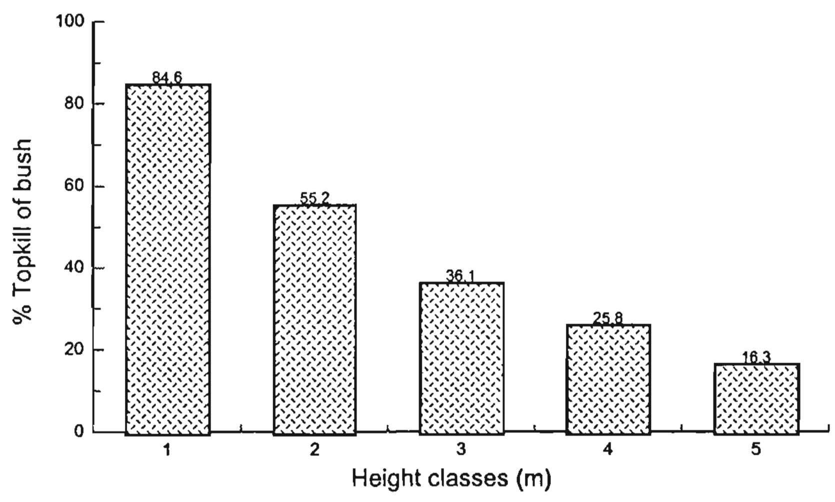

Figure 2.3 Effect of height on the topkill of bush subjected to a fire intensity of 3 000 $kJ.s^{-1}.m^{-1}$ in the Kruger National Park.

The effect of season of burning

The effect of season of burning on tree and shrub vegetation is difficult to quantify because it is confounded with fire intensity. Fire intensities are not determined so much by season, but primarily by fuel load and moisture, and the fire intensity experienced in a particular season may not be unique to that season. However general trends relating to fuel load, temperature and relative humidity can be recognised. In winter the grass layer is dormant, dry, and able to support intense fires, whereas during summer the grass is green and fires are much cooler. West (1965) postulated that trees and shrubs are probably more susceptible to fire at the end of the dry season when the plant reserves are depleted due to the new spring growth. Wade and Johansen (1986) concluded that the seasonal variations in tree physiology or phenology are critically important in determining the susceptibility of trees to fire. I refer to this as the 'phenophase' hypothesis, which postulates that mopane trees differ in their response to fire owing to their potentially variable sensitivity to fire at different phenological stages *ie.* increased susceptibility shortly after leaf expansion, than in winter when the trees are leafless.

Glitzenstein *et al.* (1995), consistent with this phenophase hypothesis, showed that deciduous oak species were least vulnerable to dormant-season burning and most vulnerable to burning in the early growing season. This was shown particularly by seasonal trends in the effect of burning on oak mortality (both topkill and complete kill) and, to a lesser extent, on oak recruitment. Detrimental effects of spring burning on oaks were partly explained by fire behaviour, but there was an important residual effect of burning season, particularly on complete kill. These results are species-specific, applying to oak species. Their results showed few systematic or predictable effects of season or frequency of burning on dynamics of longleaf pine (*Pinus palustris*).

Trollope *et al.* (1995) showed that the 1.3% mortality of bush after fires, had been applied to bush ranging from dormant to actively growing plants. With such a low mortality over such a range of phenological states, it was concluded that the woody vegetation is not sensitive to season of burn in the Kruger National Park.

The effect of frequency of burning

Results relating to the effects of frequency of burning are generally conflicting. Frequency of burning in the Kruger National Park, over 42 years, appears not to have had any significant effect on the density of woody plants (van Wyk 1971). However, frequent burning has a highly significant effect on the physiognomy of tree and shrub communities in savanna areas. Plots with 14 years of annual burning at the Matopos Research Station, Zimbabwe, showed a 70% reduction in woody phytomass by comparison with plots completely excluded from fire (Kennan 1971). In the arid savanna of the Eastern Cape annual burning caused a 65% reduction in the woody phytomass, over an 11 year period (Trollope 1983).

No quantitative data for the effect of frequency of burning on changes in tree and shrub phytomass are available from the long-term burning trials in the Kruger National Park. Visually, however, the difference in woody phytomass between the control plots that are completely protected from fire and the annual, biennial and triennial burning treatments show a dramatic decline in the woody phytomass with an increase in burning (Trollope *et al.* 1996). Any worthwhile investigation into the effects of frequency of fire on mopane woodland density and structure will need to concentrate on the effects over long periods because the event-dependent effects of fire behaviour during a single fire event may show accumulative effects over time. Repeated burning will suppress Gulliver individuals, and in combination with selective browsers such as black rhino and elephant, may result in low recruitment of new individuals into the system. Not only the low height classes, but also the larger trees, will be impacted by more frequent burning. Continued defoliation by annual fires will result in coppicing from aerial and basal regions. Post-burn browsing pressure may lead to removal of this regenerative growth, leading over the long term, to a reduction in plant vigour and a structural change.

Conclusions

It is evident that the factors affecting mopane woodlands are numerous and highly complex. The tree density, physiognomic structure and species diversity of a particular site is determined by a combination of the following: autogenic factors (self-thinning and competition with the grass sward), and allogenic factors (climate, edaphic conditions and environmental factors).

Fire is an environmental factor that is a major determinant of mopane woodland dynamics. If co-occurring with elephant impacts, this combination can be critical in driving vegetation change, even overriding other factors. The reaction by mopane to fire regime (type and intensity of the fire, and season and frequency of burning) is similar to that of other tree and shrub species in southern Africa. Profuse coppicing occurs after high intensity fires and, in conjunction with browsing by elephants, results in a highly significant decrease in the phytomass of the canopy, but very little change in the density of trees. An area lacking in understanding is the degree to which mopane reacts to the different components of the fire regime, especially the type and intensity of fire.

Owing to its ecological distribution, being found on low potential and xeric soils, the opportunity for intense fires is limited. This is further exacerbated by mopane's strong competitive ability, as it is shallow-rooted and is able to utilise water at matric potentials lower than grasses. Therefore, even if tree density is reduced, the areas opened up may not support vigorous grass production. This will still exclude the potential for intense fires, and lead to no long-term change in tree density as a result of fire alone. However, in combination with elephants and drought, the structure of the mopane woodland may well change dramatically. The following flow diagram is proposed for mopane woodland in the south-eastern lowveld of Zimbabwe:

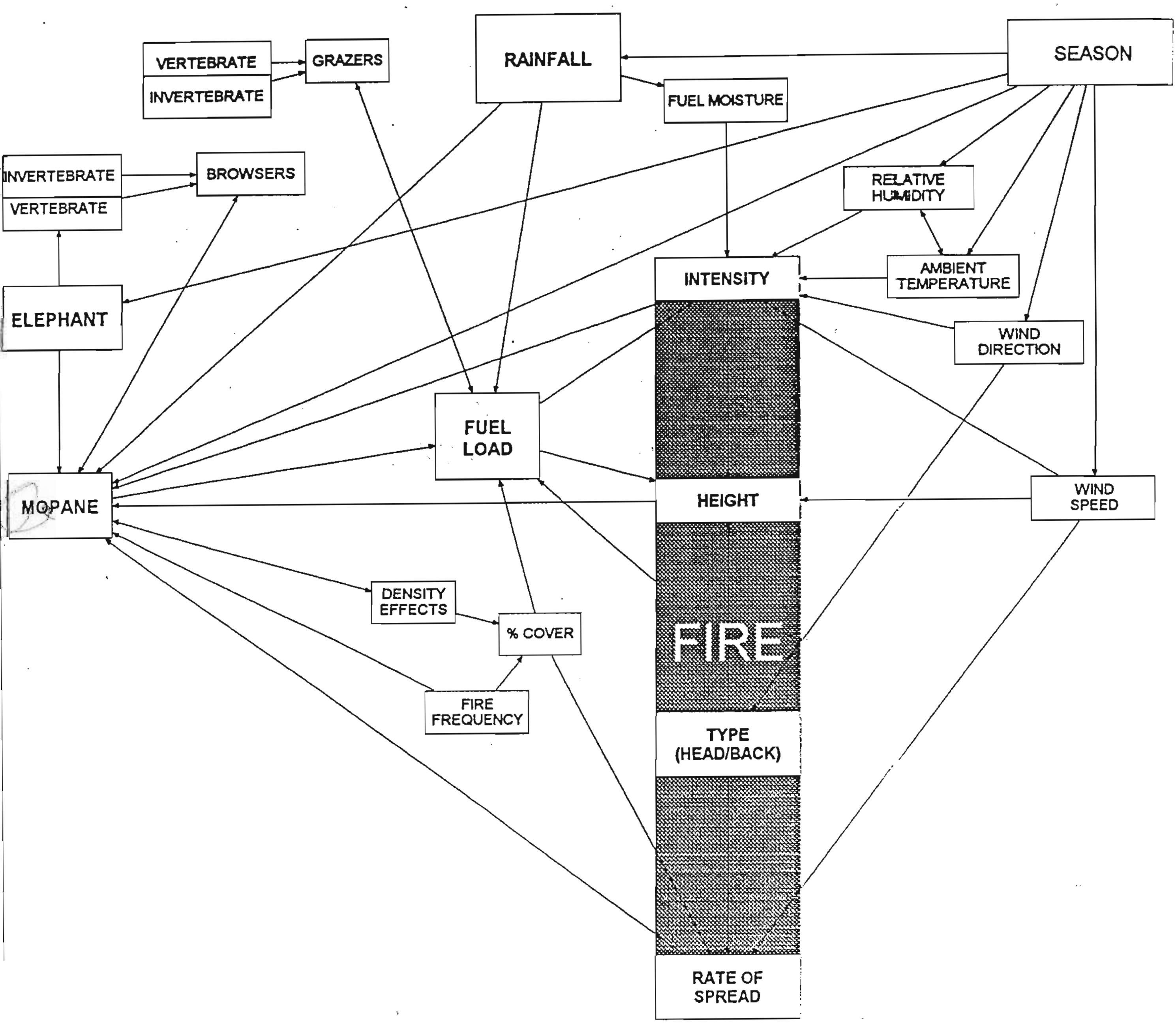

Figure 2.4 Conceptual model of fire dynamics in mopane woodland in the south-eastern lowveld of Zimbabwe (interpret arrows as interactions, with the direction of the arrows determining the dependent/independent components of the interaction/s. Arrows that cross are not linked).

It is concluded that the factors determining mopane woodland structure and functioning are numerous and complex. This suite of factors interact in response to each other, and to a highly variable environment. The available literature does not include much quantitative data, or elucidate principles, relating to the effects of fire regime on the population dynamics of mopane vegetation. It is concluded however that mopane is a strong competitor with the grass layer, is highly adapted to its environment (climatically and edaphically), and is both stable yet resilient where it occurs. Fire, although being a major determinant of mopane population dynamics, does not alter the stand density or species diversity of mopane woodlands, but together with elephant impacts, leads to a change in the structure of the vegetation. This change is generally an opening up of the woodland. The degree of this change will depend on the type and intensity of fires, the frequency and season of burning, and the extent of elephant impact. Further research into the effects of fire on the population dynamics of mopane, and aspects of its physiological response to fire, is necessary for a more accurate and complete approach to mopane woodland management.

The complexity of the factors involved in determining mopane woodland structure and functioning are obvious. The major determinants however are the following:

1) climate (*ie*. rainfall),

2) elephants, and

3) the fire regime.

Key questions and hypotheses

Standing crop dynamics

1) It was hypothesized that owing to the variability in grass sward structure through the year, one standard disc pasture meter calibration equation cannot suffice to predict standing crop for the whole year. Is there one standard equation applicable to all seasons, or are there equations suitable for different seasons because of the varying growth forms of the grass sward through the season? In addition, is the standard disc pasture meter procedure the most accurate to estimate the standing crop of the mopane woodland vegetation?

2) It was hypothesized that standing crop for a particular month is highly dependent on the effective rainfall for the previous month. Can a predictive equation for determining standing crop (for a given month) from standing crop and/or effective rainfall for the previous month, be determined? With this equation, standing crop, and therefore fuel load, can be accurately estimated.

3) It was hypothesized that peak standing crop is positively related to annual rainfall, and can be predicted. Is there a quantifiable relationship between peak standing crop and effective rainfall? With this it will be possible to estimate the potential peak standing crop (fuel load) from the effective rainfall over the season. This peak standing crop figure is the theoretical maximum from which standing crop through the dry season will decline.

4) It was hypothesized that standing crop declines through the dry season as effective rainfall decreases. Can a 'decrease function' for the decline in standing crop through the dry season be described? It is expected that standing crop will decline from peak standing crop as effective rainfall drops. Knowing this decline function will allow the estimation of standing crop for a specific month, given the peak standing crop.

Mopane leaf quantification

1) In order to successfully describe and interpret the effects of fire on mopane woodlands an appropriate quantitative description of individual trees was required. A method to estimate leaf dry mass using tree dimensions was developed by Smit (1994) in mopane veld north of the Soutpansberg in South Africa. However it was hypothesized that the mopane leaf quantification equations for Malilangwe Estate are different to those developed for the Soutpansberg. Is the mopane leaf quantification equation for the south-eastern lowveld of Zimbabwe different to that determined for the Soutpansberg in South Africa? Owing to the differences in the growth forms encountered in the two areas (Malilangwe having shorter, more shrub-type stands), it is expected that the two equations will be different.

Effect of season and type of fire

1) It was hypothesized that the damage to a mopane tree through fire is largely determined by the phenophase of the plant. Trees burnt in the late dry season will be damaged more than those burnt in the early dry season, with those burnt in the mid dry season being impacted least.

2) It was hypothesized that within the same season the damage to a mopane tree is largely determined by the type of fire. Head fires lead to greater damage than back fires. What is the effect of season of burning and type of fire on mopane woodlands in the south-eastern lowveld of Zimbabwe? It was proposed by West (1965) that trees and shrubs are probably more susceptible to fire at the end of the dry season, when plant reserves are depleted after initiating new growth. Because of this phenophase sensitivity, mopane trees burnt in different seasons may differ in their response to fire. The type of fire (back fire or head fire) was investigated as trees are sensitive to various types of fire because of the differences in the vertical distribution of the release of heat energy (Trollope *et al.* 1996). In other savanna areas it has been shown that head fires cause the highest topkill of stems and branches, because the concentration of heat energy is at levels closer to the terminal buds of the tree (Trollope 1980).

I have assumed that the principles and trends described for other semi-arid savanna tree species should give some guidelines as to the possible responses of mopane to the factors influencing it. However, it is my intention to test specific hypotheses in this thesis, in order to gain a better understanding of how mopane woodland responds to different seasons and types of fires. In order to answer the questions posed above, an empirical investigation into the effects of different seasons of burning and types of fire on mopane woodland in the south-eastern lowveld of Zimbabwe was undertaken, incorporating the following:

1) To grasp the present state of understanding and knowledge of the effect of fire on mopane woodlands, a comprehensive literature review of the determinants of mopane woodland dynamics in the south-eastern lowveld of Zimbabwe was undertaken.
2) To record the primary determinants of savanna grass production, monthly rainfall and pan evaporation figures were recorded over the study period.
3) In an attempt to accurately predict standing crop (fuel load) in the mopane woodland areas, a predictive equation for determining standing crop, for a given month, from the previous month's standing crop and effective rainfall, was determined. Also, the determination of the relationship between peak standing crop and rainfall was calculated. Using this relationship to determine peak standing crop, a 'decrease function' for the decline in standing crop as effective rainfall decreases through the dry season (to estimate standing crop as it declines from peak standing crop) was

4) It was realised that the form of the mopane trees occurring in the south-eastern lowveld of Zimbabwe were different to those found in the Soutpansberg of South Africa, and therefore the leaf quantification equations determined by Smit (1995) may be inappropriate. This led to the development of a mopane leaf quantification equation for the south-eastern lowveld of Zimbabwe (to estimate leaf dry mass by measuring the spatial canopy volume of individual trees).

5) The recording of rainfall/evaporation data, the prediction of standing crop (fuel load) over the study period and the derivation of two leaf quantification equations for mopane, were required to undertake the major focus of the study: the investigation and quantification of the effect of fire on mopane woodlands by recording the impact of different seasons of burning and types of fire on tree height, number of stems, maximum canopy diameter and leaf dry mass of mopane trees.

Chapter 3

Study area

The study area refers to Malilangwe Estate (ME), which is a privately owned commercial wildlife operation, managed by the Malilangwe Conservation Trust (MCT). This area was previously known as Lone Star Ranche.

Location

Malilangwe Estate lies approximately 20°58'- 21°15' S and 31°47'- 32°01' E, and covers an area of 40 600 ha. This includes what was previously two wildlife ranches situated in the south-eastern lowveld of Zimbabwe (Figure 3.1). Maranatha Ranch forms the northern section, and is 12 100 ha in size. Lone Star Ranche is the larger southern section, being 28 500 ha in size.

The southern boundary of ME is contiguous with the Gona-re-Zhou National Park, with a twin-cable game fence that allows for the free movement of all game species in and out of the Park. The western boundary borders with the Chiredzi River, ie. Hippo Valley Estates game section, with a short distance running along Matibi II Communal Land. The boundary with the communal land is fenced with a game-proof fence. The eastern boundary is Resettlement Land, also with a game-proof fence having been erected. This fencing extends along the northern boundary (the Triangle/Tanganda tar road).

History of Malilangwe Estate

Before the arrival of white settlers the area was inhabited by small numbers of agro-pastoral Tsonga people, who had settled along the Chiredzi, Nyamasikana and Runde rivers (as well as other smaller tributaries and artesian wells). During 1934 the adjacent Chipinda Pools area was proclaimed the Gona-re-Zhou Game Reserve (the fifth National Park to be established in Rhodesia). This large reserve stretches from the Mabalauta area in the south to the Save river in the north.

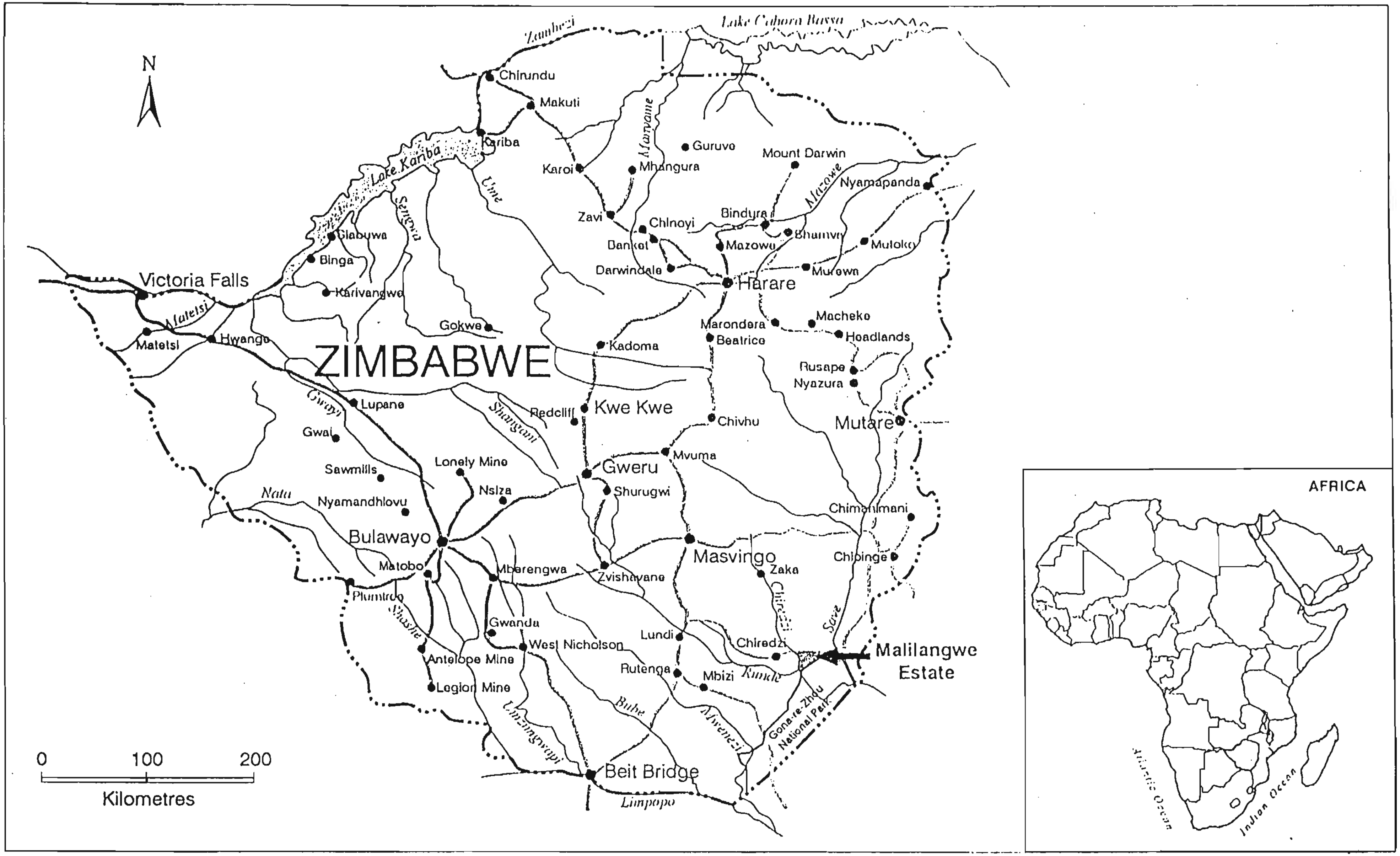

Figure 3.1 Malilangwe Estate (in relation to Zimbabwe and Africa).

After World War II areas of land were allocated to returning servicemen by the then Land Settlement Board of the Federation of Rhodesia and Nyasaland. Mr Ray Sparrow was allocated land in the Masvingo District, but applied for an area of land in the lowveld, in exchange for this. This was authorized, and he and his family moved down, in 1949, to what became known as Lone Star Ranche. The ranch was originally 4 000 ha in size, and was situated to the south of the Malilangwe Hills. Over the following 30 years he bought a further 24 500 ha of the surrounding Crown Land, and this was much the same area that is today ME.

From 1949 to 1969 cattle were the sole income from Lone Star Ranche. Even so, the majority of wildlife species (excluding predators) were conserved on the ranch. An indication of the dedication of Mr Sparrow to conserving wild game species, was the measures he took from 1972 onwards to keep buffalo, while pressure was applied by the Veterinary Department to eradicate this species in the lowveld. This matter was eventually decided in court, and Mr Sparrow erected a buffalo-proof fence to retain his population within the Lone Star Ranche. From the early seventies the Sparrow family began running organised hunting safaris on the land. During the 1983 drought nearly 80% of the cattle were lost, but by this stage the trophy hunting operation was well established. By 1985 the last remaining cattle were driven off the land completely. Once these animals were removed predator control was relaxed and the populations of resident species (predators and ungulates) increased. Trophy hunting continued to be the main income until 1987, when photographic safaris began. The severe drought of 1992/93 significantly reduced the numbers of wildlife species however.

In March 1994 the ranch was sold to the Malilangwe Conservation Trust, which is a board of trustees set up to manage funding coming into the country from an American sponsor, for the purpose of conserving wildlife, and extending the benefits of renewable natural resource management into the local communities. Consumptive and non-consumptive wildlife utilisation continues today, with additional programmes for the re-introduction of locally extinct species and research into the functioning and management of the various ecosystems in the area.

Climate

The south-eastern lowveld of Zimbabwe has a warm, arid climate with a distinct wet season (December to March), cool dry season (April to August) and hot dry season (September to November). The mean annual temperature exceeds 18°C (van Rooyen *et al.* 1981). Temperatures are high, with daily maxima above 32°C and peak temperatures often over 45°C. Winters are mild, the lowest recorded temperature being 10°C, and no record of frost exists.

Daily rainfall figures for ME have been recorded since July 1951. These records, as supplied by the Department of Meteorological Services (Harare) in June 1996, and updated monthly since then, were used to examine past rainfall patterns, determine long-term monthly and annual means and medians, and to represent graphically the monthly rainfall for the 1995/96 to 1997/98 seasons. A 5-year running mean technique was used to 'smooth' the long-term annual rainfall figures. This was done to examine possible wet and dry periods. Daily pan evaporation figures were obtained from the Zimbabwe Sugar Association (ZSA) in Chiredzi. These figures were totalled to obtain monthly pan evaporation figures. The long-term mean annual pan evaporation was also supplied by the ZSA (1991).

As at June 1998, ME had a long-term mean and median annual rainfall of 542 and 574 mm respectively (Appendix 1). This describes a negatively skewed distribution, where the occurrence of a number of very low values bias the mean downwards. As is so characteristic of semi-arid savanna areas, annual rainfall is highly unpredictable and variable (standard error about the mean is 180.4 mm). Figure 3.2 presents the annual rainfall from 1951 to 1998.

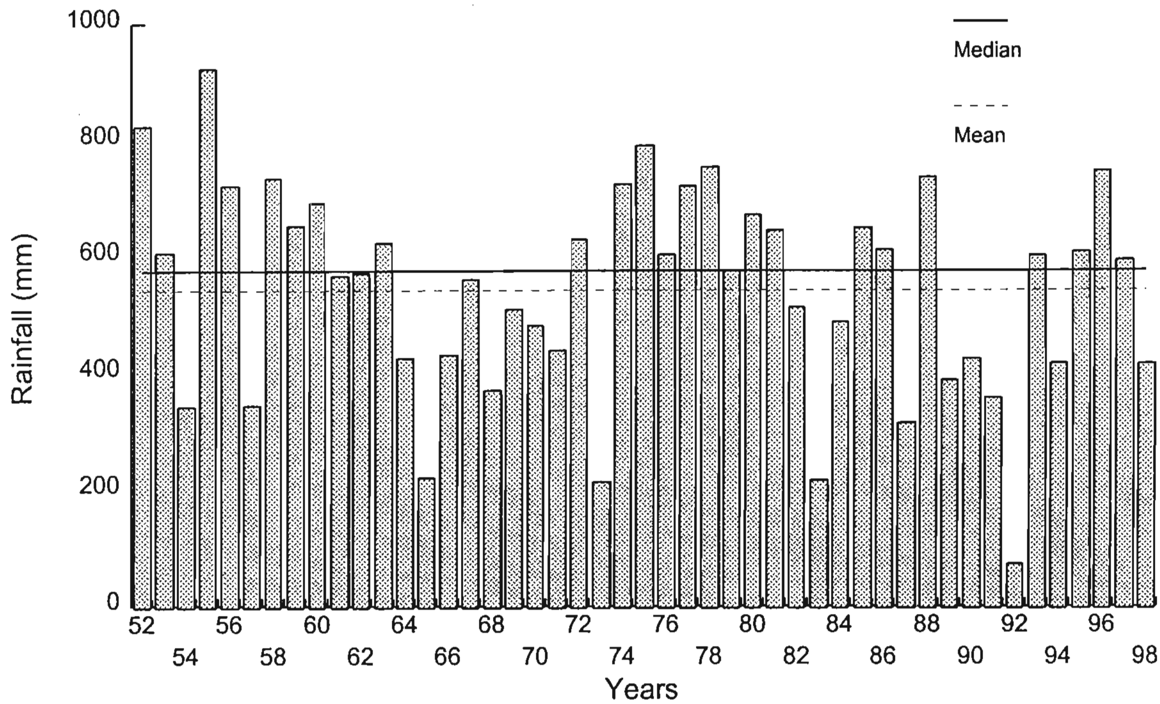

Figure 3.2 Annual rainfall for Malilangwe Estate, from 1951/52 until 1997/98, in relation to the long-term median and mean.

The variability in year-to-year rainfall has been large (up to 30%), and, with the exception of the last two decades, has shown little sustained trend (Hulme 1996). Much of this variation is random. However, within the record, real and significant non-random components are clearly identifiable. Contained within the generally random year-to-year rainfall variability is this underlying non-random component which has varied systematically for over 80 years. This is strong enough to have imparted a degree of regularity to rainfall variations, that cannot be ignored (Preston-Whyte and Tyson 1988). A feature of Southern African rainfall is the apparent cycles of wet and dry periods. Eighteen-year cycles of nine dry and nine wet years occur in the summer rainfall areas of South Africa. A similar wet/dry oscillation is evident for ME (Figures 3.2 and 3.3). Records from 1951 to 1998 show periods of above and below average rainfall. These periods are clearly observed in Figure 3.3, in which a five-year moving-average technique is applied to smooth the data. Above-average periods were 1952-1963 and 1974-1981. Below average periods were 1964-1973 and 1982-1994. No predictions can be made from the data presented in Figures 3.2 or 3.3.

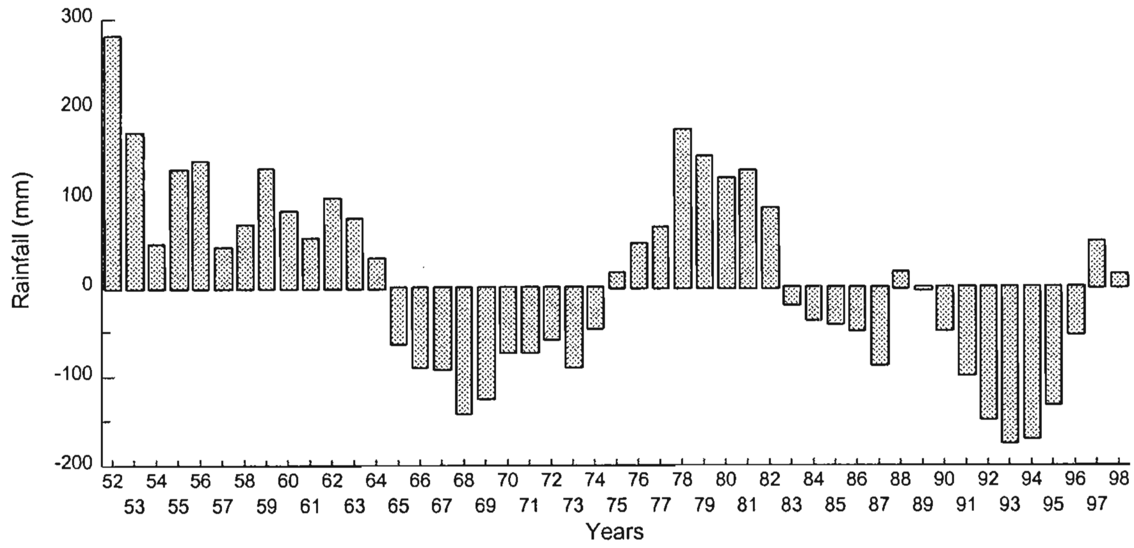

Figure 3.3 Five-year moving-average annual rainfall for Malilangwe Estate, presented as positive or negative deviation about the long-term mean of 542mm.

The 1995/96, 1996/97 and 1997/98 rainfall figures are presented in Table 3.1.

Table 3.1 Long-term (1951-1998) mean and annual rainfall (mm), s.e and CV% figures for Malilangwe Estate, on a monthly basis (Department of Meterological Services, Harare)

Month	**1951-98**	**1995/96**	**1996/97**	**1997/98**
July	6.5	42.5	33.5	8.5
August	4.6	0	6	0
September	12.6	0	4	9.5
October	24.8	0	2.5	17
November	63.7	32	64.5	40.2
December	109.4	82	66.5	70.4
January	116.5	300	167.5	184.3
February	115.1	205	119.5	63
March	44.5	33	72.5	17.9
April	26.8	33	36	3.8
May	10.2	13.5	20	0
June	7.2	5	0	0
Total		746	592.5	414.6
Means	542.0	543.7	544.8	542.0
S.E	180.4			
CV%	33.3			

The 1995/96 season was 37.2% in excess over the long-term mean of 543.7 mm for that season, 1996/97 an 8.8% excess and 1997/98 a 23.5% deficit. The 1995/96 season was the fourth highest rainfall season recorded at Malilangwe. Rains fell late, but when they did fall, 67.7% of the annual total fell in January and February (Figure 3.4). Seven of the twelve other months were below the long-term monthly mean.

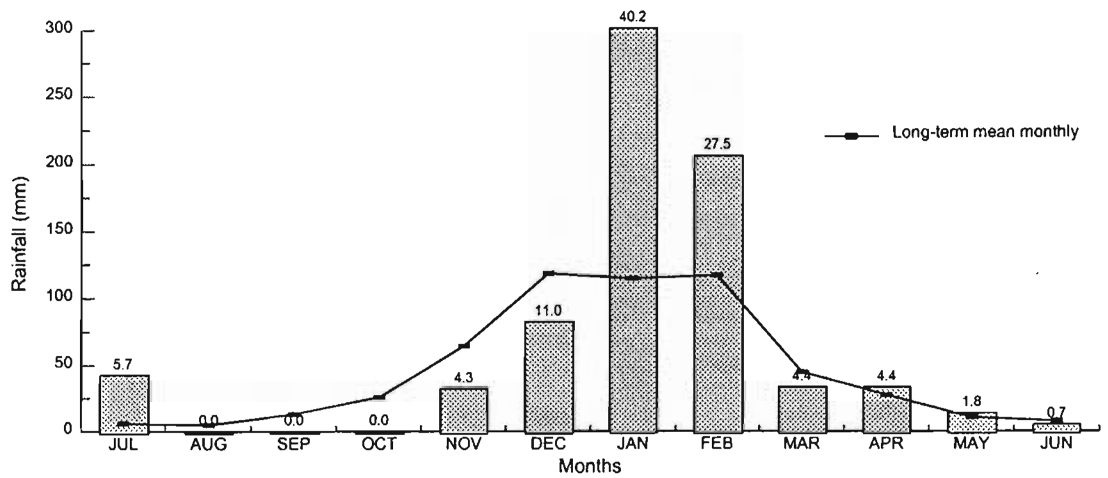

Figure 3.4 Monthly rainfall for Malilangwe Estate for 1995/96 in relation to long-term monthly mean and percentage contribution to annual rainfall.

The 1996/97 rainfall season was characterised by above-average rainfall in eight out of twelve months, and only 48.5% of the annual rain fell in January and February (Figure 3.5).

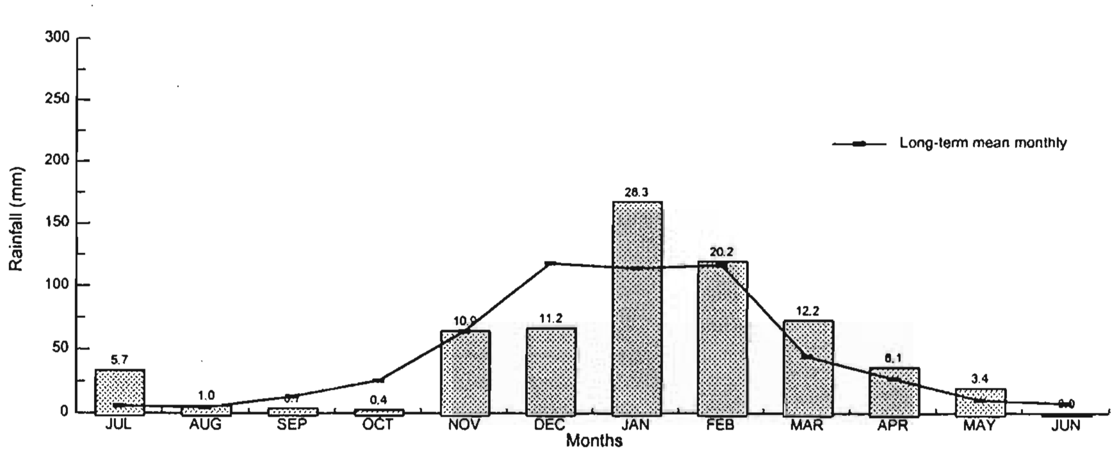

Figure 3.5 Monthly rainfall for Malilangwe Estate for 1996/97 in relation to long-term monthly mean and percentage contribution to annual rainfall.

This pattern started in July 1996, with uncharacteristically high falls, and continued into the wet season. Two weeks of early rains in November 1996 resulted in early grass growth and wet conditions that made burning impossible.

The 1997/98 season had only two months with above-average rainfall. December, January and February accounted for 76.6% of the annual rainfall, with January alone contributing 44.5% of the annual total (Figure 3.6).

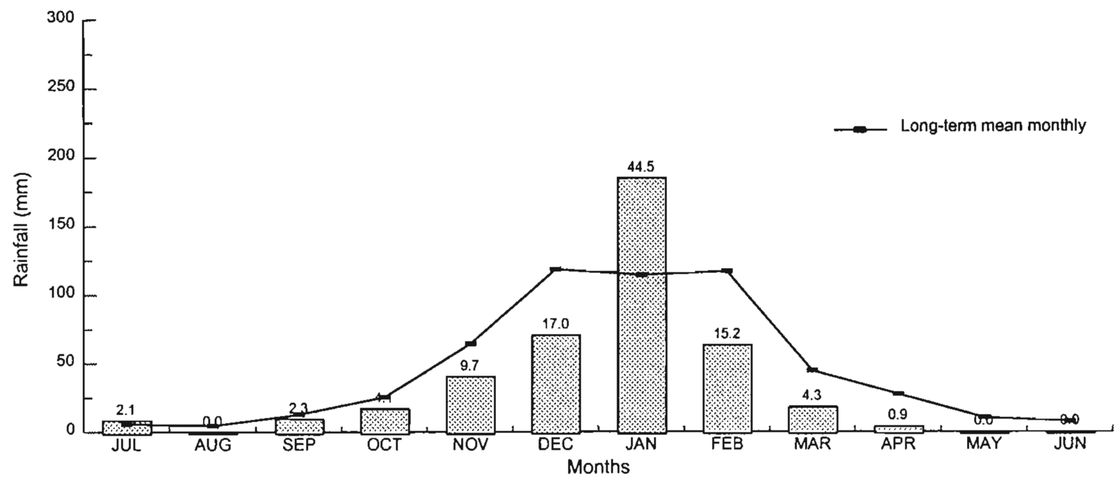

Figure 3.6 Monthly rainfall for Malilangwe Estate for 1997/98 in relation to long-term monthly mean and percentage contribution to annual rainfall.

The average annual rainfall is considerably lower than the world average of 860 mm. Over most of the country annual pan evaporation ranges between 1 100 mm and 3 000 mm, with ME being estimated as 1 900 mm (Zimbabwe Sugar Association 1991).This is well in excess of the annual rainfall, as well as that recorded on a monthly basis (Figure 3.7). January 1998 was the only month during the study period in which rainfall exceeded pan evaporation.

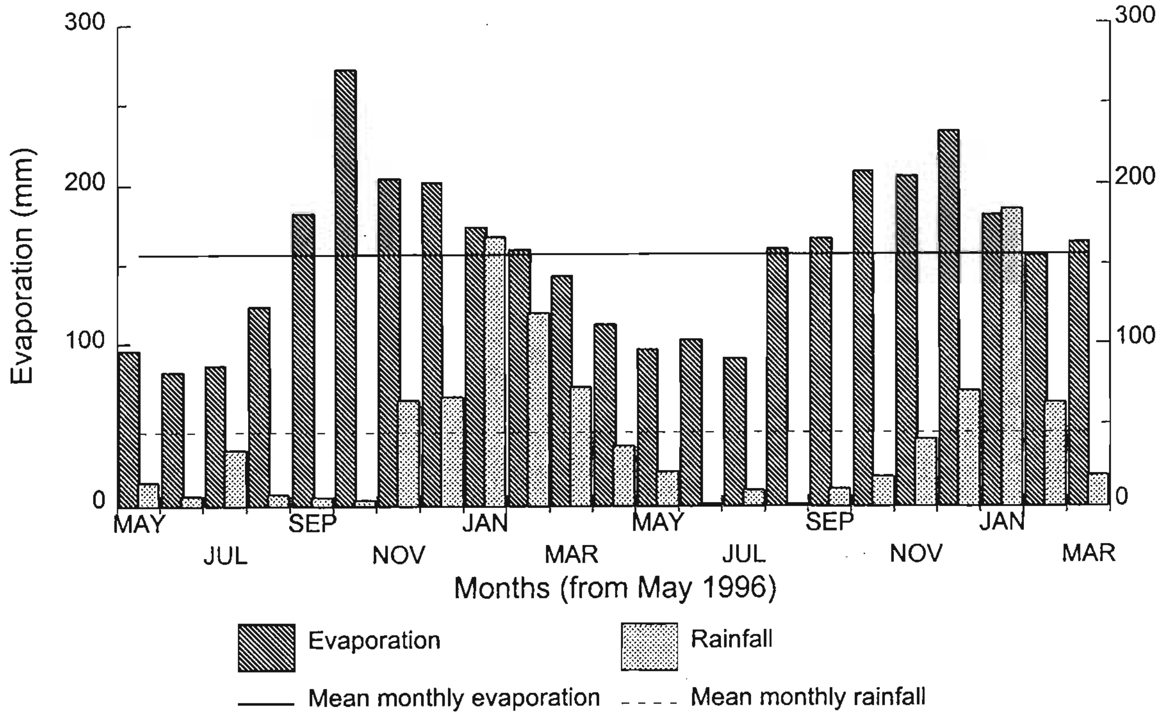

Figure 3.7 Monthly pan evaporation and rainfall for Malilangwe Estate, in relation to mean monthly pan evaporation and rainfall.

From this figure it is clear that ME is in a continuous situation of moisture deficit, both on a monthly and annual basis.

The rainfall records for ME Headquarters are assumed to be representative of the rainfall occurring at the treatment blocks, which is approximately 9 km distant. No rain gauges are located at the nearest game scout picket, and the purchase and installation of one or more rain gauges within the study site was regarded as too costly and unnecessary.

The factors influencing the rainfall patterns, under the influence of the South East Trade Winds which penetrate inland from the Mozambique Channel, appear regional rather than local (Booth 1991). Therefore the spatial variation in rainfall over the treatment blocks, within the study site, is considered to be not great enough to influence treatments. The temporal scale is also important when considering the population dynamics and life-class interactions within a community, especially when the species under consideration is adapted to low soil moisture conditions.

November to March is considered to be the rainy season, as approximately 82% of the annual rain falls within this period (Figure 3.8). However, the majority of this falls in turn during the three months December to February (62%).

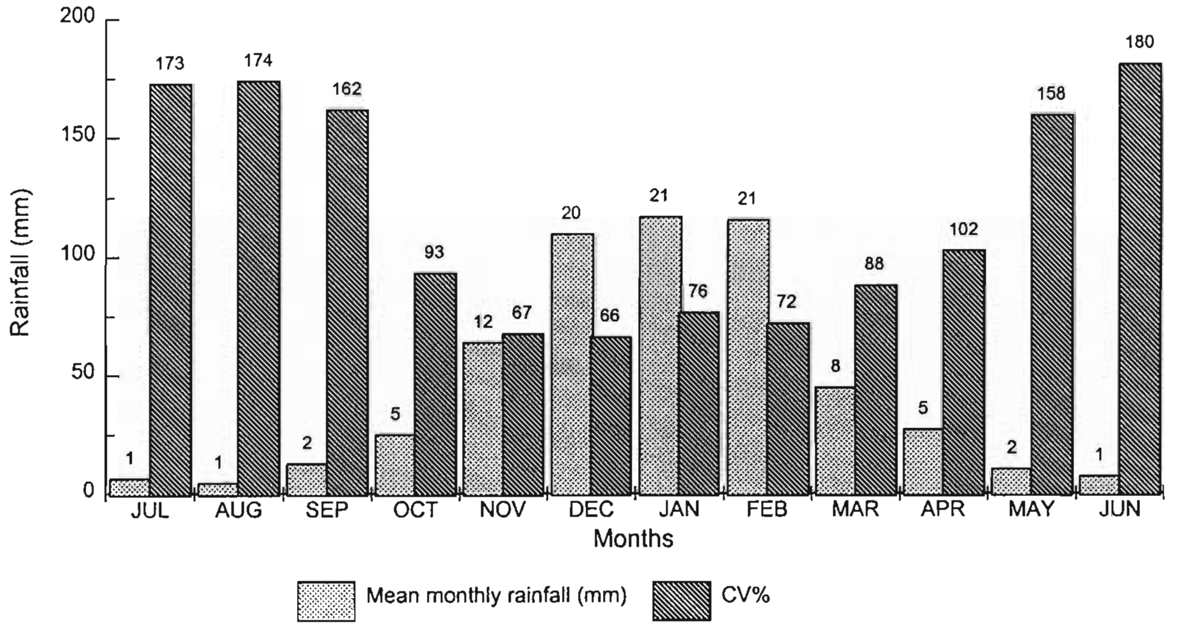

Figure 3.8 Long-term mean monthly rainfall, percentage contribution to long-term mean annual rainfall and CV%'s for Malilangwe Estate.

Average monthly rainfall for December, January and February is very similar. The point to note though is the fact that January rainfall is more variable than either December or February. The months with the least variability are November, December and February. In contrast, the low rainfall (drier) months are highly variable and unpredictable (CV%'s over 135%).

During most years the arid and semi-arid savannas of the south of Zimbabwe (below 600 mm) are characterized by a mid-season "drought". High rainfall is experienced at the start of the season, whereafter there is a period of lower rainfall during the middle of the wet season, often January. This contributes to the high variability of January rainfall.

A winter period of "guti" rain (soft drizzle) is characteristic of the south eastern lowveld of Zimbabwe. The 1995/96 season had a marked winter rainfall period (Figure 3.4), and this resulted in extended grass production and high fuel loads. The same occurred in the 1996/97 season.

Soils and geology

The Malilangwe Range dominates the central and northern areas of ME, consisting of Stormberg sandstone, cut by many faults, and resulting in a broken rocky landscape. North of this range, the area is dominated by paragneiss with numerous dolerite intrusions. Most of the area south of this sandstone range is covered by basaltic soils, and extends into the Gona-re-Zhou National Park. The soils near the Malilangwe Range are of low base status (dystrophic sandy soils), derived from the sandstone. The soils of the basalt plains are deep, heavy clays (vertisols), having a high base status (eutrophic).

The main river systems in the area are the Chiredzi, Runde (previously the Lundi) Nyamasikana and Mahande rivers. To the south of the Nyamasikana gorge, and overlying the basalt derived soils are palaeo-delta deposits comprising mesotrophic red sandy loam soils. Lastly, two narrow, well weathered, alluvial belts exist along the incised Chiredzi and Runde rivers. These rivers flow strongly during the rainy season, but are dry during the dry season. A large dam has been constructed on the Nyamasikana river, as well as other smaller weirs and reservoirs on the tributaries leading from the hills into the basalt plains.

Vegetation

The area falls within the Mopane vegetation of the Sudano-Zambezian Region (Werger and Coetzee 1978). This corresponds to Acocks (1988) veld type 15 (Mopane veld). The area is a deciduous savanna, and the vegetation has been recently described by Stalmans (1994). A list of vegetation communities is presented in Table 3.2. Nomenclature of species follows van Wyk and van Wyk (1997).

Table 3.2 The different vegetation communities of Malilangwe Estate (after Stalmans 1994)

Vegetation community
Coleochloa - Danthaniopsis
Brachystegia glaucescens- Androstachys johnstonii
Julbernardia globiflora - Diospyros usumbarensis
Newtonia hildebrandtii - Gyrocarpus americanus
Colophospermum mopane - Grewia spp.
Colophospermum mopane - Combretum apiculatum
Colophospermum mopane - Heteropogon contortus
Colophospermum mopane - Brachiaria eruciformis
Croton megalobotrys - Phyllanthus reticulatus
Eriochloa - Echinochloa
Sporobolus iocladus - Chloris gayana
Acacia tortilis - Grewia spp.
Acacia nigrescens - Combretum imberbe
Combretum imberbe - Setaria sphacelata
Acacia borleae - Brachiaria deflexa
Kirkea acuminata - Acacia erubescens
Albizia sp. - Dalbergia melanoxylon
Androstachys johnsonii - Mundulca sericea

The sandstone outcrops are dominated by miombo vegetation that is dominated by *Julbernardia globiflora* and *Brachystegia glaucescens* (approximately 10% of the area). Belts along the major rivers consist mainly of *Loncocarpus capassa, Acacia nigrescens*, *Acacia borleae* and *Combretum imberbe* (approximately 10% of the area). *Acacia tortilis* and *Grewia* spp. dominate the small areas which were cleared for habitation by the Tsonga people, and along the Chiredzi and Nyamasikana rivers (approximately 8% of the area) where tsetse clearing took place (1959-1964).

Away from the Malilangwe Range, *Colophospermum mopane* is the most common and widespread woody species in the study area (approximately 72% of the area). Two mopane-dominated communities were identified on the basalt plains by Stalmans (1994):

1) on better drained stony soils a *Colophospermum mopane-Heteropogon contortus* community occurs, with associated species such as *Sclerocarya birrea* and *Pterocarpus brenanii* being present, and
2) nearer the Chiredzi and Runde Rivers clay percentage increases dramatically and drainage is impeded. A *Colophospermum mopane-Brachiaria eruciformis* community was identified on these heavier soils, but the trees are stunted and occur as dense stands. Both in cover and bulk of the grass layer *Panicum maximum* and *Urochloa mosambicensis* form the largest component (Stalmans

1994). The treatment blocks were chosen in these mopane-dominated communities.

This vegetation type is structurally varied, ranging from shrublands to taller closed woodlands. Mopane woodland dominates the low-lying areas, particularly in the southern and northern areas. Other tree species in these vegetation types are *Dalbergia melanoxylon, Acacia nigrescens, Sclerocarya birrea, Grewia* spp. and *Combretum apiculatum.* Grasses include *Urochloa mosambicensis, Cenchrus ciliaris, Heteropogon contortus, Aristida adscensionis* and *Enneapogon cenchroides*. The grass component is dominated by Increaser species, with very low percentage abundance of Decreaser species (Stalmans 1994).

Fire History

Pre-settlement fire history is vague, but the occurrence of periodic fires through the area is accepted, as the fire history of the adjoining Gona-re-Zhou National Park and Mozambique bear testimony to the regular burning of large tracts of mopane woodland. With the introduction of cattle however, the removal of forage through fire was avoided at all costs, and fire exclusion was actively implemented. This, along with the reduction in standing crop through removal by cattle, led to approximately 50 years of no burning, or very low intensity burns.

After the formation of Malilangwe Estate fire was introduced as part of the management programme, albeit on a small and exploratory scale, because of the inhibition of management staff. However isolated fires entered through the eastern boundary fence from Government Resettlement Land , and burned small areas. Together with management burning, the following areas were burnt: 1994 (2 430 ha or 6%), 1995 (9 340 ha or 23%), 1996 (1 625 ha or 4%) and 1997 (4 060 ha or 10%). The non-management fires occurred as head fires moving from the eastern boundary in a westerly direction, while management burns were carried out within management blocks (back fires were implemented along the boundaries, and head fires implemented thereafter from the windward boundaries). These management and non-management fires burned through mopane-dominated vegetation types, as well as small river course vegetation (more open grassland areas).

Chapter 4

Standing crop production in response to effective rainfall

Introduction

Technically the term grass biomass refers specifically to living grass material, and standing crop to living and dead material. For the purposes of this study, standing crop is synonymous with fuel load, as it is the grass layer which forms the greatest proportion of available fuel for burning. The accurate estimation of standing crop was therefore regarded as fundamental to determining the potential fuel load of the mopane woodlands of ME.

The objectives of this exercise were:

1) To successfully calibrate the disc pasture meter over a number of months,
2) determine whether derived regression equations were significantly different,
3) to monitor monthly standing crop and effective rainfall, and
4) to investigate the relationship between what I termed effective rainfall (ER - calculated by dividing monthly rainfall by monthly pan evaporation) and standing crop.

Procedure

Experimental design

The study of standing crop production in response to effective rainfall and the relationship between peak standing crop and rainfall was carried out in two of the control treatment blocks. These sites are representative of the mopane-dominated areas, and are situated within the same vegetation type as the burning treatments. During the study period these blocks were not burnt at all, and had been burnt in 1995 as part of the management burning programme. The age of the grass sward in these two areas was therefore approximately one year at the outset of the study, and had recovered fully from the previous years burn.

1) Disc pasture meter calibration

Standard procedure (Bransby and Tainton 1977)

In an effort to ensure accuracy and applicability to the study area, a bi-monthly calibration approach was used to develop a predictive equation for estimating standing crop using a standard disc pasture meter (Bransby and Tainton 1977). Two areas were chosen (one in each of the control blocks) that were representative of the mopane woodlands of the treatment blocks (the same vegetation type with respect to species composition and structure). Fifty disc meter readings (25 per area) were taken, and the respective grass material harvested from beneath the disc for drying. Drying was carried out at the ZSA laboratory, at 60°C until constant mass was reached, and the samples then weighed. For each calibration, a scatterplot was used to determine the relationship between disc height and dry matter. Linear regression analysis was then applied with disc pasture meter reading (cm) as the independent variable, and standing crop (g) as the dependent variable.

Revised procedure (Trollope and Potgieter 1986)

In addition to the method described above, the revised procedure described by Trollope and Potgieter (1986) was also carried out. This method included the following:

1) Calibration was carried out using a square, 4 m^2, quadrat.
2) Thirty sample points were selected, covering the seven major vegetation communities found on ME, and one quadrat sampled per sample point.
3) Within each quadrat nine disc readings were taken, giving a mean settling height.
4) All herbaceous material was harvested from within each quadrat.
5) The 30 harvested grass samples were dried at the ZSA at 60 °C until constant mass was reached, and the samples then weighed.

The 30 points were located in the vegetation communities presented in Table 4.1. Within each vegetation community, sample sites were chosen that covered widely different potential fuel loads, so as to obtain as wide a range of regression points as possible.

Table 4.1 The seven vegetation communities of Malilangwe Estate in which calibration data were collected for the revised procedure (adapted from Stalmans 1994)

Number	Vegetation community
1	*Colophospermum mopane - Grewia spp.*
2	*Colophospermum mopane - Combretum apiculatum*
3	*Colophospermum mopane - Heteropogon contortus*
4	*Colophospermum mopane - Brachiaria eruciformis*
5	*Acacia nigrescens - Combretum imberbe*
6	*Combretum imberbe - Setaria sphacelata*
7	*Julbernardia globiflora - Diospyros usambarensis*

Due to financial cut-backs by the Zimbabwean Department of Agriculture, the facilities at the ZSA were no longer available after October 1997, and the bi-monthly standard calibration could not be continued. The months for which standard calibration equations were developed were: June, August, October and December 1996; and February, June, August and October 1997. The revised procedure was only carried out once: February 1997.

2) Covariance analysis of regression equations

To establish whether there is a significant difference between the eight calibration equations, covariance analysis was used to test for the homogeneity of regression coefficients and intercepts. Hereafter pair-wise multiple comparisons were carried out among pairs of regression coefficients and intercepts, in order to determine which months are different from which others. To test the influence of season on the calibration equation, the effect of effective rainfall and standing crop on the slope estimates was carried out.

3) Monitoring of monthly standing crop

The recording of standing crop was carried out on a monthly basis from June 1996 to March 1998. The method developed by Bransby and Tainton (1977) was used, as it was considered to be a favourable, robust and quick technique. This measurement was obtained using a standard disc pasture meter, in the two representative control areas. Four transects, each containing 50 recordings (one every five paces), were carried out in each area. This gave a total of 400 points in the two areas.

4) The relationship between effective rainfall and standing crop

Monthly rainfall was believed to be too simple and inadequate a measure of the moisture available to the grass sward for production, because of the losses that take place through evaporation, evapotranspiration and run-off. Without having to take intensive soil moisture readings on a monthly basis, and divide incoming rainfall into its various components, it was decided to use rather an effective rainfall (ER) figure. This ER figure, albeit robust, was determined on a monthly basis, using the respective monthly rainfall and pan evaporation figures, being calculated as the ratio of monthly rainfall divided by monthly pan evaporation.

Standing crop was monitored on a monthly basis over the study period. The relationship between ER and standing crop was then investigated. Linear regression analysis was applied with ER as the independent variable, and standing crop ($kg.ha^{-1}$) as the dependent variable. The variable 'previous month' (standing crop for the preceding month) was then added in an attempt to elucidate more fully the relationship between standing crop and ER. This was done because the standing crop recorded in any particular month is largely dependent on that which exists the previous month, as well as the effective rainfall for that month.

Results

1) Disc pasture meter calibration

Standard procedure (Bransby and Tainton 1977)

The linear regression equations for the eight months are presented in Table 4.2.

Table 4.2 Linear regression values for eight months, including lower and upper 95% confidence limits (for each month degrees of freedom = 49)

Month	Intercept	Slope	R^2	F prob.
Jun 96	11.25	2.12	0.72	<0.001
Aug 96	28.33	3.69	0.39	<0.001
Oct 96	50.23	2.03	0.42	<0.001
Dec 96	33.12	2.63	0.40	<0.001
Feb 97	32.27	3.31	0.41	<0.001
Jun 97	33.64	2.34	0.58	<0.001
Aug 97	24.84	3.28	0.51	<0.001
Oct 97	29.42	3.02	0.46	<0.001

	Intercept		Slope	
	Lower 95%	Upper 95%	Lower 95%	Upper 95%
Jun 96	7.57	14.94	1.75	2.50
Aug 96	13.24	43.41	2.38	4.99
Oct 96	42.51	57.95	1.36	2.71
Dec 96	22.35	43.88	1.72	3.54
Feb 97	21.22	43.32	2.19	4.43
Jun 97	27.38	39.90	1.77	2.92
Aug 97	15.95	33.74	2.37	4.19
Oct 97	21.21	37.64	2.09	3.94

The linear regression equations were all highly significant (F prob. <0.001), with adjusted R^2 values between 39% and 72%. Figures 4.1 and 4.2 present these intercept and slope data.

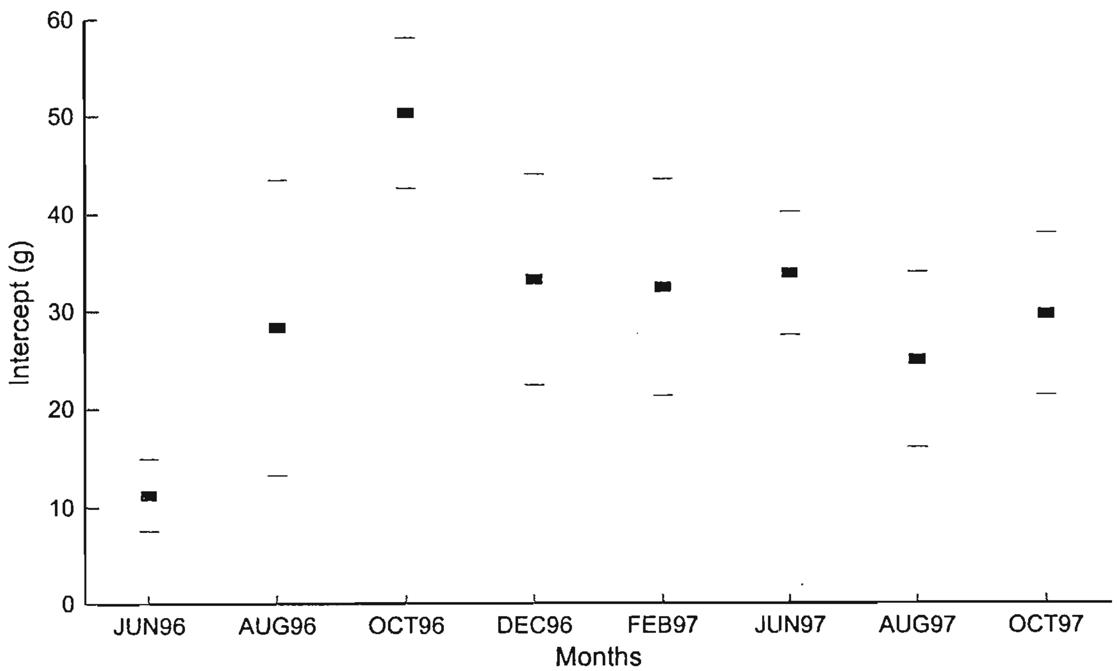

Figure 4.1 Intercept estimates (with 95% confidence limits) for eight regression equations.

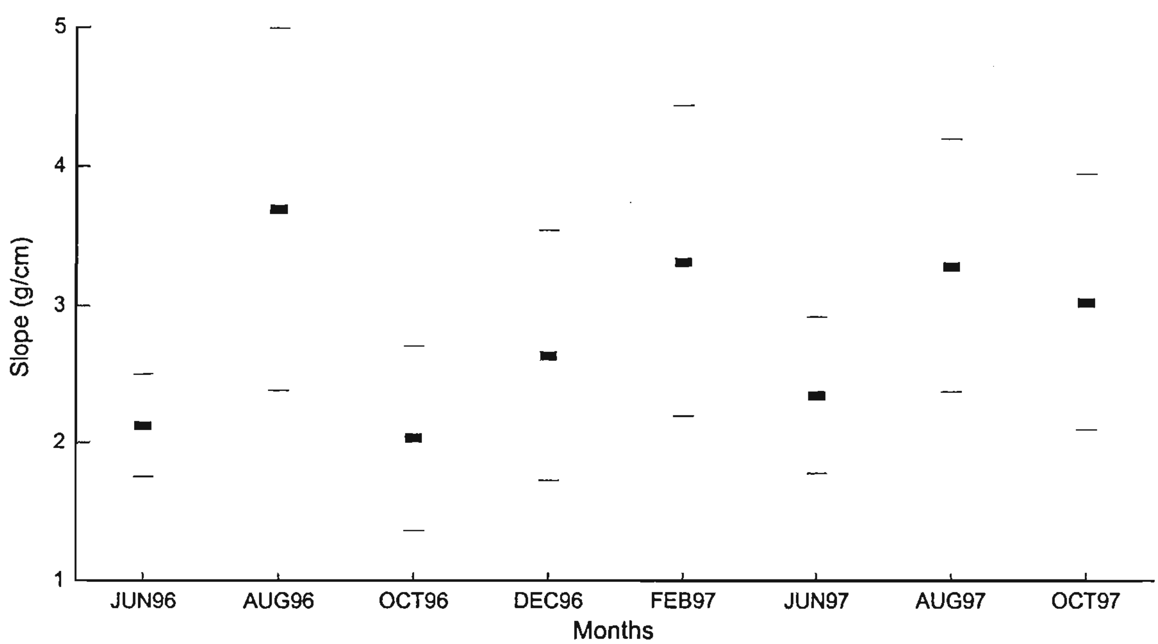

Figure 4.2 Slope estimates (with 95% confidence limits) for eight regression equations.

From the linear regression equations, it is obvious that both the intercepts and slopes of some months are significantly different to others, and that there is inconsistency in the trends of slopes and intercepts for the different months.

Revised procedure (Trollope and Potgieter 1986)

Regression analyses were conducted with the dependent variable standing crop ($kg.ha^{-1}$) and the independent variable (disc height). The independent variable was then subjected to logarithmic (ln x), square (x^2), square root ($x^{0.5}$) and reciprocal (1/x) transformations. Five points were found to be resulting in an appreciable reduction in the coefficient of determination. These points all had a high degree of lodged grass material, and because of this were unrepresentative, and these points were therefore excluded. The linear regression equations are presented in Table 4.3.

Table 4.3 The linear regression between disc height (cm), transformations of disc height, and standing crop ($kg.ha^{-1}$), (degrees of freedom for each analysis = 24)

Transformation	n	R^2	Intercept	Slope
x	25	0.88	376	197
ln (x)	25	0.85	-74	1 190
x^2	25	0.79	980	9
$x^{0.5}$	25	0.90	- 850	1 081
1/x	25	0.54	2 629	-2 467

R^2 = coefficient of determination

It was found that the square root transformation of the independent variable resulted in the best fit of the linear regression, for which the coefficient of determination was highly significant ($R^2 = 0.90$, $P<0.01$). The linear regression equation derived using the revised procedure is thus:

$$\mathbf{Y = -849.95 + 1081(X)}$$

where: Y= estimated standing crop ($kg.ha^{-1}$)

X = square root of disc height (cm)

The linear regression for the square root of disc height and standing crop is presented in Figure 4.3.

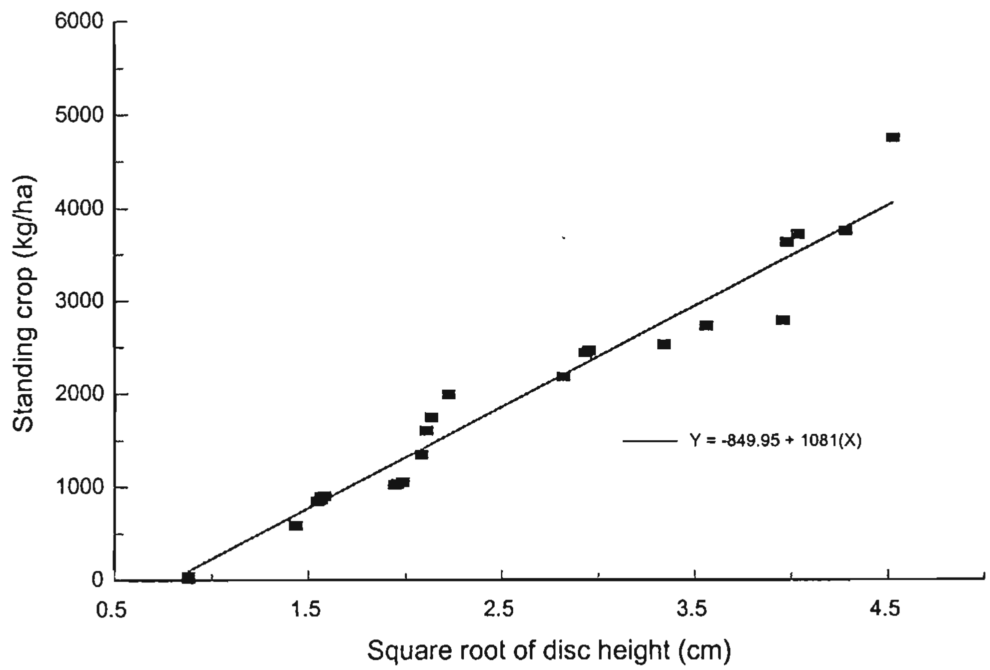

Figure 4.3 Calibration equation for revised procedure (Trollope and Potgieter 1986) covering seven vegetation types on Malilangwe Estate.

2) Covariance analysis of regression equations

The analysis of covariance carried out on the eight regression equations, gave the following results (Table 4.4).

Table 4.4 Covariance analysis results for intercept and slope

Intercept	Slope
F = 2.20	F = 15.60
F (7,384) = 2.04	F (7,391) = 2.04

On the basis of these tests, at the 95% confidence level, one concludes that the intercepts and slopes for the eight regression equations are significantly different. The multiple pair-wise comparisons between months was carried out for intercept, and then slope estimates.

Table 4.5 Intercept and slope t-test probabilities (read columns as comparisons between months)

Intercept

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97
Jun 96							
Aug 96	0.004						
Oct 96	<0.001	<0.001					
Dec 96	<0.001	0.480	0.012				
Feb 97	<0.001	0.557	0.008	0.903			
Jun 97	<0.001	0.394	0.008	0.936	0.831		
Aug 97	0.028	0.602	<0.001	0.234	0.280	0.170	
Oct 97	0.006	0.877	0.003	0.613	0.694	0.534	0.525

Slope

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97
Jun 96							
Aug 96	0.005						
Oct 96	0.873	0.004					
Dec 96	0.372	0.070	0.304				
Feb 97	0.059	0.552	0.046	0.299			
Jun 97	0.683	0.016	0.576	0.612	0.124		
Aug 97	0.065	0.522	0.050	0.318	0.968	0.134	
Oct 97	0.212	0.352	0.175	0.602	0.706	0.347	0.732

A more easily understood representation of Table 4.5 is presented in Table 4.6.

Table 4.6 Intercept and slope t-test probabilities (read columns as comparisons, months without letters in common are significantly different at the 95% level)

Intercept

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97	Oct 97
Jun 96	A							
Aug 96	B	B						
Oct 96	B	C	C					
Dec 96	B	B	D	D				
Feb 97	B	B	D	D	D			
Jun 97	B	B	D	D	D	D		
Aug 97	B	B	D	D	D	D	D	
Oct 97	B	B	D	D	D	D	D	D

Slope

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97	Oct 97
Jun 96	A							
Aug 96	B	B						
Oct 96	A	C	C					
Dec 96	A	B	C	C				
Feb 97	A	B	D	C	C			
Jun 97	A	C	C	C	C	C		
Aug 97	A	B	D	C	C	C	C	
Oct 97	A	B	C	C	C	C	C	C

The multiple comparisons between intercepts shows that the first three equations (Jun, Aug and Oct 1996) are significantly different to each other, and the other equations. The remaining five intercepts are not significantly different from each other, but are all different from the first three. The intercept estimate aids in defining the regression line, and may in fact be a sample statistic prone to misleading interpretations (Zar 1984). In this situation for example, discussion of the intercepts may require extrapolation of the regression lines far below the range of disc heights sampled.

The multiple comparisons between slopes are more complex. As with the investigation of intercepts, the five latter months are not significantly different to each other. However, the first three months have a number of significant and non significant relationships with other slope estimates. Using Table 4.5 to aid in examining these relationships, it was concluded that the derivation of a single combined regression equation was unacceptable. as the interrelatedness of slope and intercept coefficients made it difficult to identify a group, or groups, of similar months.

One would expect there to be an effect of season (dry versus wet) on calibration equations for the pasture disc meter. To test the effect of season, linear regression was applied with effective rainfall and standing crop as the independent variable, and the slope estimate as the dependent variable. The standing crop figures used were the dry mass samples from the calibration clipping quadrats. These two variables were chosen as they are two of the most easily obtainable variables available to the landowner. The results of the linear regression analyses are presented in Table 4.7.

Table 4.7 Linear regression values for effective rainfall and standing crop, over eight months (degrees of freedom = 7)

Variable	Intercept	Slope	R^2	P.
Effective rainfall	2.56	0.5200	0.10	0.23
Standing crop	2.05	0.0004	0.07	0.49

From these analyses it is clear that neither effective rainfall nor standing crop are significant in determining the slope coefficients over the eight months of calibration.

An attempt was made to develop a single combined regression equation for determining standing crop. The regression values for this equation are presented in Table 4.8.

Table 4.8 Regression values for common calibration equations using untransformed and transformed independent variables (degrees of freedom = 49)

Regression	Intercept	Slope	R^2	Sig (95%)
Untransformed	29.68	2.90	0.42	<0.001
Transformed	2.76	18.87	0.47	<0.001

The square root transformation of the independent variable led to an increase in the R^2 value, but only by 5%. The common calibration equation can be represented by Figure 4.4.

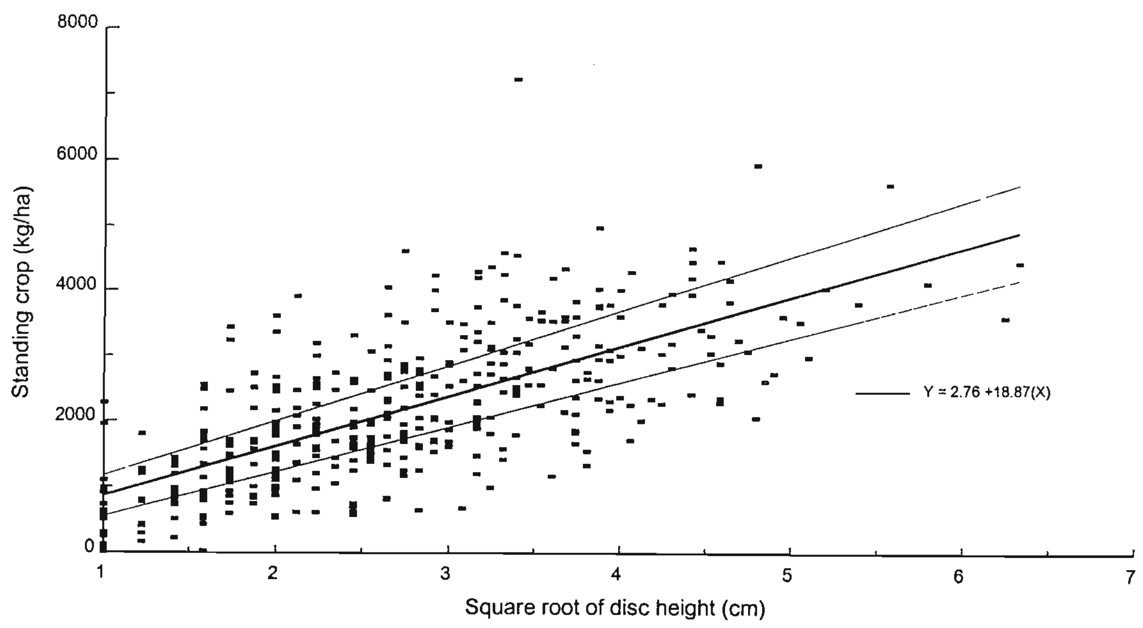

Figure 4.4 Common calibration equation for Malilangwe Estate, showing 95% confidence limits.

The range in variability for a specific disc height is up to 4 000 kg.ha^{-1}. This is exceptionally high, and cannot justify the use of a single equation.

3) Monitoring of monthly standing crop

Standing crop (kg.ha^{-1}), monthly rainfall (mm) and effective rainfall were recorded on a monthly basis from June 1996 to March 1998. These data are presented in Table 4.9. Burning took place as follows: mid dry season (MDS) in September 1996, early dry season (EDS) in June 1997 and late dry season (LDS) in November 1997.

Table 4.9 Monthly rainfall, effective rainfall and standing crop estimates (bold=burn month)

Month	Rainfall (mm)	Effective rainfall	Standing crop (kg.ha^{-1})
Jun 96	5	0.061	913.10
Jul 96	34	0.388	1011.25
Aug 96	6	0.049	1587.37
Sep 96	**4**	**0.022**	**1591.43**
Oct 96	3	0.009	703.14
Nov 96	65	0.316	753.69
Dec 96	67	0.330	1326.18
Jan 97	168	0.965	1385.16
Feb 97	120	0.751	1906.32
Mar 97	73	0.509	1558.21
Apr 97	36	0.321	1802.25
May 97	20	0.186	1543.49
Jun 97	**0**	**0.000**	**1070.28**
Jul 97	9	0.094	1008.75
Aug 97	0	0.000	1106.91
Sep 97	10	0.057	1077.39
Oct 97	17	0.082	1033.42
Nov 97	**40**	**0.196**	**931.36**
Dec 97	70	0.303	1245.97
Jan 98	184	1.020	1643.68
Feb 98	63	0.406	2506.24
Mar 98	18	0.109	1569.94

These data are presented in Figure 4.5.

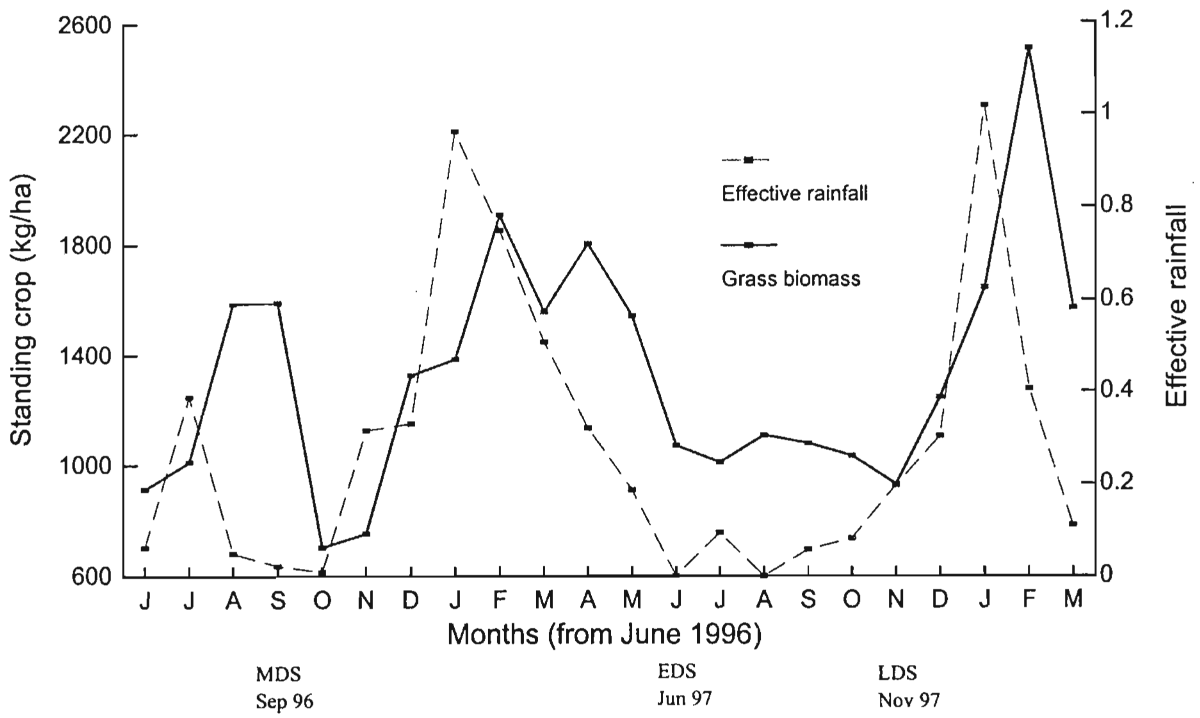

Figure 4.5 Standing crop and effective rainfall plotted over the study period (burns: MDS mid dry season, EDS early dry season, LDS late dry season).

4) Relationship between effective rainfall and standing crop

The regression analysis for standing crop, as determined by effective rainfall from the previous month, is highly significant.

Table 4.10 Multiple regression values for standing crop as the dependent variable, and previous month's effective rainfall (ER) as the independent variable

Adjusted R^2	0.73			
Sig.	<0.001			
Variable	**Estimate**	**P prob.**	**Lower 95%**	**Upper 95%**
Intercept	999.88	<0.001	858.16	1141.59
ER	1214.63	<0.001	872.86	1556.41

The equation for determining standing crop is:

$$\textbf{Standing crop (kg.ha}^{-1}\textbf{)} = \textbf{999.88} + \textbf{1214.63(ER)}$$

This regression is presented in Figure 4.6.

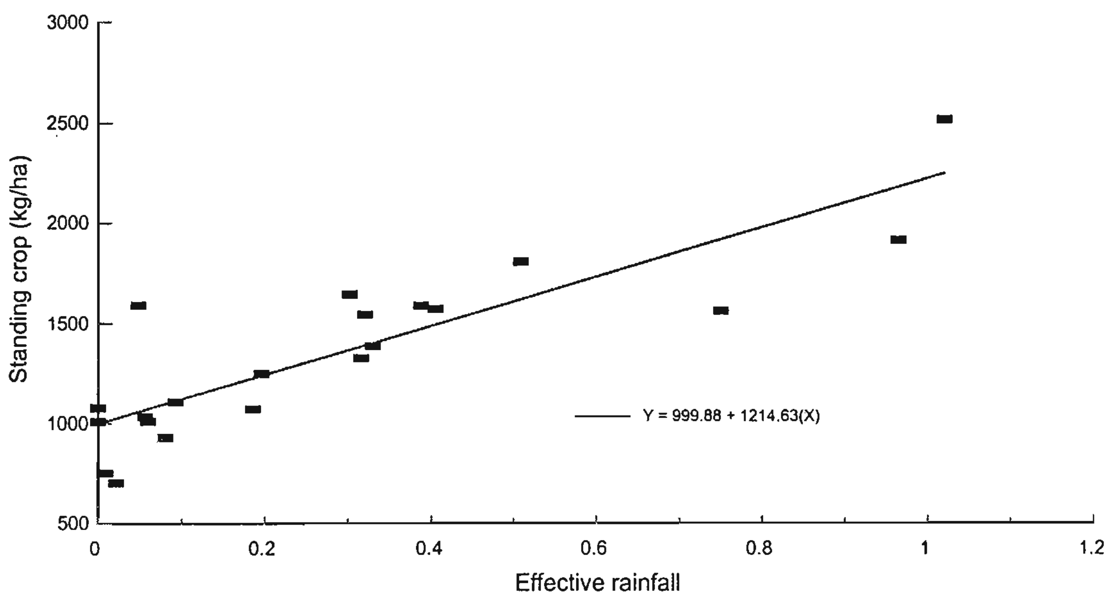

Figure 4.6 Linear regression for determining standing crop from previous month's effective rainfall

Discussion

Disc pasture meter calibration

The calibration of the disc pasture meter was carried out, and eight separate calibration equations were determined. However in five of the eight calibrations the settling height of the disc accounted for less than 50% of the variability in the standing crop of grass. The R^2 values varied between 39% and 72%, illustrating clearly the variability between months. This variability is characteristic of the low basal cover of the grass sward in the mopane woodlands, and the lack of precision represented by the high variation is accepted. The results are accepted as accurate owing to the large number of samples (50), this number of sampling events being representative of the sampling population. In order to increase the degree of variability accounted for by the falling disc, Trollope and Potgieter (1986) developed a revised procedure for calibrating the disc pasture meter for grass swards that have a very low basal cover. This revised procedure showed that disc height accounted for more than 90% of the variation in the standing crop of grass (Trollope and Potgieter 1986). This approach was carried out once on ME, over seven of the major vegetation types. As with the findings by Trollope and Potgieter (1986), more than 90% of the variation in standing crop was accounted for by disc height. This is very encouraging, but was developed over a wide range of vegetation types. It was felt that the sampling population represented by this approach was too broad *ie.* covered unrepresentative vegetation types with different grass species compositions and sward structures to those found in the mopane woodland areas. In light of this, and the fact that a large sampling population (50) was sampled using the standard procedure, the calibration equations developed for the standard disc pasture meter procedure were chosen. Their inherent imprecision is acknowledged as being representative of the variation in the grass sward, but the accuracy and specificity of the equations to the mopane woodlands being investigated, is viewed as being greater than that of the equations developed for the revised procedure.

There were significant differences between the intercept and slope estimates for each of the standard calibration equations. The degree of variability for each equation was itself highly variable (as shown by the 95% confidence limits). The June 1996 and June 1997 variability was very low, and similar. However the August 1996 variability was extremely high. The reason for the high variability of this calibration may be the effect of the extremely high rainfall for July 1996. This rainfall resulted in unseasonal grass growth. The response of particular grass species may have been different to the normal grass growth experienced during the growing season months. Although there were significant differences between the regression equations for different months (Table 4.2), it was extremely difficult to separate any group, or groups, of months as being distinctly different to all others, because of the number of significant and non significant relationships between slope and intercept values. After examining the multiple comparisons between intercept and slope estimates, it was decided that the development of a single common regression equation, that will suffice over all months and seasons, was not possible (Figure 4.5). Although being applicable in monospecific planted pasture situations, the efficacy and applicability of the use of the pasture disc meter for multispecific veld conditions is less extensive (Danckwerts and Trollope 1980). The basic requirement of any method of estimating grass biomass is that the method be capable of sampling adequately across the spatial heterogeneity in vegetation, as well as seasonal conditions and different operators (Friedel *et al.* 1988). This study shows conclusively that for highly heterogenous grass swards, that vary spatially and temporally, the use of the standard disc pasture meter procedure, as described by Tainton and Bransby (1977), is questionable. Unfortunately the pasture disc meter has been used since 1994 for annual estimation of grass yield on ME, and the standard calibration equation developed by Trollope and Potgieter (1986) for the Kruger National Park, has been used to determine the standing crop. In light of this study the following approach is recommended: the procedure described by Trollope and Potgieter (1986) should be followed, but (1) specific calibration equations should be developed for individual vegetation types, and (2) that the effect of season on the calibration equations be considered. This approach overcomes the problem of spatial variation within the grass sward, but does not imply that one regression equation will suffice over different seasons. It is felt that it will be necessary to calibrate the disc pasture meter annually, before the estimation of standing crop is carried out. This is highly recommended if management is striving to implement research findings regarding the effect of fire on savanna vegetation on Malilangwe Estate.

Relationship between effective rainfall and standing crop

The regression analysis for standing crop, as determined by the effective rainfall from the previous month, was highly significant. Using effective rainfall (monthly rainfall divided by monthly pan evaporation) from the previous month, standing crop can be estimated using the standing crop equation. This is a valuable tool for the land manager, as potential fuel loads and grazing capacities can be estimated.

Chapter 5

The relationship between peak standing crop and rainfall, and the development of a decrease function of standing crop

Introduction

From chapter four it is evident that the estimation of standing crop at time (t+1 month) is largely dependent on the effective rainfall at time (t). This allows one to estimate standing crop for the coming month (if given the present months rainfall) or the existing standing crop (given last months rainfall). This equation is however limited to monthly rainfall figures in the range 1-250 mm. At levels higher than this upper limit (the maximum recorded monthly rainfall), the estimation of standing crop is not possible, as this range is beyond that of the monthly rainfall figures sampled. To overcome this, and to develop a start-point for the decline function of standing crop from the end of the growing season, it was decided to investigate the relationship between annual peak standing crop and annual rainfall. However, the study period at ME gave only one season of peak standing crop (PSC) recording, which was inadequate. It was therefore necessary to utilise data from other mopane-dominated areas, with similar soils and climates.

Procedure

Peak standing crop in relation to rainfall

The following annual peak standing crop and respective annual rainfall figures were sourced.

Table 5.1 Source, number of years and area from which data on peak standing crop were sourced

Source	Number of years	Area
Walters	1	Malilangwe Estate
Stalmans (pers. comm.)	3	Malilangwe Estate
Kelly (1977)	2	Gona-re-Zhou National Park (Zimbabwe)
Zambatis (pers. comm.)	9	Landscapes 22, 23 and 24 of Kruger National Park

Nine years of records are available for each of the three landscapes in the Kruger National Park. These landscapes are (after Gertenbach 1983):

22) *Combretum* spp./*Colophospermum mopane* rugged veld,

23) *Colophospermum mopane* shrubveld on basalt, and

24) *Colophospermum mopane* shrubveld on gabbro.

Linear regression analysis was applied with annual rainfall (mm) as the independent variable and peak standing crop ($kg.ha^{-1}$) as the dependent variable. The range of independent values (rainfall) for the south-eastern lowveld (ME and Gona-re-Zhou) were extremely limiting, leading to an inappropriate and poor regression result. On the basis of these findings, the south-eastern Zimbabwe values were not considered for any further analyses.

From the initial regression analyses the slope estimates were compared. No significant differences were found between the three Kruger National Park slope estimates. Hereafter regression analysis was repeated, but with a constant slope estimate being used. From these results, two regression equations were derived.

The decrease function of standing crop from PSC

The monthly standing crop figures for ME, from February 1997 (PSC) to November 1997, were plotted (Figure 4.4). This showed an initial decrease in standing crop from February (month 0) to March. There was then an increase in April, after which there was a sharp decrease until July. After midwinter rainfall in July ("guti") there was an increase in August, after which there was another decrease until November (month 9). Non-linear regression analysis was applied with month as the independent variable and standing crop ($kg.ha^{-1}$) as the dependent variable.

Results

Peak standing crop in relation to annual rainfall

The results of linear regression analysis for three landscapes in the Kruger National Park and south-eastern Zimbabwe are presented in Table 5.2.

Table 5.2 Linear regression values for three landscapes in the Kruger National Park (KNP22, KNP23, KNP24) and south-eastern Zimbabwe (SEZ), including lower and upper 95% confidence limits (degrees of freedom: KNP22 = 8, KNP23 = 8, KNP24 = 8, SEZ = 5)

Area	Intercept	Slope	R^2	P.
KNP22	460.5	2.62	0.07	0.245
KNP23	1153.3	4.61	0.43	0.033
KNP24	959.4	3.57	0.27	0.089
SEZ	1272.9	1.04	0.23	0.797

	Intercept		Slope	
	Lower 95%	Upper 95%	Lower 95%	Upper 95%
KNP22	-1688.8	2609.9	-2.3	7.5
KNP23	-575.9	2882.5	-0.5	8.7
KNP24	-798.7	2717.6	-0.7	7.9
SEZ	-5099.0	7644.9	-9.5	11.5

At the 5% level, only the KNP23 regression equation is significant. KNP24 is significant at the 10% level. The high F probability and lower/upper 95% confidence limits for the SEZ regression analysis are an indication of the inappropriateness of the regression equation. This is clear from Figure 5.1.

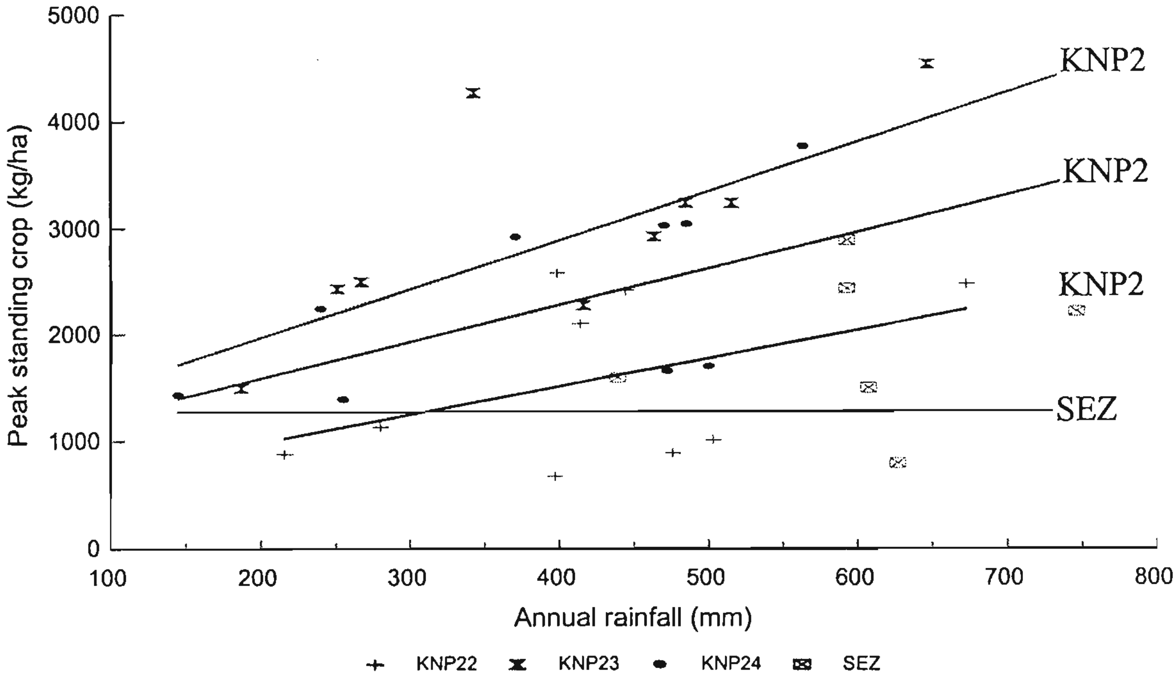

Figure 5.1 Scatterplot of peak standing crop (kg.ha^{-1}) and annual rainfall (mm) for three landscapes in the Kruger National Park (KNP22, KNP23, KNP24) and south-eastern Zimbabwe (SEZ).

From this figure it is clear that the data for SEZ do not cover a wide enough range of rainfall variation. Four of the six points are extremely close to the 600 mm rainfall level. This results in a very poor data set with which to attempt linear regression analysis. In light of this, it was decided to ignore the SEZ values (due to their narrow independent value range), and continue further analyses with the Kruger National Park landscapes only. It must be noted at this stage that landscape 23 (*Colophospermum mopane* shrubveld on basalt) is the most similar, of the three landscapes, to the treatment blocks on ME, as the climate, soils and vegetation communities of these blocks are very similar to those found in landscapes 23 and 24.

The slope coefficients (with 95% confidence limits) for the three landscapes are displayed in Figure 5.2.

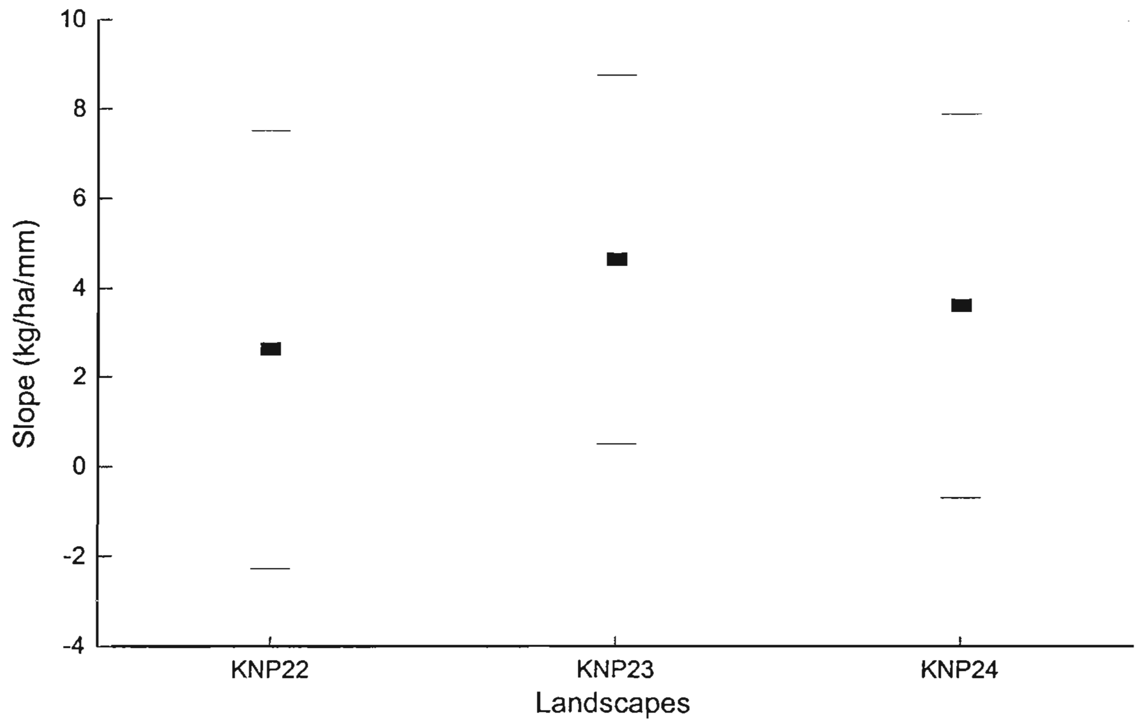

Figure 5.2 Slope coefficients for linear regression equations of three landscapes in the Kruger National Park.

It is clear that there is no significant difference between the slopes of any of the three landscapes. This led to the regression analysis of the three landscapes being repeated, with a 'common' slope and individual intercepts being determined.

Table 5.3 Regression analysis values for three landscapes in the Kruger National Park, incorporating a 'common' slope and individual intercepts (degrees of freedom = 26)

Adjusted R^2	0.51
F prob.	<0.001

Variable	**Estimate**	**s.e.**	**t prob.**
Slope	3.67	1.04	0.002
KNP22	17	500	0.973
KNP23	1524	339	<0.001
KNP24	919	340	0.014

Multiple comparisons between the three intercept estimates gave the following results.

Table 5.4 Intercept t probabilities (read columns as comparisons between landscapes)

Intercept

	KNP22	KNP23
KNP22		
KNP23	<0.001	
KNP24	0.014	0.087

A more easily understood representation of Table 5.4 is presented in Table 5.5.

Table 5.5 Intercept t probabilities (read columns as comparisons between landscapes, months without letters in common are significantly different at the 95% level)

Intercept

	KNP22	KNP23
KNP22	A	
KNP23	B	B
KNP24	B	B

This indicates that the intercept estimates for landscape 23 and 24, although non-significantly different to each other, are significantly different to landscape 22. From this the following two regression equations can be derived.

Table 5.6 Regression analysis values for landscape 22 and landscape (23/24)

(degrees of freedom: 22 = 8, 23/24 = 17)

Landscape	Intercept	Slope	s.e.	t prob.
22	17	3.67	500	0.973
23/24	1205	3.67	340	0.008

The regression analysis results for landscape 22 indicates that the linear relationship between PSC and rainfall is inadequate (t prob.= 0.973). This equation is therefore unacceptable, and the combined equation for landscape 23/24 is the only equation that can be used to estimate PSC from annual rainfall.

The regression equation for these landscapes is:

Landscape (23/24): PSC = 1205 + 3.67(Annual rainfall)

This equation was assumed to be applicable to the treatment blocks on ME, because of their similarity.

The decrease function of standing crop from PSC

On ME peak standing crop was achieved in February. Over the study period, only one recording of the decline in standing crop from peak standing crop at the end of the growing season, was possible. The results for the non-linear regression analysis applied to months from peak standing crop as the independent variable, and standing crop as the dependent variable, are presented in Table 5.7.

Table 5.7 Non-linear regression analysis results (degrees of freedom = 9)

F prob. =	0.002
R^2 =	0.79
s.e. =	166

Variable	**Estimate**	**s.e.**
R	0.826	0.119
B	1203	387
A	715	432
Equation	$Y = A + B(R^x)$	

(Where Y=standing crop, R=rate of exponential increase, B=range between the asymptote and the value when x=0, A=the asymptote, and x=month after peak standing crop).

The equation to estimate standing crop for a particular month, after peak standing crop has been reached, is:

Standing crop (month x) = 715 + 1203 (0.826^x)

The exponential relationship between standing crop (kg.ha^{-1}) and months from peak standing crop is presented in Figure 5.3.

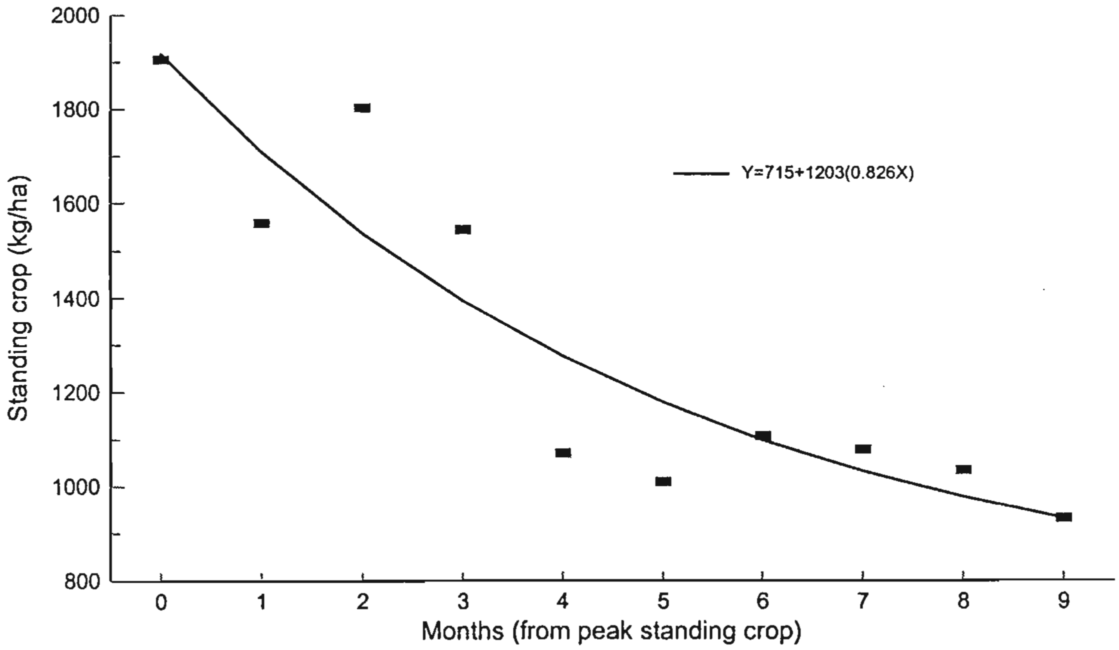

Figure 5.3 The exponential relationship between standing crop and months from peak standing crop.

Discussion

The monthly monitoring of standing crop and effective rainfall shows that there is a distinct lag-effect between effective rainfall and change in standing crop. The resolution of this study (monthly intervals) indicates that the lag period is one month. However, the response by the grass sward to changes in soil moisture (especially during the early and mid growing season) is in most cases shorter than one month. The effective change in standing crop may very well be shorter than one month after a rainfall event. The monitoring interval of the grass sward by a land manager will very seldom be less than one month, and the results are therefore considered acceptable. The effect of effective rainfall, from the previous month, on standing crop was found to be highly significant ($R^2 = 0.73$, $P<0.001$). The standing crop for a particular month can be estimated by using the effective rainfall from the previous month. The standing crop values recorded for the treatment areas were not indicative of the expected standing crop values within a given year.

Intuitively, standing crop declines from peak standing crop (February/March) through the dry season. This is as a result of increasing dormancy of the grass plants, removal by grazing ungulates and termites, flattening by animal movement, and decreasing rainfall. The earlier the burning takes place the higher the expected fuel load *i.e* mid dry season burns should have a higher fuel load than late dry season burns, because of the decline in standing crop as the dry season progresses. The paradoxical situation in the recorded fuel load values, where the early dry season burns had the highest fuel load, and mid dry season the lowest (Table 7.5), can be explained by the increased effective rainfall in July, September and October 1997, which led to an increase in standing crop from August 1997. This resulted in the late dry season treatments having higher than normal fuel loads. The very high mid dry season fuel loads were as a result of the exceptionally high June and July 1996 rains (Figure 4.4). This high effective rainfall led to fuel loads higher than one would expect for the middle of the dry season. These fuel load and fire intensity figures were not recorded within the same season, and therefore inferences from the mid dry season head and back fires (being from the previous year) must be treated with caution.

Chapter 6

A leaf quantification equation for mopane trees in the south-eastern lowveld of Zimbabwe

Introduction

At the outset of the study it was recognized that the successful description and interpretation of the effects of fire on mopane woodlands would require an appropriate quantitative description of tree populations. The number, ecological status (dead, living or coppicing) and structure of sampled individuals (during base-line and monitoring exercises) would be the fundamental parameters with which to compare and study the effects of different seasons of burning and types of fire. The approach needed to be rapid, robust and account for a large proportion of the variation in leaf dry mass.

The approach adopted by Smit (1994) was accepted as a comprehensive and repeatable method whereby tree dimension measurements could be obtained, and from these an accurate estimate of leaf dry mass determined. To test the significance of treatment effects (season and type of fire) the accurate estimation of tree-leaf dry mass was critical.

Procedure

The technique followed a regression analysis approach, whereby the relationship between the spatial volume of a tree and its true leaf dry mass was determined. The leaf quantification technique of Smit (1994) was developed for coppicing and non-coppicing trees in the Soutpansberg area of the Northern Province of South Africa. It was felt however that the tree structure in the aforementioned study area differs to that found on ME in Zimbabwe, owing to different soils and rainfall. It was therefore decided to determine two alternative leaf quantification equations for the south-eastern lowveld of Zimbabwe specifically, one for coppicing and one for non-coppicing individuals.

Two areas were chosen in which to harvest mopane trees, each being approximately five hectares in size. The first area had been burnt the previous year and coppicing was prevalent on the majority of trees. The second area had not been burnt within recent history, and contained non-coppicing individuals. Thirty mopane trees from each of the areas, representative of the mopane woodlands occurring on the basalt-derived soils and ranging in size, were selected for harvesting.

Before harvesting commenced, the dimensions of each tree was measured. Hereafter the trees were felled, and all leaves hand-picked. The leaf samples were air-dried for three days before being sent to the ZSA, where they were oven-dried at 60°C until constant mass, and then weighed. Regression analysis was applied with true leaf dry mass as the dependent variable and calculated spatial volume as the independent variable. The spatial volume of each tree was calculated using the procedure presented by Smit (1994). This procedure involves the estimation of five tree dimensions:

(A) tree height (height of top foliage),
(B) height of maximum canopy diameter,
(C) height of first leaves,
(D) maximum canopy diameter, and
(E) base diameter of foliage at height (C), as well as the calculation of two more
(F) (A-B), and
(G) (B-C).

Smit (1994) elucidates on the calculation of tree canopy volume, regardless of its shape or size, using the dimension measurements above and the volume formulae of an ellipsoid, right circular cone, frustum of right circular cone or a right circular cylinder. Tree canopy volume can then be calculated using these shapes, and two tree segments (Smit 1994). All trees were assumed to be symmetric. This was done for both coppicing and non-coppicing trees. The formulae for calculating tree canopy volume are presented on pages 10 and 11 of Smit (1994).

Results

The summary of the data for the 30 coppicing and non-coppicing trees are presented in Table 6.1.

Table 6.1 Minimum, maximum, mean and s.e. tree dimension values for coppicing and non-coppicing trees

	Number of Stems	Stem diameter (cm at 25 cm)	Tree height (cm)
Coppicing			
Min.	1	3	75
Max.	12	22	410
Mean	4.43	9.8	225
s.e.	3.44	4.5	97.6
Non-coppicing			
Min.	1	1	80
Max.	3	12	475
Mean	1.13	6.4	281
s.e.	0.43	2.5	91.7

The linear regression analysis for coppicing trees was highly significant (Table 6.2).

Table 6.2 Linear regression values for coppicing trees, with spatial volume (cm^3) as the independent variable and leaf dry mass (g) as the dependent variable (degrees of freedom = 29)

Adjusted R^2	0.83
Prob.	<0.001

Variable	Estimate	F. prob.	Lower 95%	Upper 95%
Intercept	133.07	<0.001	88.52	177.61
Spatial Volume	0.00024	<0.001	0.0002	0.00029

The scatter-plot and linear regression line are presented in Figure 6.1.

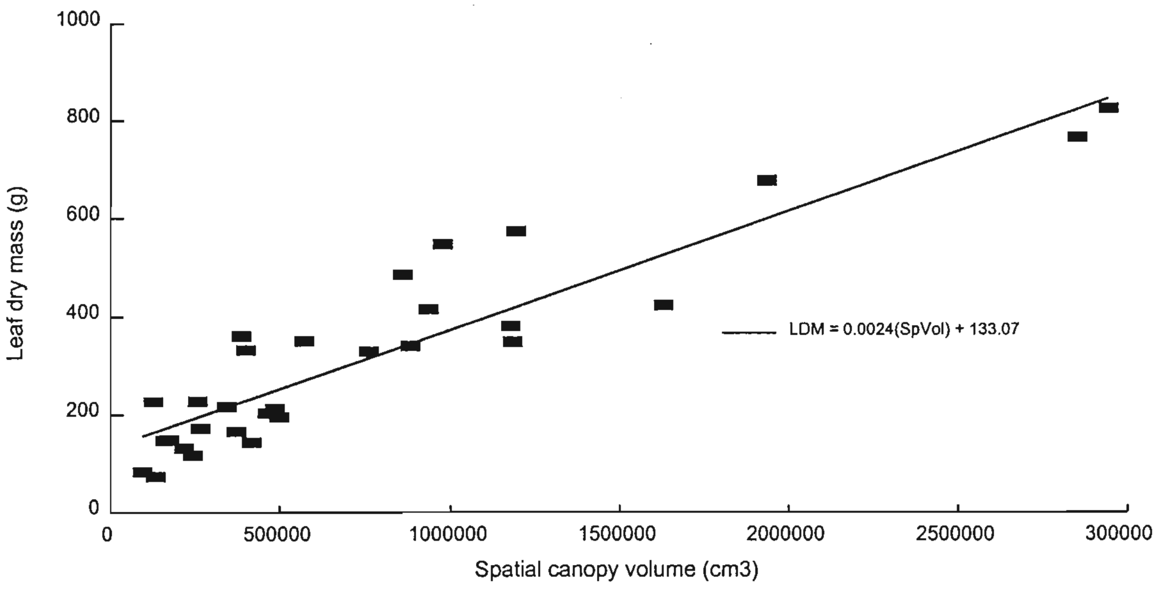

Figure 6.1 Scatter-plot and linear regression of leaf dry mass (g) and spatial canopy volume (cm^3) for coppicing trees.

The regression analysis for non-coppicing trees was also highly significant (Table 6.3).

Table 6.3 Linear regression values for non-coppicing trees, with spatial volume (cm^3) as the independent variable and leaf dry mass (g) as the dependent variable (degrees of freedom = 29)

Adjusted R^2	0.87			
Prob.	<0.001			
Variable	Estimate	F. prob.	Lower 95%	Upper 95%
Intercept	101.97	<0.001	24.08	179.85
Spatial Volume	0.00032	<0.001	0.00027	0.00037

The scatter-plot and linear regression line for non-coppicing trees is presented in Figure 6.2.

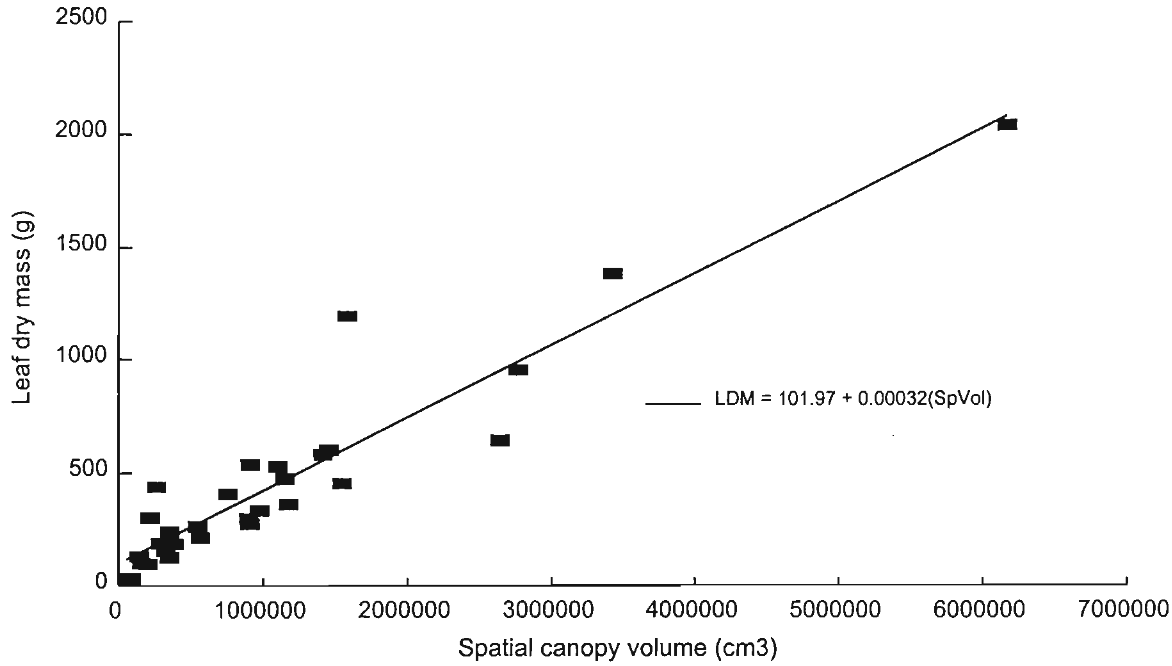

Figure 6.2 Scatter-plot and linear regression of leaf dry mass (g) and spatial canopy volume (cm^3) for non-coppicing trees.

Discussion

Two leaf quantification equations (coppicing and non-coppicing) for mopane, in the south-eastern lowveld of Zimbabwe, were developed to estimate leaf dry mass ($kg.ha^{-1}$) from spatial canopy volume (cm^3). Both analyses were highly significant (Table 6.2 and 6.3), coppicing trees ($R^2 = 0.83$, $P<0.001$) and non-coppicing trees ($R^2 = 0.87$, $P<0.001$). These equations were found to be highly similar to equations developed by Smit (1994) for mopane veld north of the Soutpansberg in South Africa. In Figure 6.3 it can be seen that for coppicing trees there is a significant difference between the leaf dry mass estimates, from the respective equations, at canopy volumes below $5.9x10^6$ cm^3 (*ie.* 15.6 $ln(cm^3)$ on the x-axis). At these canopy volumes, the Soutpansberg equation gives significantly higher leaf dry mass estimates.

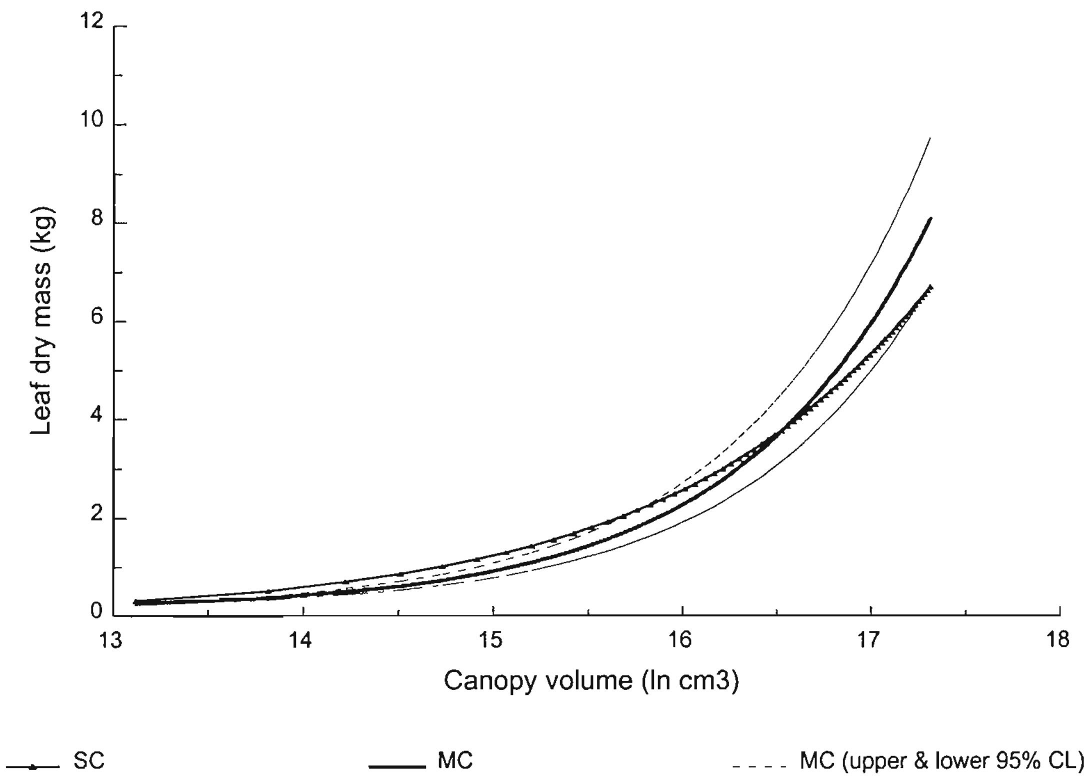

Figure 6.3 Linear regression equation lines of the relationship between tree canopy volume and leaf dry mass of coppicing trees for Soutpansberg (SC) and Malilangwe Estate (MC), as well as the 95% confidence limits (CL) for MC.

From Figure 6.4 it can be seen that for non-coppicing trees there is a significant difference between the two estimates at canopy volumes greater than 1.2×10^6 cm^3 (*ie.* 14.0 ln(cm^3) on the x-axis). At these canopy volumes, the Soutpansberg equation gives significantly lower leaf dry mass estimates.

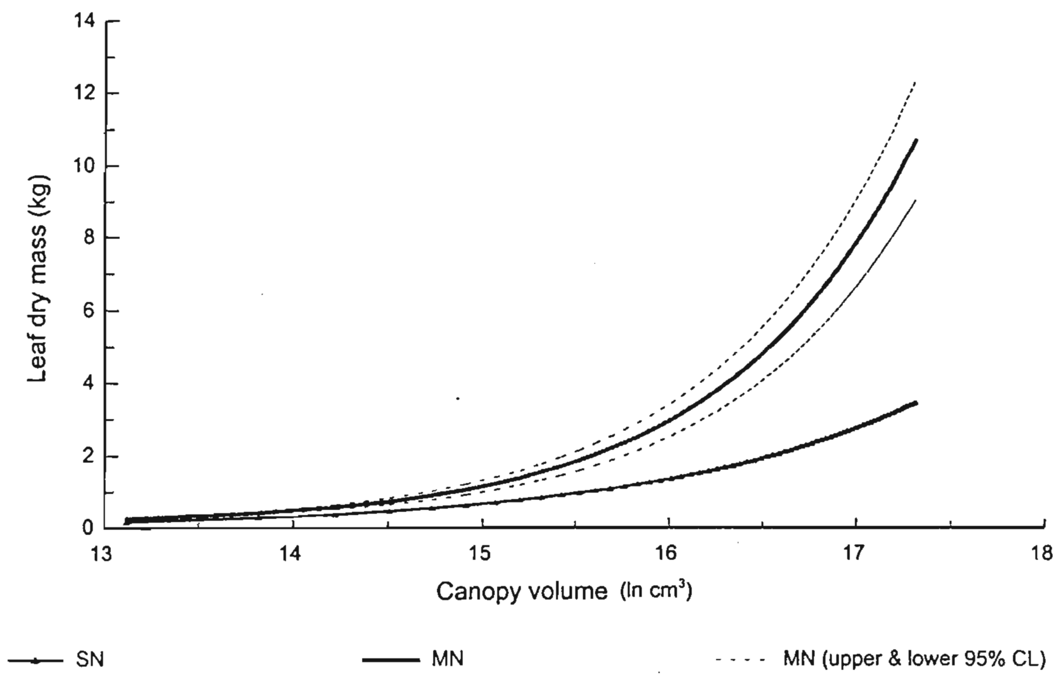

Figure 6.4 Linear regression equation lines of the relationship between tree canopy volume and leaf dry mass of non-coppicing trees for Soutpansberg (SN) and Malilangwe Estate (MN), as well as the 95% confidence limits (CL) for MN.

The Soutpansberg equation gives significantly lower leaf dry mass estimates. This can be explained by the difference in tree sizes harvested for determining the leaf quantification equations in the two areas *i.e* the average height of harvested trees on ME was only 2.4 m, whereas in the Soutpansberg the trees were up to 7 m in height (Smit 1994). Larger trees have increasingly fewer leaves per unit canopy volume, and this explains the higher leaf dry mass for a given non-coppicing tree canopy volume on ME, than that for the Soutpansberg. However, the trees harvested for the leaf quantification study on ME are representative of the woodlands found there, and the equations are specific for that region.

Chapter 7

Effect of season of burning and type of fire on mopane woodland

Introduction

It is accepted that climate and soils may set the limits for plant growth, but that fire and herbivory determine vegetation patterns in the region. Fire sometimes competes with, sometimes replaces and sometimes facilitates herbivory (Bond 1997). The impact of fire can be described at different scales: individual plants (fire responses to burning), plant populations (how burning influences community ecology) and vegetation patterns (landscape and subcontinental level). In this study the effect of season of burning and type of fire is investigated at the individual tree level, as well as the population (woodland) level.

Fire affects tree populations in the following manner (review in Chapter 2):

1) tree seedlings may be killed by fire (whereas larger individuals may survive),
2) burning of the canopy causes topkill,
3) coppicing takes place from the base or from surviving buds (the degree of topkill and coppicing increases with increasing flame height and fire intensity),
4) the architecture of large trees (> 3 m) is unaffected by burning (unless damage occurs through a crown fire or to the trunk bark), and
5) fire changes the structure of the canopy and/or the number of stems.

It was postulated by West (1965) that trees and shrubs are probably more susceptible to fire at the end of the dry season, when plant reserves are depleted after initial spring growth. Because of this phenophase sensitivity, mopane trees burnt in different seasons may differ in their response to fire. The type of fire (back fire or head fire) was investigated because trees are sensitive to various types of fire owing to the differences in the vertical distribution of the release of heat energy. It has been shown that head fires cause the greatest topkill of stems and branches (Trollope *et. al.* 1996), because the concentration of heat energy is at levels closer to the terminal buds of the tree.

Objectives

The objectives of this study were to investigate the following seven parameters, in terms of the effect of season of burning and type of fire on them:

1) the species composition of the treatment areas,
2) the fire parameters and fire intensities of the burning treatments,
3) effect of treatment on stem diameter,
4) effect of treatment on percentage topkill,
5) effect of treatment on tree density,
6) structural response of individuals to burning treatments
    - change in tree height
    - change in number of stems
    - change in maximum canopy diameter (MCD), and
7) effect of treatment on leaf dry mass (LDM).

Procedure

Treatment blocks and treatment areas

Experimental burning took place in three seasons: early dry season (E), mid dry season (M) and late dry season (L). Two types of fire were implemented: head fire (H) and back fire (B), with three replications set up for each treatment. Six controls were also set up (C).

Malilangwe Estate is divided by a network of roads and tracks. These roads, as well as some river courses, are used as the boundaries of the 127 management blocks. In the mopane-dominated vegetation communities, on the basalt plains, six management blocks were chosen as treatment blocks, and treatments allocated as follows: to accommodate the three replications, two treatment blocks were allocated for each of the three season treatments (E,M and L). Within each of these blocks, three treatment areas were then chosen. These treatment areas were chosen in areas where mopane is the dominant species and where soil properties and elevation are similar. Season of burning and type of fire treatments were identified as follows:

Table 7.1 Season of burning (E early, M mid. L late dry season) and type of fire treatment allocations (H head, B back fire), including size of treatment burn and year of last burn

Early	**Mid**	**Late**	**Controls**	
(812 ha)	(815 ha)	(406 ha)		
EB1 - EB3	MB1 - MB3	LB1 - LB3	C1 - C6	
EH1 - EH3	MH1 - MH3	LH1 - LH3		
Last Burn				
EB 1995	MB pre-1994	LB 1997	C1	1994
EH pre-1994	MH 1995	LH 1997	C2/3/4	1995
			C5	pre-1994
			C6	1995

Permanent transects

Ten permanent transects were laid out in each treatment area. Control transects were laid out in similar vegetation, but in areas allocated not to be burned. Five transects were placed in each of the six control areas.

Transects were placed at least 15 m from the road, and 20 m apart. The starting point (a tree) of each transect was marked with yellow paint, and an aluminium disc nailed to it. A 50 m tape was then laid out from this point, and the compass bearing for the transect taken. Another disc was placed at the end of the transect. This allowed for the accurate monitoring of individual trees over time, within a 100 m^2 transect. Transect start-points were recorded using a GPS (Appendix 2).

Data collection

This included the following:

1) Base-line data

Data for the early (E) and mid (M) dry season treatments, as well as the control (C96) treatment were collected in May 1996. The base-line data for the late (L) dry season treatment were collected in May 1997.

The following parameters were recorded for each individual tree encountered:

1) species,

2) status (living or dead),

3) number of stems per individual (counted, but cognisance taken of the fact that underground root stocks may give rise to numerous stems i.e one individual with many stems),

4) the presence or absence of topkill (the occurrence of topkill may be as a result of damage to the extremities of the plant due to drought, and was recorded as such. Effect of topkill on mopane woodland was only considered with regard to damage by fire),

5) spatial canopy volume (the spatial canopy volume of each individual was estimated using five measured, and two derived, dimensions: **(A)** tree height (of living leaf material), **(B)** height of maximum canopy diameter, **(C)** height of first leaves, **(D)** maximum canopy diameter, **(E)** base diameter of the foliage at height **(C)**, **(F)** height of tree crown (**A-B**), and **(G)** height of tree base (**B-C**)),

6) the presence/absence of coppice stems,

7) the number of (a) aerial and (b) coppice stems, and

8) the height to which coppice stems have grown.

This approach was used in Chapter 6 to determine a leaf quantification equation applicable to mopane in the south-eastern lowveld of Zimbabwe. Using these equations (one for non-coppicing individuals and one for coppicing individuals), the estimation of leaf dry mass (LDM) of individual trees was possible. Leaf dry mass is an indicator of competitive ability with herbaceous vegetation for moisture because it is a descriptor of the evapotranspiration potential of the tree. Therefore, it was felt that effects of season of burning and type of fire on mopane would be best interpreted by the change in the competitive ability of the individual or population *i.e* change in leaf dry mass. This is by implication an indirect measure of the plant's competitive ability, and should be viewed more as an indicator of potential change in competitive ability. The mean relationship between leaf volume and leaf dry mass for mopane is 1:0.519 (Smit 1994).

2) Fire intensity data

During the two days prior to burning the following parameters were recorded:

i) fuel load (100 disc pasture meter readings per area)

ii) fuel moisture (25 $1m^2$ grass samples cut, dried and weighed per area)

During the burning of each area, the following parameters were recorded five times during the burning event:

i) ambient temperature (°C)

ii) relative humidity (%, with a whirling psychrometer)

iii) wind speed ($m.s^{-1}$, with a wind anemometer or talcum powder drift speed)

iv) rate of spread ($m.s^{-1}$, time taken for flame front to cover distance between two poles 5 m apart).

A fire intensity formula was developed by Byram (1959) to estimate fire intensity of surface head and back fires. The formula for predicting fire intensity is:

$$\mathbf{I = H*w*r}$$

Where: I = fire intensity ($kJ.s^{-1}.m^{-1}$)
H = heat yield ($kJ.kg^{-1}$)
w = mass of available fuel ($kg.m^{-2}$)
r = rate of spread of the fire front ($m.s^{-1}$)

For the burning treatments fire intensity was estimated using the heat yield values (Byram 1959) and the fuel load and rate of spread values collected.

3) Burning

Early dry season burns were carried out in June 1997, mid dry season burns in September 1996 and late dry season burns in November 1997. Each treatment block was burnt in a day. Burning began when environmental conditions were most conducive to achieving intense and effective fires. Roads were used as fire-breaks, with a back fire put in first to act as a further protective measure. Once this back fire was in place, a head fire was set along the windward side of the block. By using this approach, the safety of the burning exercise, as well as the objective of achieving both head and back fires was met. Control areas were not burnt.

4) End-of-season data

The same individuals that were recorded during base-line data collection, were monitored to ascertain plant responses to treatments. Early and mid dry season (E and M), as well as control (C97) areas were monitored in May 1997, and late dry season (L) and control (C98) areas in April 1998.

The change in any particular parameter was determined by calculating the absolute difference between the base-line and end-of-season values. Comparisons between burning treatments and controls, as well as across treatments, were carried out. Due to the temporal variation inherent in the data (as a result of different years and times of treatment application) the following changes and comparisons against controls for the three treatment seasons were possible (Table 7.2).

Table 7.2 Collection of data for different seasons of burning

(E early, M mid, L late dry season, and C control)

	Early	Mid	Late
Base-line	E96	M96	L97
End-of-season	E98	M97	L98
Control	C98-C96	C97-C96	C98-C97

5) Analysis of data

Analysis of variance (Genstat 5.41) was carried out to test for the effects of season of burning, type of fire and height class on fire intensity, stem diameter and percentage topkill. Analysis of covariance (Genstat 5.41) was carried out to test for the effects of the same variables on the changes in tree density, as well as an attempt to accommodate the influence of initial tree density. For these analyses comparisons were made across treatments *i.e* tests between the three seasons of burning (early, mid and late dry season), two types of fire (head and back fire) and four height classes, including interactions. Owing to the unbalanced nature of the data set (*i.e* an unequal number of replications between controls and treatments) conventional analysis of variance techniques could not be employed. The residual maximum likelihood (REML) method was used (Genstat 5.41) where the estimation of variance components is possible. The

REML algorithm estimates the treatment effects and variance components in a linear mixed model (i.e a linear model with both fixed and random effects). Unlike regression, it can account for more than one source of variation in the data. This approach was taken to test for significant differences between seasons and types of fire, for each of the three parameters. REML analysis was undertaken to test for significant differences between seasons and types of fire for changes in tree height, number of stems, maximum canopy diameter and leaf dry mass. Comparisons across seasons, and against the control treatments were carried out. It is assumed that the control treatments, owing to them not being burnt, are an effective control, and comparisons between burning treatments and control treatments would give an accurate analysis of burning treatment effects.

Note

The environmental conditions, burning parameters, fire intensities and percentage occurrence of mopane in the treatment areas are presented. These give an insight into the potential damage, and therefore potential change, that the burning treatments incurred. The effect of season of burning and type of fire on stem diameter (at 25 cm above ground level) and percentage topkill are also presented. These parameters were only measured in April 1998, not having been measured during the base-line collection period, and therefore no analysis of change is possible. However, differences were investigated for the sake of completeness.

It must be remembered that the results gained from the tests for significant differences between season of burn and type of fire, for stem diameter and percentage topkill cannot be taken as true effects of treatments. The "once-off" nature of the treatment applications do not allow for long-term prediction or appreciation of past treatments. Significant differences in stem diameter or percentage topkill may reflect the inherent variation in the population, rather than variation due to treatments. However if the percentage topkill in the control areas was significantly lower than in the treatment areas, then the extent of topkill in the treatment areas could well be ascribed to treatment effects.

Results

1) Species composition of treatment areas

The treatment areas were all dominated by mopane (Table 7.3).

Table 7.3 Mean percentage occurrence of mopane per treatment area

Treatment	% Mopane
Early Back	85.6
Early Head	69.4
Mid Back	87.8
Mid Head	82.2
Late Back	63.6
Late Head	64.4
Controls	77.4
Overall	75.8

Other woody species that occured in the treatment areas are listed (Table 7.4):

Table 7.4 Additional tree species occurring in the treatment areas of Malilangwe Estate

Combretum imberbe	*Pterocarpus brenanii*
Combretum apiculatum	*Peltophorum africanum*
Lonchocarpus capassa	*Dichrostachys cinerea*
Newtonia hildebrandtii	*Dalbergia melanoxylon*
Grewia bicolor	*Grewia flavescens*
Dovyalis longispina	*Grewia villosa*
Ormocarpum trichocarpum	*Flueggea virrosa*
Acacia nigrescens	*Balanites aegyptiaca*
Lannea schweinfurthii	*Rhus dentata*

2) Fire parameters and fire intensities of burning treatments

The fire parameters, and fire intensities, of the treatment burns are presented in Table 7.5.

Table 7.5 Mean (±S.E.) of fuel load, rate of spread and fire intensity, and heat yield values (Byram 1959) for season of burning and type of fire treatments in mopane woodlands (degrees of freedom = 2 for each treatment)

Treatment	Fuel load ($kg.m^{-2}$)	Rate of spread ($m.s^{-1}$)	Heat yield ($kJ.kg^{-1}$)	Fire intensity ($kJ.s^{-1}.m^{-1}$)
Early Back	0.23 (0.01)	0.04 (0.05)	17 781	153 (176.7)
Early Head	0.23 (0.02)	0.49 (0.56)	16 890	1833 (2019.8)
Mid Back	0.11 (0.01)	0.02 (0.01)	17 781	30 (15.3)
Mid Head	0.11 (0.01)	0.41 (0.36)	16 890	378 (63.1)
Late Back	0.20 (0.01)	0.06 (0.05)	17 781	236 (158.3)
Late Head	0.24 (0.01)	0.40 (0.37)	16 890	1585 (1408.9)

Table 7.6 (a) Analysis of variance of season of burning and type of fire on fire intensities of the treatment areas

Variate: Fire intensity

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Season	2	2256964	1128482	1.11	0.363
Type	1	5700826	5700826	5.58	0.036
Season.Type	2	1443081	721540	0.71	0.513
Residual	12	12250275	1020856		
Total	17	21651146			

(b) LSD-tests

Type	Mean	Comparisons LSD(0.05) 1037.8
Head fire	1265	a
Back fire	140	b

(Read comparisons down columns, types of fire with letters in common are not significantly different)

It is evident that the fire intensities of the treatment burns implemented in different seasons were not significantly different (Table 7.6). The effect of type of fire was significant however, with head fires being more intense than back fires, over all seasons. This difference was very large, with head fires being almost ten times more intense than back fires.

3) Effect of treatment on stem diameter

Table 7.7 Analysis of variance of season of burning and type of fire on stem diameter (cm) of the treatment areas

Variate: Stem diameter

Source of variation	d.f.	S.S.	M.S.	V.r.	F pr.
Season	3	185.24	61.75	10.6	<0.001
Type	2	2.14	1.07	0.18	0.833
Height class	3	2305.48	768.5	132.0	<0.001
Season.Type	1	23.25	23.25	3.99	0.05
Season.Height class	9	138.2	15.36	2.64	0.01
Type.Height class	6	0.93	0.15	0.03	1.00
Season.Type. Height class	3	98.06	32.69	5.61	0.002
Residual	68	395.98	5.82		
Total	95	3149.27			

There were no significant differences between type of fire for stem diameter at 25 cm. The other two main effects, season and height class, were highly significant. The interaction effects were all significant at the 5% level, except the type-height class interaction. The interactions are presented in Figures 7.1 and 7.2.

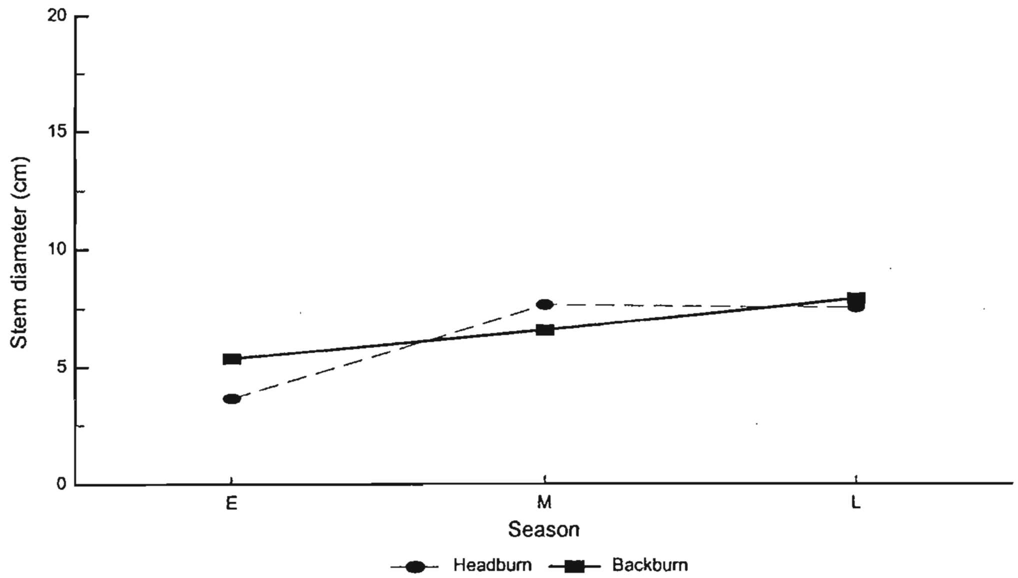

Figure 7.1 Mean stem diameter (cm) at 25 cm above ground level, for season and type of fire, for (E) early, (M) mid, and (L) late dry season burns.

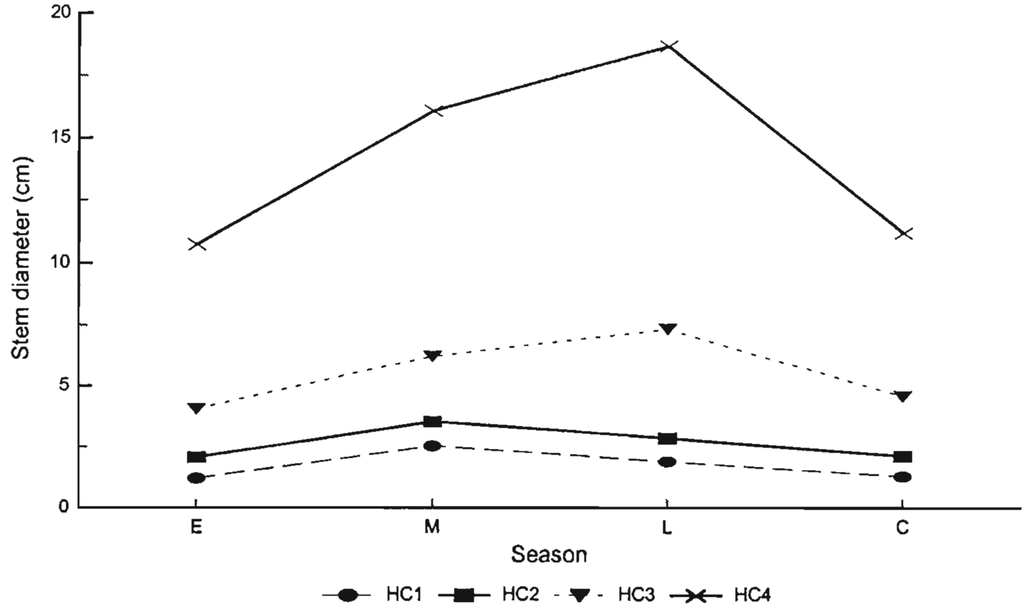

Figure 7.2 Mean stem diameter (cm) at 25 cm above ground level, for season and height class (HC), for (E) early, (M) mid, (L) late dry season burns and (C) control; HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

The season-type-height class interaction is highly significant, indicating that the third order interaction of the three variables is more significant than the second order interactions. The interaction effects give insight into the direction and/or magnitude of levels of season, type and height class as they affect each other at respective levels of the other. The stem diameter of trees headburnt in the early and mid dry season are smaller than those backburnt in the same seasons. The stem diameter of trees headburnt in mid dry season are greater than trees in backburnt areas. This might indicate that head fires in the early and late dry seasons (the two seasons with the highest fire intensities, Table 7.4 b) impacted the trees in such a manner that increase in stem diameter was reduced.

The effect of season of burning on stem diameter is more pronounced on larger trees (Figure 7.2). Trees in areas burnt during the mid and late dry seasons had greater stem diameters than trees burnt in the early dry season, or not at all. This trend was similar for all height classes.

4) Effect of treatment on percentage topkill

Analysis of variance of treatment effects are presented in Table 7.8.

Table 7.8 (a) Analysis of variance of season of burning and type of fire on percentage topkill of the treatment areas

Variate: Percentage Topkill

Source of variation	d.f.	S.s.	M.s.	V.r.	F pr.
Season	2	2853.3	1426.7	4.21	0.021
Type	1	1345.1	1345.1	3.97	0.052
Height class	3	58186.5	19395.5	57.17	<0.001
Season.Type	2	446.2	223.1	0.66	0.523
Season.Height class	6	2927.3	487.9	1.44	0.220
Type.Height class	3	1339.3	446.4	1.32	0.280
Season.Type. Height class	6	788.5	131.4	0.39	0.883
Residual	48	16283.2	339.2		
Total	71	84169.4			

(b) Means and 95% Confidence Limits for percentage topkill of season of burn, type of fire and height class

Season

	Early	Mid	Late
Upper	53.8	59.0	69.0
Mean	**43.0**	**48.2**	**58.2**
Lower	32.3	37.5	47.5

Type

	Back fire	Head fire
Upper	54.27	62.87
Mean	**45.50**	**54.10**
Lower	36.73	45.33

Height class

	HC1	HC2	HC3	HC4
Upper	86.2	88.1	56.3	18.1
Mean	**73.8**	**75.7**	**43.9**	**5.7**
Lower	61.4	63.3	31.5	-6.7

Height classes
HC1 0-50 cm
HC2 51-150 cm
HC3 151-350 cm
HC4 >351 cm

These results are presented graphically in Figures 7.3 to 7.5.

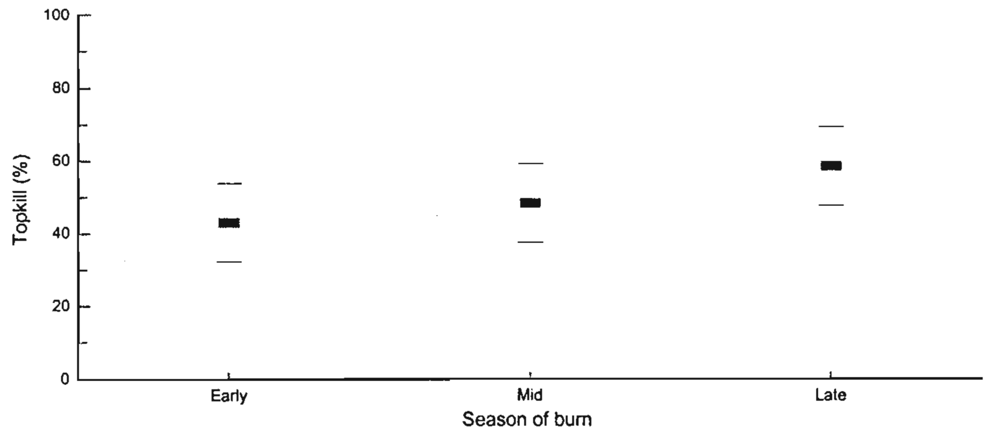

Figure 7.3 Mean percentage topkill for season of burning (±95% Confidence Limits).

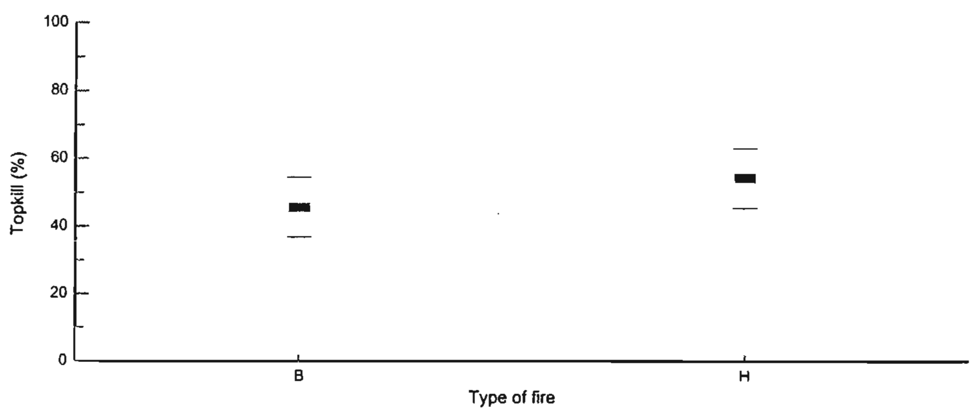

Figure 7.4 Mean percentage topkill for type of fire (±95% Confidence Limits).

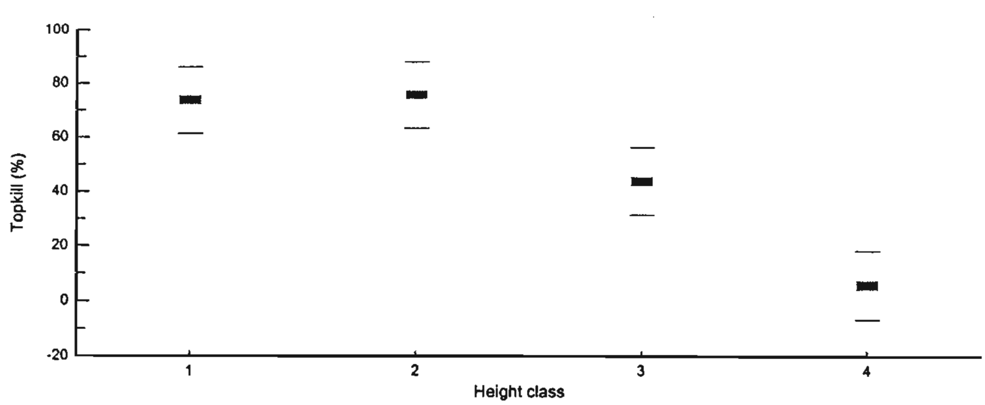

Figure 7.5 Mean percentage topkill for height classes (±95% Confidence Limits), HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

From the analysis of variance it is evident that there are significant differences between the three seasons of burning, between head and back burns and between height classes (Table 7.8a). Percentage topkill after late dry season burns is significantly higher than topkill after early dry season burns, by an average of 15.2%. There is no significant difference between mid and late dry season burns (Table 7.8 b). Topkill in areas burnt as a head fire experienced significantly higher levels of topkill, at the 6% level, with head fires having on average 8.6% more topkill (Figure 7.4). Height class 3 and 4 (43.9% and 5.7%) experienced significantly less topkill than height classes 1 and 2 (73.8% and 75.7%), while height class 2 was not significantly different to class 1. Height classes 2, 3 and 4 are significantly different to each other (Figure 7.5). The interaction effects are all non significant.

5) Effect of treatment on tree density

The population response to burning is presented as the change in population density *i.e* the absolute change in the number of individuals, on a per hectare basis. This is presented in Table 7.9.

Table 7.9 Mean initial population density, mean change in number of individuals and mean percentage change for the burning treatments on Malilangwe Estate

Treatment	Mean initial density (ha^{-1})	Mean change (ha^{-1})	Mean percentage change (%)
Early Back	4750.0	216.7	4.6
Early Head	3500.0	316.7	9.1
Mid Back	4141.7	66.7	1.6
Mid Head	4683.3	91.7	2.0
Late Back	2683.2	33.3	1.2
Late Head	2458.3	266.7	10.9

All burning treatments showed a nett recruitment of individuals, rather than a nett loss of individuals. Covariance analysis (Genstat 5.41) was carried out in an attempt to factor out the influence of initial population density, and thereafter determine whether season of burning, type of fire and height class had an effect on tree density.

Table 7.10 Analysis of covariance of season of burning, type of fire and height class on change in tree density (initial population density as covariate)

Variate: Change in tree density

Source of variation	d.f.	S.S.	M.S.	F.	P.
Season	2	4.34E+06	2.17E+06	1.93	0.157
Type	1	1.17E+04	1.17E+04	0.01	0.919
Height class	3	4.94E+07	1.64E+07	14.63	<0.001
Season.Type	2	1.36E+05	6.79E+04	0.06	0.941
Season.Height class	6	1.64E+07	2.73E+06	2.42	0.040
Type.Height class	3	3.98E+06	1.32E+06	1.18	0.328
Season.Type Height class	6	6.61E+06	1.10E+06	0.98	0.450
Covariate	1	2.47E+06	2.47E+06	2.20	0.415
Residual	47	5.29E+07	1.13E+06		
Total	71	1.75E+08			

There is no significant difference between the burning treatments (season or type of fire). The only significant main effect was height class. Burning had no impact on the recruitment or loss of individuals after one burning event, irrespective of season of burn or type of fire. The season-height class interaction was significant (Figure 7.6).

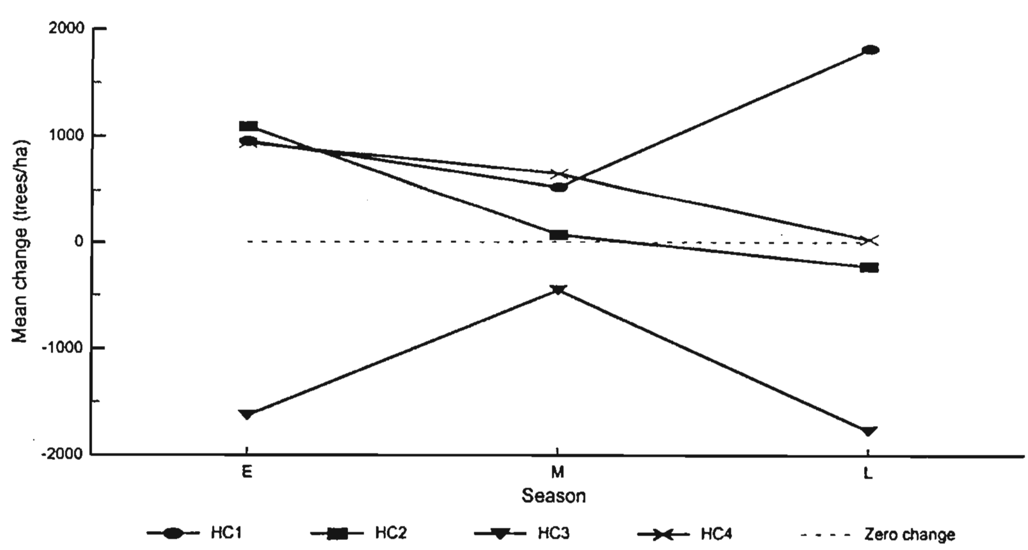

Figure 7.6 Mean change in density of trees, for season of burning and height class, for (E) early, (M) mid, and (L) late dry season burns; HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

For all seasons of burning, there was an increase in the number of individuals in height classes one and four (Figure 7.6). In height class one, high intensity burns (late dry season) led to the largest increase in individuals, whereas early and mid dry season burns led to smaller increases in tree density. In height class two only early and mid dry season burns led to an increase in tree density, whereas late dry season burns led to a decrease in tree density. For all seasons of burning height class three experienced a decrease in tree density. Late and early dry season burns (the two highest intensity burns) led to the largest decrease, while mid dry season burns did not experience such dramatic decreases in tree density. For all seasons of burning height class four experienced an increase in tree density, with late dry season burns having very little change, but mid and early dry season burns increasing. Height class one (0-50 cm) and three (151-350 cm) are impacted most by fire, height class two (51-150 cm) and four (>351 cm) less markedly. Late dry season burns led to the largest increase in height class one, but the largest decrease in height class three. Mid dry season burns led to the least change in these two height classes, while early dry season burns showed the same trends as late dry season burns.

6) Structural response of individuals to season of burn and type of fire

The change in the following three parameters were chosen as being of ecological and physiological value, and therefore good indicators of effects of season and type of fire on mopane woodland:

1) change in tree height,
2) change in the number of stems, and
3) change in the maximum canopy diameter.

For each parameter the base-line and end-of-season data were used to calculate the change in the particular parameter under investigation. Analysis of this change was then undertaken to determine whether season of burning, type of fire or interactions thereof were significant.

1) Change in tree height

Results of REML analysis are presented in Table 7.11.

Table 7.11 (a) Wald test for treatment effects, degrees of freedom and significance of change in tree height (cm)

Term	Wald statistic	d.f.	Significance
Treatment	46.9	2	P<0.001

(b) Mean change in tree height (cm), including 95% Confidence Limits

Early			
	Control	Early Back	Early Head
Upper	39.14	32.43	17.48
Mean	**18.07**	**11.36**	**-3.590**
Lower	-3.000	-9.710	-24.66
Mid			
	Control	Mid Back	Mid Head
Upper	27.14	14.11	11.67
Mean	**7.271**	**-5.759**	**-8.203**
Lower	-12.60	-25.63	-28.07
Late			
	Control	Late Back	Late Head
Upper	19.12	0.220	-6.060
Mean	**11.61**	**-7.290**	**-13.57**
Lower	4.100	-14.80	-21.08

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	0.62	P>0.5
Control vs. Early Head	2.01	P<0.05
Control vs. Mid Back	1.29	P<0.2
Control vs. Mid Head	1.53	P<0.2
Control vs. Late Back	4.92	P<0.001
Control vs. Late Head	6.57	P<0.001
Early Back vs. Early Head	1.39	P<0.2
Mid Back vs. Mid Head	0.24	P>0.5
Late Back vs. Late Head	1.64	P<0.2

These results are graphically presented in Figures 7.7 to 7.10.

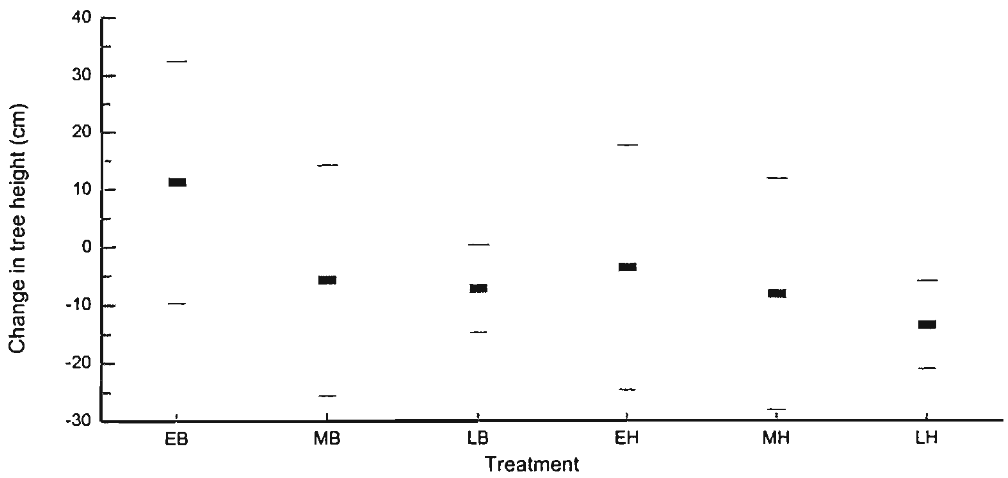

Figure 7.7 Mean change in tree height (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late and B back fire, H head fire) and length of monitoring periods (Figure 4.4).

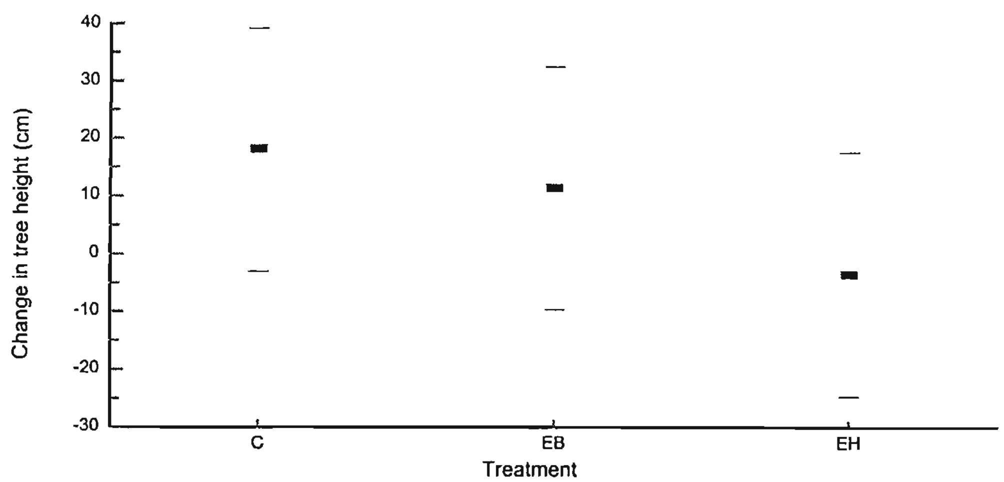

Figure 7.8 Mean change in tree height for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

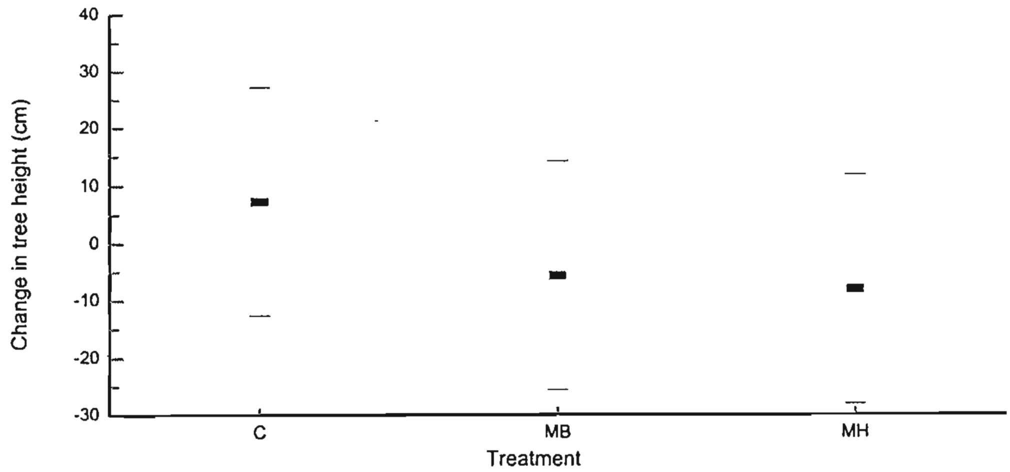

Figure 7.9 Mean change in tree height for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

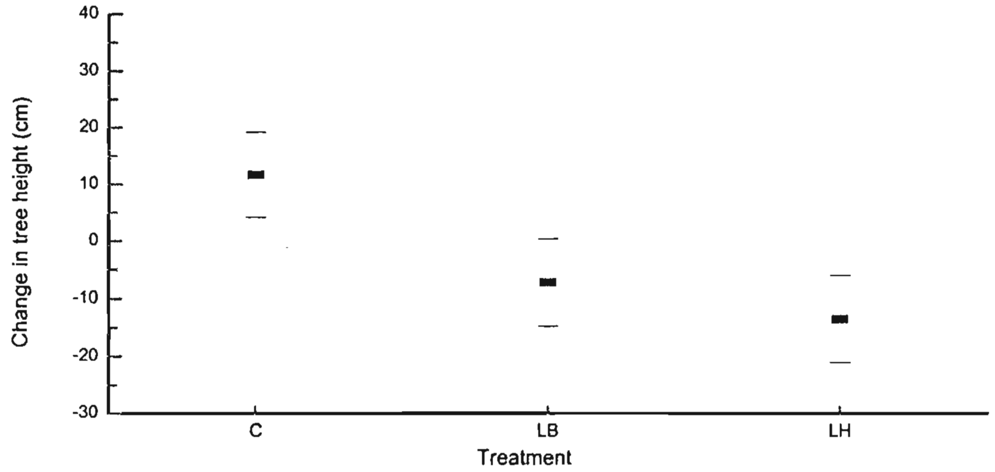

Figure 7.10 Mean change in tree height for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The change in tree height for treatments was significant ($P<0.001$). For all seasons there was a mean increase in tree height in the control areas. In contrast to this, only the early back fires led to an increase in tree height (Table 7.11b). Early head fires resulted in a significant reduction in tree height, while early back fires were not significantly different. This can be attributed to the very high fire intensities attained during the early dry season head fires (Table 7.5). There was no significant difference between the mid dry season burns and the control, nor between the two types of fire. Notably however, the mid season burning treatments both led to a reduction in tree height, even though low fire intensities were recorded. For late dry season burns there was no significant difference between the two types, but trees in the control area showed a significant increase in height, whereas the treatment trees were reduced in height.

2) Change in number of stems

Results of REML analysis are presented in Table 7.12.

Table 7.12 (a) Wald test for treatment effects, degrees of freedom and significance of change in number of stems per tree

Term	Wald statistic	d.f.	Significance
Treatment	159.2	2	P<0.001

(b) Mean change in number of stems per tree, including 95% Confidence Limits

Early	Control	Early Back	Early Head
Upper	0.562	1.468	2.186
Mean	**-0.098**	**0.808**	**1.526**
Lower	-0.758	0.148	0.866

Mid	Control	Mid Back	Mid Head
Upper	1.023	3.799	3.554
Mean	**0.133**	**2.909**	**2.664**
Lower	-0.757	2.019	1.774

Late	Control	Late Back	Late Head
Upper	0.178	2.073	2.474
Mean	**-0.222**	**1.673**	**2.074**
Lower	-0.622	1.273	1.674

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	-2.69	P<0.01
Control vs. Early Head	-4.83	P<0.001
Control vs. Mid Back	-6.10	P<0.001
Control vs. Mid Head	-5.56	P<0.001
Control vs. Late Back	-9.27	P<0.001
Control vs. Late Head	-11.23	P<0.001
Early Back vs. Early Head	-2.13	P<0.05
Mid Back vs. Mid Head	0.54	P>0.5
Late Back vs. Late Head	-1.97	P<0.05

These results are presented in Figures 7.11 to 7.14.

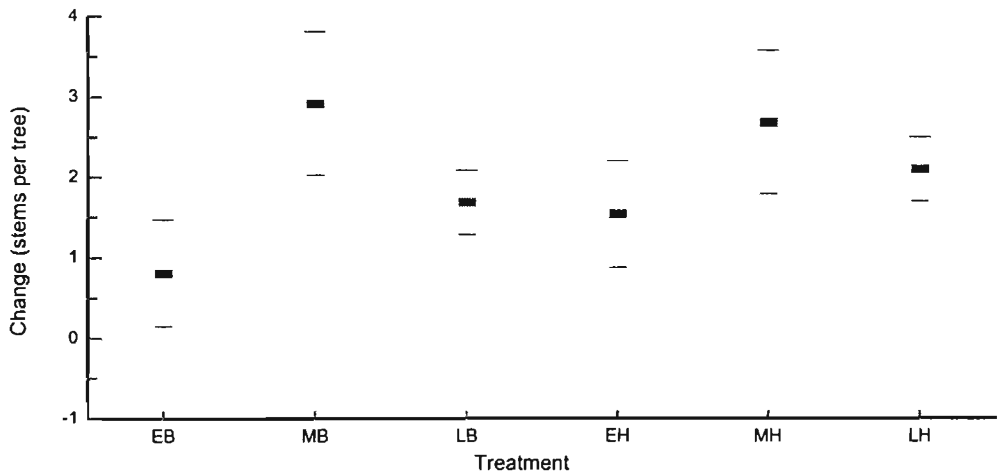

Figure 7.11 Mean change in number of stems per tree (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

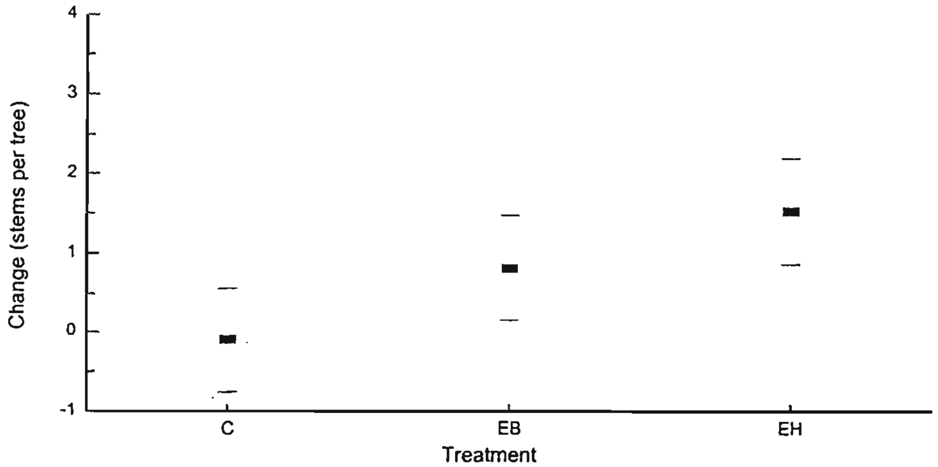

Figure 7.12 Mean change in number of stems per tree for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

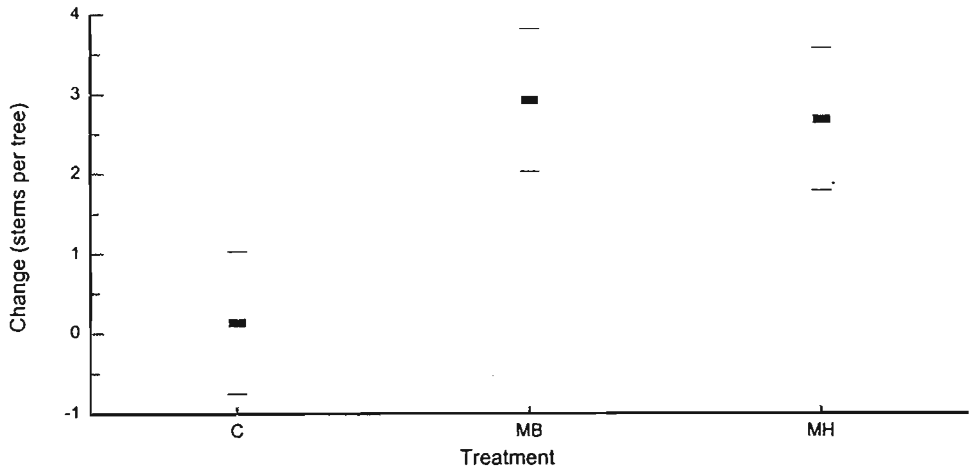

Figure 7.13 Mean change in number of stems per tree for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

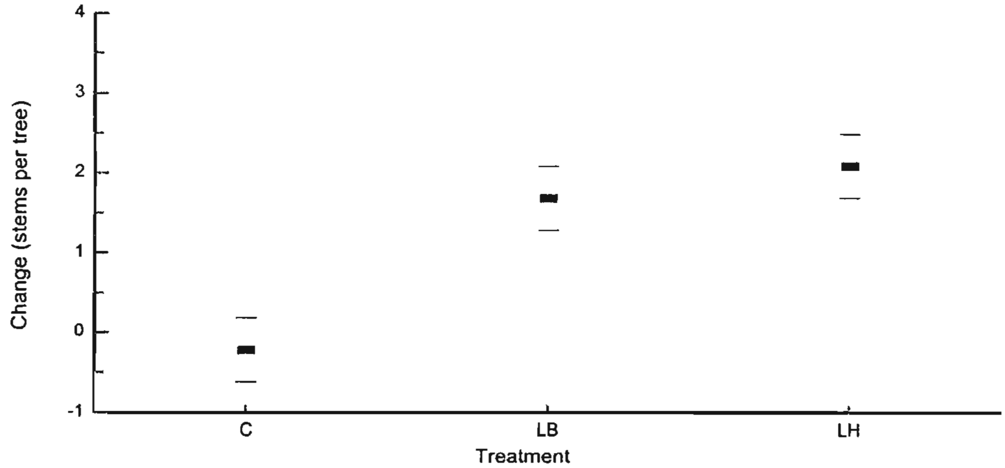

Figure 7.14 Mean change in number of stems per tree for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The effect of treatment was significant ($P<0.001$). In comparison with the control treatment, all burning treatments had a significantly greater increase in number of stems per tree. For early and late dry season treatments the control area showed a reduction in the number of stems. Both head and back fires in the early dry season led to a significant increase in the number of stems, whereas the control area had a reduction in the number of stems. This result also applied to the mid and late dry season burns. Early head fires had a significantly greater increase in number of stems than back fires, this being in response to the higher fire intensities attained by the head fires. For mid dry season burns there was no significant difference between types of fire. Late dry season head fires also had a significantly greater number of stems, than trees in back fire treatments. For late dry season burns there was a significantly greater number of stems as a result of coppicing in response to head fires, than back fires. Mid season back and head fires led to the largest increase in the number of stems, whereas early dry season burns had the lowest increase in stems (Figure 7.10). This trend (Figure 7.11) would indicate that, for intense fires, head fires lead to a greater increase in coppicing stems than do back fires, but that high intensity fires (early and late dry season) lead to a smaller increase in number of stems than low intensity fires (mid dry season).

3) Change in maximum canopy diameter

Results of REML analysis are presented in Table 7.13.

Table 7.13 (a) Wald test for treatment effects, degrees of freedom and significance of change in maximum canopy diameter (cm)

Term	Wald statistic	d.f.	Significance
Treatment	42.4	2	P<0.001

(b) Mean change in maximum canopy diameter (cm), including 95% Confidence Limits

Early			
	Control	Early Back	Early Head
Upper	30.57	11.92	8.05
Mean	**15.91**	**-2.743**	**-6.61**
Lower	1.249	-17.40	-21.3
Mid			
	Control	Mid Back	Mid Head
Upper	18.8	-6.64	-12.45
Mean	**5.34**	**-20.1**	**-25.94**
Lower	-8.15	-33.6	-39.43
Late			
	Control	Late Back	Late Head
Upper	17.77	0.279	-4.23
Mean	**10.45**	**-7.041**	**-11.5**
Lower	3.134	-14.36	-18.9

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	2.49	P<0.02
Control vs. Early Head	3.01	P<0.01
Control vs. Mid Back	3.70	P<0.001
Control vs. Mid Head	4.55	P<0.001
Control vs. Late Back	4.68	P<0.001
Control vs. Late Head	5.89	P<0.001
Early Back vs. Early Head	0.52	P>0.5
Mid Back vs. Mid Head	0.84	P<0.5
Late Back vs. Late Head	1.21	P<0.3

These results are graphically presented in Figures 7.15 to 7.18.

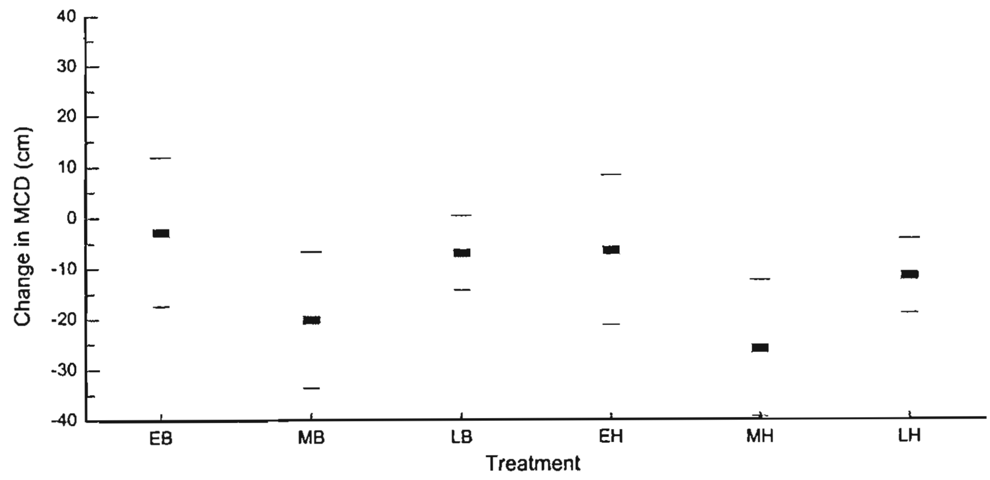

Figure 7.15 Mean change in maximum canopy diameter (MCD) (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

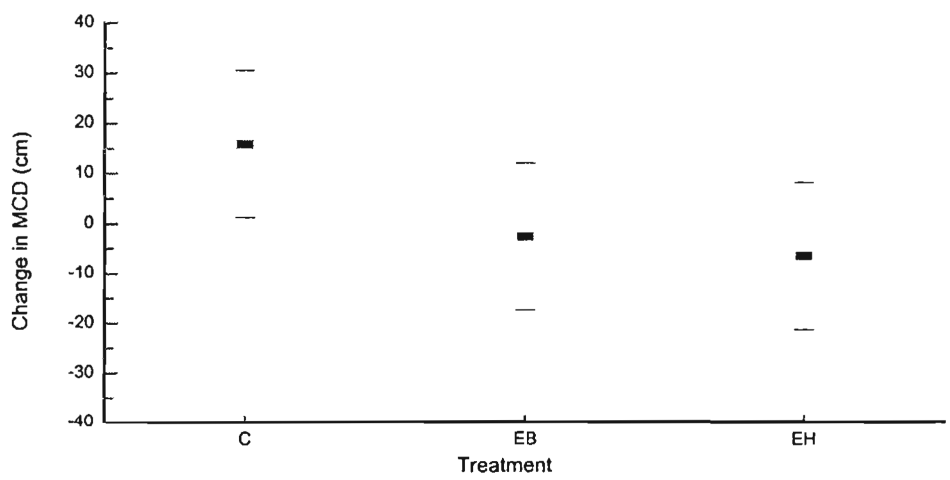

Figure 7.16 Mean change in maximum canopy diameter (MCD) for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

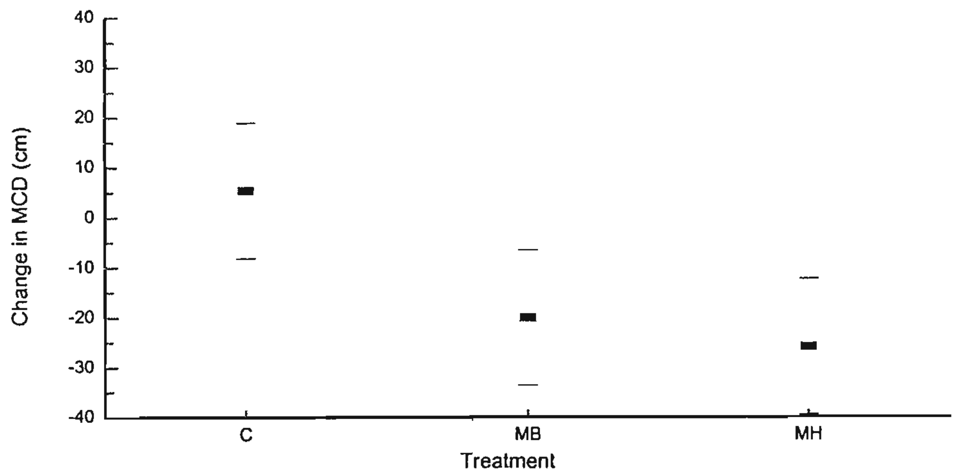

Figure 7.17 Mean change in maximum canopy diameter (MCD) for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

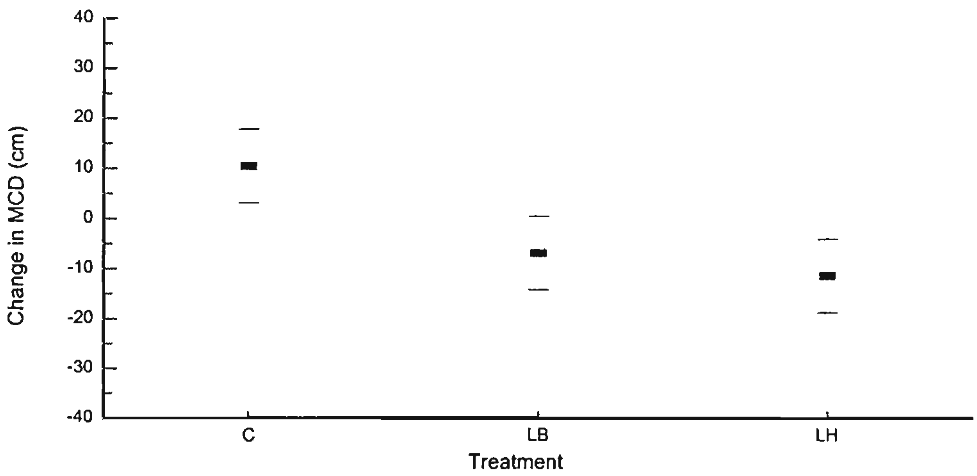

Figure 7.18 Mean change in maximum canopy diameter (MCD) for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

Treatment effects were significant ($P<0.001$). Early dry season burns led to a significant reduction in MCD, whereas the control area had an increase in MCD. The same trend was found for mid and late dry season burns. There were no significant differences between head and back fires for any season. For both head and back fires, the mid dry season treatment led to a significantly greater reduction in MCD than either early or late burns (Figure 7.14).

7) Effect of treatment on leaf dry mass

The equations developed in Chapter 5, for estimating leaf dry mass of mopane individuals using the estimated spatial canopy volume, were used to calculate the leaf dry mass of mopane individuals.

Results of REML analysis are presented in Table 7.14.

Table 7.14 (a) Wald test for treatment effects, degrees of freedom and significance of change in leaf dry mass (kg)

Term	Wald statistic	d.f.	Significance
Treatment	57.3	2	P<0.001

(b) Mean change in leaf dry mass (kg) including 95% Confidence Limits

Early			
	Control	Early Back	Early Head
Upper	0.345	-0.02	-0.03
Mean	**0.195**	**-0.17**	**-0.18**
Lower	0.045	-0.32	-0.33
Mid			
	Control	Mid Back	Mid Head
Upper	0.174	-0.08	-0.08
Mean	**0.014**	**-0.24**	**-0.24**
Lower	-0.146	-0.40	-0.40
Late			
	Control	Late Back	Late Head
Upper	0.3598	-0.0246	-0.2759
Mean	**0.1798**	**-0.2046**	**-0.4559**
Lower	-0.0002	-0.3846	-0.6359

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	4.67	P<0.001
Control vs. Early Head	4.83	P<0.001
Control vs. Mid Back	3.11	P<0.01
Control vs. Mid Head	3.11	P<0.01
Control vs. Late Back	4.15	P<0.001
Control vs. Late Head	6.86	P<0.001
Early Back vs. Early Head	-0.004	P>0.5
Mid Back vs. Mid Head	2.85	P<0.01
Late Back vs. Late Head	2.71	P<0.01

These results are graphically presented in Figures 7.19 to 7.22.

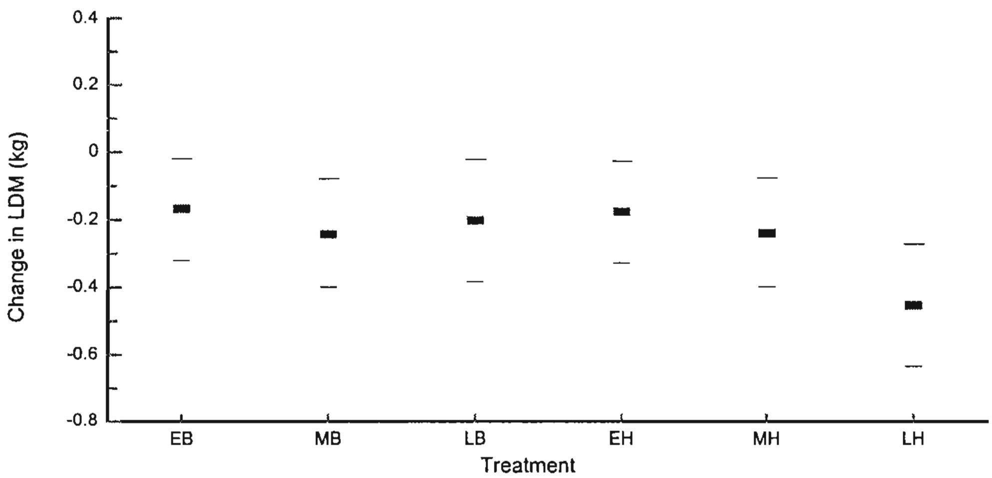

Figure 7.19 Mean change in leaf dry mass (LDM) (± standard error of the difference) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

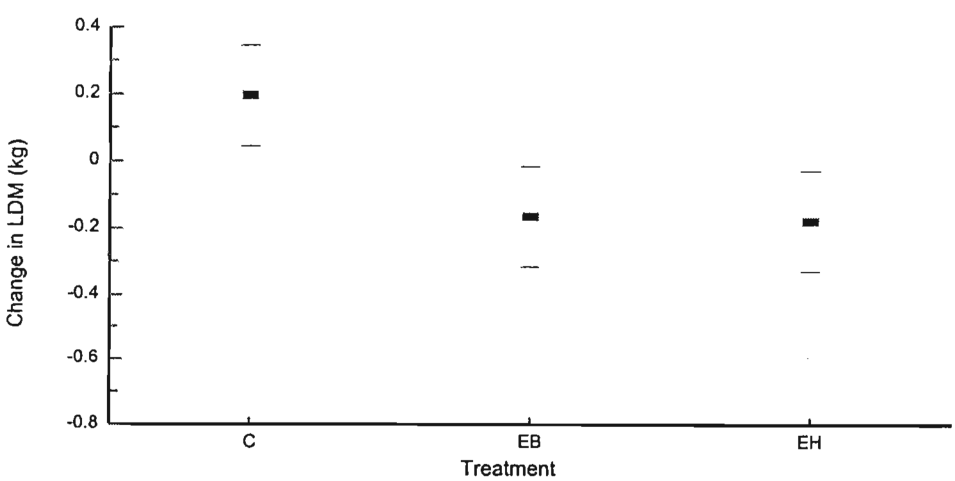

Figure 7.20 Mean change in leaf dry mass (LDM) for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

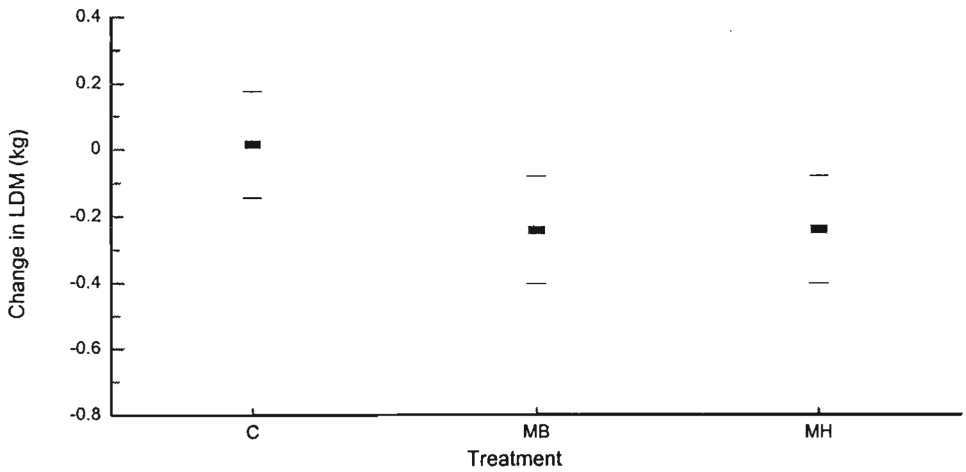

Figure 7.21 Mean change in leaf dry mass (LDM) for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

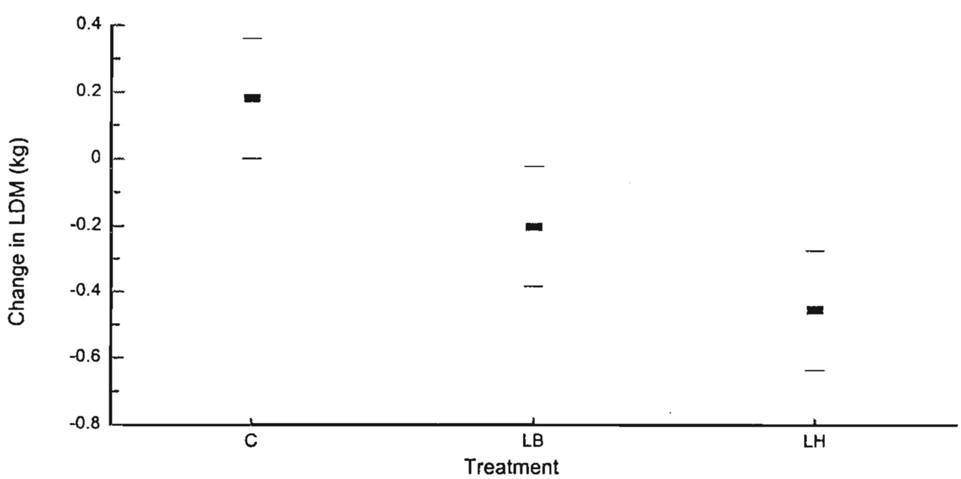

Figure 7.22 Mean change in leaf dry mass (LDM) for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The treatment effects were significant ($P<0.001$). All burning treatments resulted in a reduction in leaf dry mass, whereas control areas had an increase in LDM. There were no differences between the early, mid and late dry season back fire treatments. The late dry season back fires led to a significant decrease in LDM, compared to mid and early dry season treatments. Early, mid and late dry season burns (both back and head fires) were significantly different to the controls (Figures 7.20 to 7.22).

Discussion

There were no significant differences between fire intensities experienced in the three seasons of burning (Table 7.6). Head fires, in all seasons, were significantly more intense than back fires ($P<0.05$). This agrees with many other findings showing that, in general, savanna head fires are more intense than back fires (Trollope and Tainton 1986 and Trollope *et al.* 1996).

It is unfortunate that the analysis of the change in stem diameter (*i.e* post-burn compared with pre-burn) was not possible. The possible effect of burning treatments on stem diameter was therefore not possible, and the variability in stem diameter that is apparent in Figure 7.2 cannot be attributed to treatment effects. However it is not conceivable that changes in stem diameter will occur after only one burning treatment, but would require extended periods of treatment application.

The late dry season treatment led to the highest percentage topkill (58.2%), and was significantly higher than the early dry season treatment. This is in accordance with the fire intensity trend, where late dry season burns were more intense than the mid and early burns. This contrasts with the findings of West (1965) and Wade and Johansen (1986), who postulated that seasonal variations in tree physiology (phenophase) are critically important in determining the susceptibility of trees to fire. There are a number of covarying factors that contribute to determining the susceptibility of trees to fire. For a given fuel load, under early and late dry season conditions respectively, they predict that the percentage topkill after late dry season burns will be greater because of the difference in tree phenophase. However the variation in the susceptibility of a tree to fire is not only determined by the variation in tree phenophase, but by the environmental and specific tree conditions that occur. These covarying factors are extraneous to the tree, being determined primarily by the climate and nature of the standing crop (fuel). These factors include ambient temperature, relative humidity, wind speed, fuel load, fuel moisture and moisture content of the tree branch extremities, which together largely determine the degree of damage to the tree by fire. Head fires led to significantly more topkill, than back fires (Figure 7.4). This finding corroborates findings by other researchers (Trollope 1980, Stocks and Trollope 1993 and Trollope *et al.* 1996). Height classes one and two experienced the greatest topkill, 73.8% and 75.7% respectively (Figure 7.5). Damage to height class three and four was significantly lower (43.9% and 5.7% respectively). Trollope *et al.* (1995) found the same trend for the effect of height on topkill of bush subjected to a fire intensity of 3 000 $kJ.s^{-1}.m^{-1}$ (Figure 1.3). This fire intensity is higher than that experienced in this study, and therefore the percentage topkill was higher.

Fire does not significantly change the stand density within mopane woodlands. The same results were found for mopane in the Kruger National Park by Tainton *et al* (1991) and Trollope *et al.* (1996), for *Acacia spp* species in Hluhluwe Game Reserve (Macdonald 1980), in the Sengwa Wildlife Research Area (Guy 1981), for *Acacia spp* in the eastern Cape (Trollope 1974), and *Pinus palustris* woodlands in the southeastern United States (Glitzenstein *et al.* 1995). These findings repudiate the claims made by Scott (1966) that fire reduces bush density by killing seedlings of trees and shrubs. They also contrast with the high levels of mortality reported by Trapnell (1959) for *Brachystegia-Julbernardia* woodlands in northern Rhodesia, where percentage mortality in late-, early- and protected plots was 17.4%, 7% and 4.2% respectively. However these figures were from woodlands in which fire-sensitive species predominate, and where mopane did not occur. As with other savanna tree species however, mopane is very resistant to fire alone (Trollope *et al.* 1996), and may be particularly tolerant of fires regardless of when they occur. Nett recruitment of individuals took place in all treatment areas, as well as controls (mean change in density for burning treatments 4.9%). This change is almost twice as high as the increase in stand density reported by Guy (1981) of 2.5% for a two year period. This difference can be explained by the differences in elephant density: the two areas being of similar size (approximately 380 km^2), but the elephant density in the Sengwa Wildlife research Area being twice as high as that found on Malilangwe Estate.

This finding, that limited recruitment took place even in burnt areas, contradicts the assumption made by Lewis (1991) that the occurrence of fire would increase seedling mortality, as well as the finding by Macdonald (1980) that fire reduced post-fire seedlings.

Norton-Griffiths (1979) elucidates upon the synergistic relationship between elephants and fire, whereby elephants open up bush thickets and encourage the growth of grass within them, which fuels more intense fires that lead to a decrease in cover density (Buechner and Dawkins 1961). For mopane woodlands however this relationship is much weaker. Owing to its occurrence on shallow, xeric soils unfavourable to many grass species, the grass layer is generally scant, and high fuel loads such as those found in Murchison Falls National Park (Buechner and Dawkins 1961) are not attained (specific fuel loads are not given, but with annual rainfall of over 1 000 mm and a tropical climate, as well as descriptions of the grass sward, it is assumed that fuel loads are a lot greater). Therefore, even when elephants do open up bush thickets, the increase in grass production may not be sufficient to support fires of the intensity needed to kill mopane trees. This suggests that fire may have the same influence as herbivory *i.e* limiting the rate at which density increases. This agrees with the findings by Dublin (1986) that annual seedling mortality by elephants and fire were 4% respectively. It also suggests that there is no increase in herbivory in burnt areas, and that there is no interactive effect of fire and browsing in reducing mopane tree density in burnt areas. However this contrasts with later findings by Dublin (1995) that browsers showed a distinct preference for seedlings in burnt plots. If large browsers such as elephant, black rhino, eland; and small browsers such as steenbok and impala, were attracted to burnt (open) areas then it is possible that tree population density should decrease in these areas. However, this was not the case, and browsers vacated burnt areas and moved into adjoining unburnt areas, possibly in an attempt to find cover from predators (personal observations). This may well have been as a result of the size of the area burnt, as the burning treatments were relatively small in size, compared to the size of natural fires. Unfortunately no quantitative data were collected regarding animal densities in the burning treatments pre- and post-burning, and these are no more than speculation. This highlights the importance of the patch dynamics of fire, and supports a more *laissez faire* point ignition approach to management burning, which results in areas of residual grass cover, and protection from predators, within the larger burnt area. With high grazer/browser densities, and the simultaneous implementation of burning large blocks, animals may be forced into burnt areas, with the result that seedlings (< 50 cm) may be eradicated, leading to a situation where no recruitment takes place. For invasive species such as *Acacia borleae* and *Dichrostachys cinerea* this may be advantageous, but for other more sensitive, or threatened, species this may be disastrous, especially if this takes place over many years and the recruitment of successive cohorts is removed.

The only burning treatments that led to significant changes in tree height were the early head fires, and both types of late dry season burns, all of which led to decreases in tree height of 3.6 cm, 7.3 cm and 13.6 cm respectively (Table 7.11). This is as a result of the removal of leaf material through topkill, and these trends are the same as those found for the effect of topkill. Belsky (1984) showed that tree height was maintained, or reduced, by browsing and that fire had little additional effect, whereas Macdonald (1980) found that fire reduced the size of three *Acacia* species. With the exclusion of browsing and fire tree height increased significantly.

As with other woodland species, and found in other studies (Dublin 1995), mopane coppices profusely in response to burning. Fire in all seasons, and using both types of burning, led to an increase in the number of stems (Table 7.12). Mid dry season burns led to the greatest increase in number of stems. This is interesting as it suggests that low intensity fires (below 1 000 $kJ.s^{-1}.m^{-1}$) led to a significant increase in the number of stems, while early and late dry season burns (fire intensities greater than 1 000 $kJ.s^{-1}.m^{-1}$), led to significantly smaller changes in the number of stems. Also, for the treatments experiencing high fire intensities (early and late dry season) the head fires led to significantly more coppice stems than back fires. If this profuse coppicing, induced by burning, can be subjected to high levels of browsing pressure, then fire can be effective in bush control (Trollope 1974), and the shrub structure may be modified. Like the major portion of southern African savannas (Trollope 1980), this semi-arid area is characterised by rainfall which is too low and unreliable to enable adequate grass material to accumulate and support frequent fires, that can burn the coppice growth and control seedlings. It is also likely that repeated, intense, fires of over 1 000 $kJ.s^{-1}.m^{-1}$will result in less profuse coppiccing, and the development of a more single-stemmed woodland population. The difficulty in this is that the potential for repeated, intense, fires is limited in these areas because of the environmental and soil characteristics that have led to the establishment of mopane, and therefore the occurrence of mopane shrubveld is inevitable, and cannot be altered by fire.

All burning treatments led to significant decreases in canopy diameter, whereas the control treatments all had increased canopy diameters (Table 7.13). This shows that burning, of any type and within any season, leads to a reduction in canopy diameter *i.e* a change in structure. As with changes in tree height, this response is also a reflection of the topkill experienced by trees during fires. Tainton et al. (1991) found the same results in the Kruger National Park, as well as van Wyk (1972) and West (1958) in Rhodesia. Mid dry season burns led to the largest decrease, followed in magnitude by the early and late head fires (Figure 7.15). Even though the mid dry season burns had the lowest fire intensity, the decrease in maximum canopy diameter is the greatest. This suggests that there is another, unrecorded, variable that is leading to this change. The inverse relationship between the increase in the number of stems and the decrease in canopy diameter of trees in the low intensity mid dry season burns can be explained in two ways:

1) Mid dry season burns result in the largest increase in number of stems, and it is this investment in additional stem growth that may lead to the canopy diameter decreasing at the expense of this investment in stems *i.e* the canopy diameter of the plant producing the most new coppice stems will decrease the most.
2) Alternatively, the photosynthetic requirements of the plant that coppices profusely are now partially met by the new coppice stems, and therefore canopy diameter can decrease as the total photosynthetic requirements are still being met. These constraints and tradeoffs have been identified in many terrestrial plants, and it is these allocation-based tradeoffs (Tilman 1990) that led to reductions in canopy diameter and canopy volume in mopane individuals. Fire and herbivory are major environmental constraints that impact the plant, and the tradeoffs that plants face in dealing with these constraints are directly attributable to differences in biomass and nutrient allocation patterns (Tilman 1990).

All seasons and types of fire led to significant decreases in leaf dry mass, whereas the control treatments increased in leaf dry mass (Table 7.14). The mean change in leaf dry mass per tree for all treatments was -0.122 kg. Although the number of stems increases in response to burning, the leaf biomass declines. This suggests that the attempt by the plant to invest in additional stem growth, in marginalising the damage incurred by fire, is not adequate, and that although there are more stems, the leaf dry mass decreases. This is an expense to the plant, and one that may impact the plants longevity over time. Guy (1981) found that biomass in mopane woodland decreased by 6%. This was also under conditions of elephant and fire damage, but at greater elephant densities. For back fires, there was no significant difference between seasons, but for head fires the late dry season burns led to a significantly greater decrease in leaf dry mass than the other two seasons (Figure 7.19). This lends quantitative support to the field observations made by Trollope *et al.* (1996) that head fires cause higher topkill of stems and branches as compared to back fires. In contrast to the effect of treatments on the change in number of stems and MCD, the change in leaf dry mass would appear to be most pronounced after high intensity fires, such as those of the late dry season head fires ($>$1 500 $kJ.s^{-1}.m^{-1}$). This suggests that, as found by Glitzenstein (1995) and Trollope *et al.* (1996), variation in fire behaviour (intensity or temperature) may be much more important than season of burning, in predicting population dynamics. The nature, behaviour and intensity of a fire is not determined by the season in which it occurs, but rather by the specific fuel load, fire regime and environmental conditions under which the fire takes place. Owing to this specificity of fire behaviour and fire intensity, and the resultant impacts on tree structure and physiology, the effects of season of burning are not predictable, nor valid in determining the effects of such fires. Rather the specific fuel load, fire intensity and fire behaviour data will be more valid in determining the effect of fire on mopane woodlands.

Chapter 8

General discussion and conclusions

As with the majority of other savanna tree species, mopane shows tremendous resilience and persistence throughout its range. This is borne out by the fact that over its range, mopane remains the dominant species and in some cases competitively excludes other trees and/or grasses. Under pressure from fire and herbivory this species shows continued resilience, through prolific basal and aerial coppicing, and emergence of new growth from underground rootstocks. In this the initial focus was on the standing crop dynamics of the grass sward in mopane vegetation, and thereafter the influence of burning during different seasons, and with different types of fires. After testing the hypotheses stated at the end of the literature review, the following was determined:

Answers to questions posed

Standing crop dynamics

One standard disc pasture meter calibration equation cannot suffice for estimating standing crop for the whole year, because of the large spatial and temporal variation in the grass sward. The standard procedure described by Bransby and Tainton (1977) is not applicable to savanna grass swards, but the revised procedure (Trollope and Potgieter 1986), with which disc height accounts for more than 90% of the variation in standing crop, is recommended. However, in order to account for the spatial variation in grass sward structure, specific calibration equations must be developed for homogenous vegetation units *eg*. mopane woodland.

Standing crop for a particular month is highly dependent on the effective rainfall from the previous month, and standing crop tracks effective rainfall closely. Peak standing crop is positively related to annual rainfall, and the potential peak standing crop can be predicted. After peak standing crop has been achieved standing crop declines through the dry season as effective rainfall decreases, and this decline in standing crop can be estimated using a decrease function.

Mopane leaf quantification

Two distinct equations were developed: one for coppicing individuals, and one for non-coppicing individuals. At certain canopy volumes these equations are different to the equations developed for mopane areas north of the Soutpansberg in South Africa, and the equations derived in this study are therefore recommended for estimating leaf dry mass in the south-eastern lowveld of Zimbabwe.

Season of burning

The effect of season of burning was not consistent over all the parameters investigated. There was no significant difference between the fire intensities of the fires implemented in the three seasons. There was also no seasonal burning effect on the change in tree density. However, the percentage topkill between different seasons was highly significant, with late dry season burns resulting in higher levels of topkill. Tree height was reduced significantly by early and late dry season burns, whereas mid dry season burns did not significantly reduce tree height. Mid dry season burns led to the greatest increase in the number of stems per individual through coppicing, whereas mid dry season burns led to the greatest decrease in maximum canopy diameter. The seasonal effect of burning on change in leaf dry mass was not evident, except where late dry season head fires led to a greater decrease in leaf dry mass than the other two seasons.

Type of fire

Head fires were more intense than back fires, over all seasons. This fire intensity effect is evident in the other parameters investigated. Head fires led to significantly more topkill of mopane trees. Within seasons there was no significant difference in the density of trees between types of fire applied. There was no significant effect of type of fire on the change in tree height, nor on change in maximum canopy diameter. For the change in the number of stems per tree early and late dry season head fires led to greater increases in the number of stems than did back fires, and for change in leaf dry mass late head fires led to a significantly greater reduction in leaf dry mass than did back fires.

Fire intensity

It was found that fire intensities did not differ between seasons, but that head fires are more intense than back fires. Owing to this, head fires led to more topkill of mopane individuals, and because of the high fire intensities (environmental conditions being conducive), the late dry season fires led to the highest topkill. Burning had no effect on the recruitment or loss of individuals, irrespective of season or type of fire. Even with low fire intensities tree height was reduced. More intense fires led to a smaller increase in the number of coppice stems. Maximum canopy diameter and leaf dry mass are reduced by fire, whereas maximum canopy diameter and leaf dry mass increases when fire is excluded.

Conclusions

The spatial and temporal variation in standing crop is highly dependent on rainfall. Owing to the low basal cover of the mopane woodland areas, and structural heterogeneity between grass species and times of year, the use of the standard disc pasture meter, as described by Bransby and Tainton (1977), is unacceptable for estimating standing crop. To account for the spatial and specific variation in standing crop the revised procedure (Trollope and Potgieter 1986) is recommended. However the use of a single predictive equation, developed for the Kruger National Park in South Africa, is questionable. The assumption cannot be made that the grass structure and basal cover of Malilangwe Estate can be accurately estimated using a single equation developed for an area 50 times larger in size, and containing vastly different vegetation types and climates. Instead it is highly recommended to management that the revised procedure be carried out for each homogenous vegetation type within which standing crop needs to be estimated. To account for the temporal variation in standing crop (between seasons) it might be necessary to calibrate the disc pasture meter, using the revised procedure, for specific sampling events. Owing to financial and other constraints this may not be possible. The study of the effect of season on the accuracy of the revised procedure, is needed.

From this study it cannot be shown conclusively that there is a clear effect of season of burning across all the parameters studied. West's (1965) postulation that plant phenophase is critical in determining their susceptibility to fire, applies only to percentage topkill. Late dry season burns did lead to a significantly higher level of topkill, than did mid or early dry season burns. It is therefore concluded that the effect of season of burning on the damage to tree stems and branches (topkill) is influenced by season of burning because there was no significant difference between the fire intensities experienced in the three seasons, but there were significant differences in percentage topkill. Plants burnt at the end of the dry season (when the plant is preparing for new growth in response to increased day temperature and photoperiod) are more susceptible to topkill than plants burnt in the early or mid dry season. This phenophase effect was not evident for the other parameters investigated.

The effect of type of fire was highly significant for a number of parameters. Over all seasons, head fires were more intense, and it is this higher intensity that led to significant differences in response to head and back fires. However there was no significant difference in the density of trees burned as head or back fires. This provides further evidence that mopane is highly resistant to fire alone, and that population density is unaffected by fire. In contrast to this is the finding that fire changes the structure of the tree significantly. This supports evidence for other savanna areas, as well as other tree species (Wlaker 1985, Trollope *et al.* 1995, Trollope *et al.* 1996). The major influence of fire is to change the above-ground physiognomy of the tree component, whereby the distribution of individuals within each height class changes. The total number of individuals does not change, but there is an increase in the number of short individuals (< 150 cm) and tall individuals (> 351 cm). This is at the expense of individuals of intermediate height (151-350 cm).

From this study it has been ascertained that the effect of season of burning was not significant, except for percentage topkill. Maximal damage to individual mopane trees, through topkill of aerial extremities, takes place after late dry season fires. Fire damage is also greater after head fires, and therefore the maximum damage will be evident after late dry season head fires.

Possible long-term effects of burning in different seasons

Other than the quantitative effects determined in this study, there is an observational aspect of great importance, and this phenomenon may well impact mopane woodland dynamics with more frequent burning. Van Wyk (1971) claimed that frequency of burning appears not to have any significant effect on the density of woody plants, but that frequent burning reduces woody phytomass. This was also found by Kennan (1971), Tainton *et al.* (1991), Trollope (1983) and Trollope *et al.* (1996). Conversely Dublin (1996) showed that seedling mortality increased greatly with increasing fire intensity and burn number. The observations made on Malilangwe Estate are as follows:

Early dry season burns

These burns took place in June 1997, and mopane trees were in full leaf carriage. The immediate response to burning was a loss of leaves (July 1997), while unburnt trees remained in full leaf carriage. This disturbance early in the dry season led to the trees photosynthetic ability being reduced, as they lose leaves when they should be carrying full leaf carriage, and also until much later in the dry season (November/December 1997). The impact on the trees was further exaggerated at the end of the dry season (December 1997), when trees in the burnt areas flushed earlier than those in unburnt areas. This is the hottest time of the year, with daily maxima over 40°C. Trees in the burnt areas were therefore flushing and carrying leaves when the climatic conditions were most unconducive to photosynthetic processes (high temperatures and low water availability during November and early December, before the onset of the rains). Physiological stress leads the plant to senesce at this time of the dry season, but fire results in the plant bearing leaves when it is most unsuitable. The implications of continued early dry season treatments such as this may be severe.

Lewis (1987), Bell and Jachmann (1984) and Jachmann *et al.* (1987) did not observe this phenomenon, but it is unlikely that this is a localised incident. They found that early dry season burning moderated habitat use by elephants in riverine mopane woodlands by deferring elephant impact away from burnt areas, and simultaneously reduced the risk of intense late dry season burns. The disadvantages of early dry season burns (*i.e* more severe damage to the basal growth of grasses) are outweighed by the greater risk of seedling mortality through a slower moving fire, and by creating a mosaic of burnt/unburnt patches that reduce the frequency and spread of late dry season burns.

Late dry season burns

Late dry season burns were undertaken in November 1997. By January 1998 trees in the unburnt areas were in full leaf. However, trees burnt two months earlier remained leafless, although climatic and soil moisture conditions were conducive to leaf carriage. The leafless plants lost out on approximately 4 weeks of photosynthetic production, in comparison with trees in the unburnt areas that were able to utilise this period. Also, grass production was advantaged by this situation as the trees shed no shade and were not photosynthesising during this period. The grass sward therefore had a competitive advantage.

These observations prompt the following questions:

1) What is the physiological expense of losing leaves at a time when leaf carriage is vitally important?
2) What is the physiological expense of carrying leaves at the hottest time of the year, when protein denaturation may occur?
3) Assuming that the effect after one fire event may not be significant, what are the consequences of repeated burning and repeated leaf loss and leaf carriage 'out of sync' with the physiological constraints of the plant?
4) What are the consequences and tradeoffs of being leafless when physiologically it is the optimal period for photosynthesis (warm and wet as the rains have just started)?
5) What are the costs of being leafless when the grass sward is actively growing?

The short duration of this study did not allow for these questions to be addressed, but the posing thereof may well lead to investigation into the effects of frequency of different seasons and types of fire on mopane woodland. Sweet (1982) found that in *Acacia nigrescens/Combretum apiculatum* savannas the density of bush increased with increasing burning interval, as well as altering the community structure. I believe that frequent burning will not only impact the physiognomy of the trees, but when interacting with drought events and high elephant densities, will begin to impact the stand density of mopane woodlands.

Management recommendations

Management burning should be carried out with the intention of achieving one of the following objectives (Tainton 1999):

1) Removing moribund grass material that has accumulated and is now unacceptable to grazing ungulates,
2) control the encroachment of undesirable pants (especially woody species),
3) maintain or develop grass cover,
4) contribute to fire control by reducing fuel loads, or
5) stimulating out-of-season grass growth to provide green feed when it does not occur naturally.

Points three to five do not apply to Malilangwe Estate in general, but the first two points are scenarios that management do encounter. The specific objective will determine the season, type and frequency of fire to be applied. From the findings of this study it is advised that the following be used as a guide-line for determining when and how to burn mopane woodlands, in an attempt to achieve objective (1) or (2):

1) Removing moribund grass material

Malilangwe Estate is a sweetveld area, and the vegetation can support grazing ungulates for the full 12 months of the year. However after periods of high grass production and simultaneous low utilisation, the grass sward can become moribund and unacceptable for grazing ungulates. It is under these conditions, when the removal thereof is required, that surface fires that burn close to the ground are required, in the form of back fires. However there is the danger that these slow-moving back fires can damage the meristematic regions of the grass plant. Alternatively cool, low intensity, fires of less than 1 000 $kJ.s^{-1}.m^{-1}$ should be applied. This level of fire intensity can be attained when the management burning takes place when the air temperature is cool (approximately 20°c) and relative humidity is greater than 45%. It is advised that these burns be carried out at the end of the dry season/start of the wet season when the grass plants are dormant and the fire hazard low, but close enough to the onset of the rainy season as to minimise the length of time that the soil will be exposed. The frequency of controlled burning to remove moribund material will depend on the rate of accumulation of such material, as determined by rainfall and grazing utilisaton.

2) Control encroachment of undesirable plants

To maintain or reduce the level of encroachment by undesirable species (especially trees) high intensity fires are required (> 1 500 $kJ.s^{-1}.m^{-1}$). These fire intensities will be achieved if the fuel load is in excess of 2 500 $kg.ha^{-1}$, the air temperature is approximately 29°C and the relative humidity less than 30%. Under these conditions, and with wind speeds not greater than 6 $m.s^{-1}$, high fire intensities will result that will lead to significant topkill of trees and shrubs up to 250 cm in height. The frequency of these burning events is species-dependent. Multiple fires may be needed, or single intense burns. If possible, the size of the burnt area should be large so that the grazing utilisation will not be excessive. These types of fires are recommended for the areas where encroachment by woody species has occurred into previously grassland areas, or where a more open savanna woodland is desired.

In the mopane-dominated areas high intensity fires will lead to topkill, but also to coppicing. High levels of coppicing are undesirable, as it leads to a more dense and aesthetically unappealing woodland. However the more intense the fire the smaller the increase in the number of stems per individual. Therefore, by implementing high intensity fires the level of coppicing will be reduced. Tree density will not be changed by fire application, but the interaction between fire and post-fire browsing by elephants and black rhino may well lead to a significant decrease in stand density.

The conclusions from this investigation must be seen for their true value: one set of insights into the effects of different seasons and types of fire on mopane woodland, with inferences to the effect of frequency of burning. The large variability in rainfall and standing crop in the south-eastern lowveld of Zimbabwe result in large spatial and temporal variations in fuel load and fuel characteristics. Also the environmental conditions and fire behaviour, both of which are specific to individual fire events, will in turn lead to variation in the effects of individual fires, in different seasons, and using different types of burning. Apart from the effects of fire alone, the interaction of fire and large browsers such as elephants and black rhino must be recognised, as together, they have a highly significant impact on the species and structural diversity of mopane woodlands, making them central in determining the potential changes that take place in these woodlands.

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Appendix 1 Monthly rainfall figures for Malilangwe Estate (1951 to 1998) as supplied by the Meteorological Services Department in Harare

	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	ANNUAL
51/52	0	11.7	34	42.9	76.2	184.4	318.3	57.4	13.7	0	15.2	69.6	823.4
52/53	7.6	0	5.1	0	67.3	177	216.7	24.4	107.2	0	0	0	605.3
53/54	0	7.9	0	16	36.6	44.7	87.4	56.1	32.5	50.3	5.3	5.6	342.4
54/55	0	0	0	6.6	138.4	258.8	260.1	143.8	76.2	38.1	0	0	922
55/56	0	0	0.8	20.3	49	173.5	34.8	348.2	77.5	6.1	0	9.7	719.9
56/57	0	0	17.5	0	75.5	47.2	72.1	78.2	35.1	13.5	5.6	0	344.7
57/58	2.5	7.4	0.5	51.1	79.2	64.5	296.7	160.3	11.2	36.8	2.8	20.1	733.1
58/59	0.8	0	17.8	29.2	25.1	105.4	240.8	123.4	26.7	59.9	7.9	13.5	650.5
59/60	22.1	8.9	14.5	2	145.3	263.9	15.2	104.4	31.2	64	0	18	689.5
60/61	6.1	0	6.6	32	88.4	99.6	60.7	130.6	50.5	59.7	0	32	566.2
61/62	6.1	4.3	0	33.8	70.4	21.1	279.1	29	107.2	16.3	2.5	0	569.8
62/63	0	0	0	2	118.4	102.6	94.5	248.4	6.4	40.4	0	8.9	621.6
63/64	0	0	0	70.1	0	83.6	28.2	210.6	22.9	3.3	6.4	0	425.1
64/65	0	0	0	0	49.3	115.3	27.9	19.8	0	1.3	2.5	5.1	221.2
65/66	0	2.5	27.2	3.8	105.2	11.4	117.6	111.3	38.9	4.3	3.8	5.1	431.1
66/67	0	0	63.5	38.9	51.1	89.4	127.8	113	48.3	18.8	7.1	2	559.9
67/68	9.1	11.4	4.3	28.2	37.8	39.4	16.3	145.3	11.9	28.2	30.7	7.4	370
68/69	0	0	0	5.1	88.6	118.9	54.1	67.6	126.5	47.2	0	0	508
69/70	9.4	0	5.8	42.2	108	137.9	51.8	85.1	5.1	3	0	33	481.3
70/71	3	0	0	10.9	31	127.5	166.9	70.9	4.6	5.6	16.5	1.8	438.7
71/72	0	0	2.5	23.6	88.8	47.3	274.7	116.9	45.8	21.4	5.9	0	626.9
72/73	1.2	0	0	13	8.5	20	92	22	31.5	19.5	0	5.5	213.2
73/74	1	30	37.5	32	46	206.2	33.5	190.5	71	69	5	0	721.7
74/75	19	0	31	4.5	192.5	121.5	83	164	48.5	75.5	46.5	3	789
75/76	0	35.5	0	0	25.5	116.5	126	49.5	157.5	22	69	0	601.5
76/77	0	0	16	0	127	89	69	325.5	66.5	25.3	0.5	0	718.8
77/78	0	19	53	9	22	154	229	142	56.8	60.2	6.4	0	751.4
78/79	5.5	0	0	35	96	131	47	100.5	129.5	4.5	23	2.5	574.5

79/80	9.5	10.5	0.6	84	88.5	96	144.5	104.5	120.5	10.5	0	0	669.1
80/81	1.5	15	81	16.5	86	61	95	178	6.5	34	68	0.5	643
81/82	4.5	0.5	41	43.5	109	17.5	76	145	26	24.5	25	0	512.5
82/83	0.4	0	0.3	32.5	25	48	47	6	25	19	8.5	5	216.7
83/84	22	20	0	42	26	173.5	70	60	49	25	0	0	487.5
84/85	3.5	0	10	84.5	58.5	124.5	217.3	94.5	0	0	37.5	17	647.3
85/86	40	0	73.5	59	58.9	76.1	112.3	25.5	20	139.8	5.5	0	610.6
86/87	0	0	0	27.5	27.5	128.5	31	91.5	8	0	0	0	314
87/88	0	5.5	20.5	24	18.5	373.5	91	61	87	1	21.5	31.5	735
88/89	0	6.5	2.5	53	36.5	30.5	25.5	131.5	24	55	0	22.5	387.5
89/90	0	4	0	56.5	49	92.5	148.7	23.5	19	30.5	0	0	423.7
90/91	0	0	11	0	33	61	51	116	69.5	0	9	6.5	357
91/92	0	0	0.5	1.5	4.5	21.5	29	0	10.5	3.5	0	1	72
92/93	10	0	0.5	5	42.5	154	79	268.5	8.5	26.5	0	6	600.5
93/94	34	5	0	51	140.5	118.5	44	10.2	11.5	0	0.5	1	416.2
94/95	0	4	2	15.5	3.9	193	39	268.5	42	25	14	0	606.9
95/96	42.5	0	0	0	32	82	300	205	33	33	13.5	5	746
96/97	33.5	6	4	2.5	64.5	66.5	167.5	119.5	72.5	36	20	0	592.5
97/98	8.5	0	9.5	17	40.2	70.4	184.3	63	17.9	3.8	0	0	414.6
MIN	0	0	0	0	0	11.4	15.2	0	0	0	0	0	72
MAX	42.5	35.5	81.0	84.5	192.5	373.5	318.3	348.2	157.5	139.8	69.0	69.6	922.0
MEAN	6.5	4.6	12.6	24.8	63.7	109.4	116.5	115.1	44.5	26.8	10.3	7.2	542.0
SD	11.1	8.0	20.4	23.1	42.9	72.2	88.7	82.4	38.9	27.4	16.4	12.9	180.4
CV%	173	174	162	93	67	66	76	72	88	102	158	180	33
%Cont	1.2	0.8	2.3	4.6	11.7	20.2	21.5	21.2	8.2	5	2	1.3	

Appendix 2: Treatments, transect numbers, GPS coordinates and magnetic compass bearings for mopane woodland transects on Malilangwe Estate

GARMIN GPS 45 (SERIAL # 34514047)
SILVA COMPASS (Type 16)

EB1

131) 21° 04' 44.0" S	31° 56' 41.9" E	160
132) 21° 04' 42.5" S	31° 56' 42.0" E	138
133) 21° 04' 43.0" S	31° 56' 41.6" E	146
134) 21° 04' 43.0" S	31° 56' 42.1" E	136
135) 21° 04' 41.8" S	31° 56' 44.0" E	160
136) 21° 04' 41.2" S	31° 56' 44.8" E	142
137) 21° 04' 41.3" S	31° 56' 45.7" E	146
138) 21° 04' 40.6" S	31° 56' 46.9" E	150
139) 21° 04' 39.9" S	31° 56' 47.5" E	164
140) 21° 04' 39.8" S	31° 56' 48.8" E	162

EB2

21) 21° 05' 12.7" S	31° 56' 31.6" E	50
22) 21° 05' 14.9" S	31° 56' 33.4" E	80
23) 21° 05' 16.1" S	31° 56' 34.2" E	64
24) 21° 05' 14.8" S	31° 56' 33.1" E	94
25) 21° 05' 16.7" S	31° 56' 35.3" E	83
26) 21° 05' 18.8" S	31° 56' 37.0" E	76
27) 21° 05' 17.5" S	31° 56' 35.0" E	68
28) 21° 05' 20.7" S	31° 56' 36.1" E	62
29) 21° 05' 19.4" S	31° 56' 36.3" E	70
30) 21° 05' 18.9" S	31° 56' 37.3" E	80

EB3

31) 21° 05' 39.1" S	31° 56' 53.2" E	64
32) 21° 05' 39.8" S	31° 56' 54.7" E	64
33) 21° 05' 39.0" S	31° 56' 55.4" E	42
34) 21° 05' 40.4" S	31° 56' 53.7" E	62
35) 21° 05' 41.1" S	31° 56' 56.3" E	60
36) 21° 05' 42.0" S	31° 56' 57.1" E	62
37) 21° 05' 42.0" S	31° 56' 55.2" E	64
38) 21° 05' 43.9" S	31° 56' 59.9" E	36
39) 21° 05' 44.0" S	31° 57' 00.9" E	60
40) 21° 05' 47.4" S	31° 57' 02.0" E	70

EH1

111)	21° 03' 40.4" S	31° 56' 08.4" E	84
112)	21° 03' 44.0" S	31° 56' 07.4" E	94
113)	21° 03' 44.0" S	31° 56' 09.6" E	80
114)	21° 03' 42.9" S	31° 56' 12.4" E	82
115)	21° 03' 41.2" S	31° 56' 11.3" E	72
116)	21° 03' 44.5" S	31° 56' 12.9" E	60
117)	21° 03' 44.8" S	31° 56' 15.0" E	76
118)	21° 03' 44.8" S	31° 56' 15.7" E	78
119)	21° 03' 46.8" S	31° 56' 12.3" E	76
120)	21° 03' 50.9" S	31° 56' 14.6" E	10

EH2

121)	21° 04' 26.2" S	31° 56' 20.4" E	92
122)	21° 04' 26.3" S	31° 56' 20.3" E	11
123)	21° 04' 26.9" S	31° 56' 21.3" E	11
124)	21° 04' 25.8" S	31° 56' 21.5" E	11
125)	21° 04' 28.5" S	31° 56' 21.1" E	118
126)	21° 04' 28.8" S	31° 56' 21.0" E	140
127)	21° 04' 27.4" S	31° 56' 20.3" E	120
128)	21° 04' 28.5" S	31° 56' 21.1" E	130
129)	21° 04' 27.3" S	31° 56' 22.5" E	109
130)	21° 04' 29.3" S	31° 56' 21.2" E	130

EH3

91)	21° 04' 43.8" S	31° 56' 44.6" E	348
92)	21° 04' 41.6" S	31° 56' 41.0" E	334
93)	21° 04' 42.3" S	31° 56' 40.4" E	360
94)	21° 04' 42.4" S	31° 56' 43.9" E	008
95)	21° 04' 41.2" S	31° 56' 42.9" E	342
96)	21° 04' 43.2" S	31° 56' 42.1" E	350
97)	21° 04' 40.0" S	31° 56' 44.7" E	350
98)	21° 04' 41.2" S	31° 56' 44.1" E	316
99)	21° 04' 41.5" S	31° 56' 44.1" E	324
100)	21° 04' 40.2" S	31° 56' 45.0" E	358

MB1

101)	21° 02' 55.4" S	31° 57' 31.3" E	164
102)	21° 02' 55.7" S	31° 57' 31.9" E	150
103)	21° 02' 55.2" S	31° 57' 30.7" E	192
104)	21° 02' 55.4" S	31° 57' 30.3" E	180
105)	21° 02' 56.4" S	31° 57' 28.3" E	170
106)	21° 02' 57.2" S	31° 57' 27.2" E	176
107)	21° 02' 58.4" S	31° 57' 27.5" E	70
108)	21° 02' 57.9" S	31° 57' 29.6" E	78
109)	21° 02' 59.2" S	31° 57' 29.0" E	70
110)	21° 02' 58.0" S	31° 57' 29.0" E	110

MB2

81)	21° 04' 11.4" S	31° 57' 43.7" E	164
82)	21° 04' 11.4" S	31° 57' 42.1" E	190
83)	21° 04' 12.4" S	31° 57' 42.9" E	180
84)	21° 04' 14.1" S	31° 57' 42.7" E	156
85)	21° 04' 13.2" S	31° 57' 41.5" E	176
86)	21° 04' 13.6" S	31° 57' 42.2" E	158
87)	21° 04' 14.0" S	31° 57' 40.5" E	158
88)	21° 04' 15.2" S	31° 57' 41.0" E	154
89)	21° 04' 15.7" S	31° 57' 39.2" E	122
90)	21° 04' 16.2" S	31° 57' 39.1" E	174

MB3

1) 21° 04' 04.1" S	31° 58' 14.9" E	276
2) 21° 04' 06.6" S	31° 58' 13.3" E	283
3) 21° 04' 06.7" S	31° 58' 12.9" E	283
4) 21° 04' 07.4" S	31° 58' 10.1" E	286
5) 21° 04' 10.0" S	31° 58' 08.7" E	316
6) 21° 04' 13.6" S	31° 58' 08.1" E	322
7) 21° 04' 12.7" S	31° 58' 12.2" E	310
8) 21° 04' 16.1" S	31° 58' 09.0" E	294
9) 21° 04' 14.7" S	31° 58' 09.6" E	294
10) 21° 04' 14.2" S	31° 58' 07.2" E	328

MH1

71) 21° 04' 11.6" S	31° 57' 45.6" E	16
72) 21° 04' 11.7" S	31° 57' 42.0" E	334
73) 21° 04' 13.3" S	31° 57' 41.3" E	340
74) 21° 04' 11.1" S	31° 57' 41.2" E	316
75) 21° 04' 13.4" S	31° 57' 40.9" E	354
76) 21° 04' 12.0" S	31° 57' 39.1" E	344
77) 21° 04' 13.5" S	31° 57' 38.3" E	340
78) 21° 04' 14.1" S	31° 57' 38.4" E	346
79) 21° 04' 13.5" S	31° 57' 36.5" E	350
80) 21° 04' 14.0" S	31° 57' 36.1" E	312

MH2

11) 21° 05' 33.5" S	31° 57' 36.3" E	308
12) 21° 05' 35.5" S	31° 57' 39.0" E	323
13) 21° 05' 39.1" S	31° 57' 38.7" E	326
14) 21° 05' 38.6" S	31° 57' 37.2" E	302
15) 21° 05' 38.1" S	31° 57' 35.4" E	316
16) 21° 05' 40.1" S	31° 57' 34.4" E	312
17) 21° 05' 40.8" S	31° 57' 34.1" E	310
18) 21° 05' 42.8" S	31° 57' 35.0" E	322
19) 21° 05' 43.2" S	31° 57' 32.6" E	302
20) 21° 05' 45.6" S	31° 57' 33.3" E	276

MH3

141) 21° 05' 52.2" S	31° 57' 06.2" E	80
142) 21° 05' 52.0" S	31° 57' 05.4" E	100
143) 21° 05' 51.9" S	31° 57' 06.3" E	110
144) 21° 05' 53.4" S	31° 57' 06.8" E	66
145) 21° 05' 53.7" S	31° 57' 06.8" E	74
146) 21° 05' 54.8" S	31° 57' 06.9" E	92
147) 21° 05' 54.6" S	31° 57' 05.9" E	70
148) 21° 05' 55.1" S	31° 57' 07.8" E	92
149) 21° 05' 53.5" S	31° 57' 09.1" E	74
150) 21° 05' 55.5" S	31° 56' 06.9" E	58

LB1

151) 21° 03' 31.7" S	31° 56' 06.4" E	24
152) 21° 03' 32.4" S	31° 56' 07.7" E	20
153) 21° 03' 32.3" S	31° 56' 08.6" E	09
154) 21° 03' 32.7" S	31° 56' 09.0" E	22
155) 21° 03' 31.5" S	31° 56' 10.4" E	16
156) 21° 03' 29.2" S	31° 56' 11.7" E	30
157) 21° 03' 28.7" S	31° 56' 11.9" E	30
158) 21° 03' 28.1" S	31° 56' 13.8" E	17
159) 21° 03' 28.0" S	31° 56' 14.7" E	354

LB2

191) 21° 03' 02.1" S	31° 58' 34.1" E	291
192) 21° 03' 01.0" S	31° 58' 34.3" E	302
193) 21° 03' 00.1" S	31° 58' 34.1" E	294
194) 21° 02' 59.2" S	31° 58' 34.5" E	292
195) 21° 02' 58.9" S	31° 58' 35.2" E	328
196) 21° 02' 58.0" S	31° 58' 34.3" E	292
197) 21° 02' 56.7" S	31° 58' 34.3" E	278
198) 21° 02' 55.8" S	31° 58' 34.0" E	290
199) 21° 02' 53.1" S	31° 58' 35.1" E	276
200) 21° 02' 51.8" S	31° 58' 36.4" E	298

LB3

201) 21° 02' 45.7" S	31° 58' 26.9" E	180
202) 21° 02' 45.9" S	31° 58' 25.9" E	160
203) 21° 02' 46.4" S	31° 58' 25.1" E	152
204) 21° 02' 45.9" S	31° 58' 24.6" E	176
205) 21° 02' 45.9" S	31° 58' 23.8" E	179
206) 21° 02' 45.5" S	31° 58' 23.4" E	189
207) 21° 02' 45.8" S	31° 58' 21.8" E	166
208) 21° 02' 46.5" S	31° 58' 21.4" E	172
209) 21° 02' 47.1" S	31° 58' 20.3" E	176
210) 21° 02' 48.0" S	31° 58' 19.0" E	178

LH1

161) 21° 03' 22.7" S	31° 56' 23.5" E	16
162) 21° 03' 22.3" S	31° 56' 24.4" E	355
163) 21° 03' 21.4" S	31° 56' 25.2" E	358
164) 21° 03' 20.5" S	31° 56' 25.6" E	357
165) 21° 03' 18.8" S	31° 56' 26.0" E	329
166) 21° 03' 18.5" S	31° 56' 26.8" E	309
167) 21° 03' 18.6" S	31° 56' 27.9" E	41
168) 21° 03' 17.9" S	31° 56' 29.1" E	339
169) 21° 03' 16.2" S	31° 56' 32.2" E	344
170) 21° 03' 16.7" S	31° 56' 35.7" E	326

LH2

171) 21° 03' 06.2" S	31° 56' 42.0" E	288
172) 21° 03' 05.1" S	31° 56' 42.3" E	276
173) 21° 03' 04.6" S	31° 56' 42.6" E	288
174) 21° 03' 01.9" S	31° 56' 42.0" E	265
175) 21° 03' 01.4" S	31° 56' 42.0" E	257
176) 21° 03' 01.0" S	31° 56' 41.7" E	280
177) 21° 02' 59.6" S	31° 56' 41.0" E	266
178) 21° 02' 58.9" S	31° 56' 40.8" E	249
179) 21° 02' 58.1" S	31° 56' 39.4" E	242
180) 21° 02' 58.1" S	31° 56' 39.1" E	225

LH3

181) 21° 03' 53.7" S	31° 58' 19.7" E	293
182) 21° 03' 53.0" S	31° 58' 20.8" E	300
183) 21° 03' 52.1" S	31° 58' 21.3" E	298
184) 21° 03' 51.5" S	31° 58' 21.3" E	318
185) 21° 03' 51.0" S	31° 58' 21.9" E	271
186) 21° 03' 50.5" S	31° 58' 21.8" E	291
187) 21° 03' 49.1" S	31° 58' 23.1" E	284
188) 21° 03' 47.6" S	31° 58' 23.9" E	290
189) 21° 03' 47.0" S	31° 58' 23.8" E	294
190) 21° 03' 46.2" S	31° 58' 23.4" E	[illegible]

C1			
51)	21° 02' 52.8" S	31° 57' 31.6" E	360
52)	21° 02' 52.6" S	31° 57' 32.3" E	348
53)	21° 02' 51.9" S	31° 57' 30.6" E	352
54)	21° 02' 51.3" S	31° 57' 28.6" E	336
55)	21° 02' 53.1" S	31° 57' 26.3" E	344
C2			
61)	21° 03' 47.5" S	31° 55' 54.7" E	256
62)	21° 03' 39.1" S	31° 56' 07.1" E	273
63)	21° 03' 41.1" S	31° 56' 07.5" E	256
64)	21° 03' 42.6" S	31° 56' 10.0" E	254
65)	21° 03' 42.6" S	31° 56' 08.6" E	262
C3			
66)	21° 04' 25.6" S	31° 56' 19.5" E	268
67)	21° 04' 27.4" S	31° 56' 19.0" E	266
68)	21° 04' 29.3" S	31° 56' 18.2" E	270
69)	21° 04' 28.8" S	31° 56' 20.1" E	273
70)	21° 04' 30.2" S	31° 56' 21.5" E	282
C4			
56)	21° 04' 39.1" S	31° 56' 20.7" E	280
57)	21° 04' 38.8" S	31° 56' 18.3" E	258
58)	21° 04' 39.6" S	31° 56' 17.7" E	270
59)	21° 04' 39.1" S	31° 56' 21.0" E	248
60)	21° 04' 42.3" S	31° 56' 23.9" E	250
C5			
41)	21° 05' 47.6" S	31° 57' 02.2" E	236
42)	21° 05' 17.4" S	31° 56' 32.3" E	238
43)	21° 05' 17.7" S	31° 56' 30.4" E	234
44)	21° 05' 17.7" S	31° 56' 31.7" E	268
45)	21° 05' 16.7" S	31° 56' 32.2" E	232
C6			
46)	21° 05' 55.7" S	31° 57' 05.1" E	230
47)	21° 05' 56.0" S	31° 57' 06.5" E	242
48)	21° 05' 54.5" S	31° 57' 10.0" E	214
49)	21° 05' 55.8" S	31° 57' 08.1" E	236
50)	21° 05' 55.8" S	31° 57' 07.6" E	208

E = Early dry season (autumn)

M = Mid dry season (winter)

L = Late dry season (spring)

C = Control (no burn)

B = Backburn

H = Headburn

EFFECT OF SEASON AND TYPE OF FIRE ON *Colophospermum mopane* WOODLAND IN THE SOUTH-EASTERN LOWVELD OF ZIMBABWE

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Degree of Master of Science in Agriculture
in the
Discipline of Grassland Science
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University of Natal, Pietermaritzburg

January 2000

Declaration

I hereby declare that the contents of this dissertation comprises my own original work, except where otherwise acknowledged or stated. This work has not been submitted for degree purposes to any other university.

....

Michael J Walters

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"Trust in the Lord with all your heart, and never believe what you think you know."
Proverbs 3:5. Thank you Lord for all that you have given me.

The commencement, execution and compilation of this thesis has been a source of great joy and learning, and this was made possible with the help and encouragement of the following wonderful people:

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Abstract

The majority of the vegetation types occurring on Malilangwe Estate, in the south-eastern lowveld of Zimbabwe, are dominated by *Colophospermum mopane* (mopane). Over the past 30-50 years the stand density of these mopane vegetation types has increased, and an investigation was undertaken to determine the effect of season of burning and type of fire on mopane woodlands. From this study the following was ascertained:

1) A single predictive equation cannot be used over all seasons to estimate standing crop (fuel load) using the standard disc pasture meter procedure. The calibration equations developed using this procedure accounted for between 39 and 72% of the variation in standing crop, illustrating the high variation in basal cover of the grass sward, as well as the variation between months. Although the revised procedure, developed for areas with low basal cover, accounts for a lot more of the variation in standing crop, this procedure was not used to estimate standing crop over the study period because the calibration equation covered a number of vegetation types, and was not specific to the mopane woodlands.

2) Standing crop tracks effective rainfall (monthly rainfall divided by monthly pan evaporation) closely, with a lag period of less than one month. Standing crop can be estimated using a predictive equation that utilizes effective rainfall from the previous month. There is a positive relationship between peak standing crop and rainfall. A predictive equation was developed to estimate peak standing crop, using annual rainfall. Standing crop declines through the dry season as effective rainfall decreases, and this 'decrease function' allows for the estimation of the standing crop for a particular month, after peak standing crop is reached.

3) Two leaf quantification equations were developed for mopane trees in the south-eastern lowveld of Zimbabwe, one for coppicing and for non-coppicing individuals. These allow for the estimation of leaf dry mass from measured canopy volume.

4) There was no significant difference between the fire intensities attained for the three seasons of burning. Over all seasons, head fires were significantly more intense than back fires.

5) Percentage topkill after late dry season burns was significantly higher than topkill after early dry season burns. There was no significant difference between mid and late dry season burns, and head fires led to significantly more topkill than back fires. Plants <150 cm experienced significantly more topkill (80%) than did individuals >150 cm (44%).

6) Fire *per se* led to an increase in stand density over all seasons and types of fire, but this change was not significant. Fire did not influence the nett recruitment of new individuals. Height class one (0-50 cm) and three (151-350 cm) were impacted most by fire. This reflects a change in tree structure, with an increase in the amount of leaf material in height class three, and a subsequent decrease in the amount of material in height class one.

7) The effect of season of burning on the change in tree height was significant, whereas the effect of type of fire was not significant. All treatments, except early dry season back fires, led to a reduction in tree height, whereas trees in the no burn areas increased in height.

8) Burning in any season, and implementing either type of fire, led to an increase in the number of stems. Mid dry season burns led to the highest increase in number of stems. However, the more intense the fire the smaller the increase in number of stems.

9) All three seasons of burning (head and back fires) led to a significant decrease in maximum canopy diameter per tree, while the maximum canopy diameter of trees in the no burn areas increased. Mid dry season burns resulted in the greatest decrease in canopy diameter.

10) The effect of burning on the change in leaf dry mass per tree was highly significant. All three seasons of burning led to a decrease in leaf dry mass, while there was no difference between head and back fires. Leaf dry mass in the control areas increased however. High fire intensities led to the greatest decrease in leaf dry mass, late dry season head fires having the greatest decrease.

This study suggests that mopane plants face a constraint due to fire and/or browsing, and a tradeoff occurs between canopy volume, canopy diameter, canopy area; and number of stems. Fire leads to an increase in the number of stems through coppicing, while canopy volume and leaf dry mass decreases. This decrease is either (i) a tradeoff in response to increasing stem number, or (ii) a reduction in canopy because additional leaves on the new stems contribute to photosynthesis.

The most important response to season of burning is the altered phenophase (phenological stage) of the plant. Early dry season burns cause the trees to be leafless during the early dry season (when unburnt trees are carrying full leaf), and then to be in leaf at the end of the dry season (when unburnt trees are leafless). It would appear that fire disturbance initiates leaf senescence after burning, and then leaf expansion earlier than normal *i.e* the whole leaf senescence/growth process is brought forward. Trees in late dry season burn areas remain leafless at the start of the rains, while trees in unburnt areas are carrying leaf. Being leafless these trees do not photosynthesize during this time, and it is proposed that the grass sward is advantaged by the reduced competition from the tree component. The consequences of these two changes in phenophase could not be addressed in this study, but are pertinent questions that must be answered if mopane woodland dynamics are to be more fully understood.

Management recommendations for (1) the removal of unacceptable moribund grass material, or (2) the reduction of encroachment by woody species on Malilangwe Estate are also given. In an attempt to combat the increase in stand density of mopane it is recommended that high intensity head fires be implemented, when standing crop (fuel load) is sufficient and climatic conditions are conducive to maintaining high intensity fires. These should be carried out at the end of the dry season, before the onset of the rains.

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Chapter 1

Introduction

The mopane vegetation of the south-eastern lowveld of Zimbabwe occurs as shrubland or woodland, and forms part of the arid, fertile, mesophyllous savanna community of southern Africa (Figure 1.1). Savannas occupy 54% of southern Africa and 60% of sub-Saharan Africa (Scholes and Walker 1993).

The main control on the recruitment of savanna trees is the interactive effects of fire, herbivory and competition with the grass layer (Frost 1985). In this study the effect of fire (season and type) was examined. It was hypothesized that trees in different phenological stages (seasons) would respond differently to fire, and that head fires would cause more damage than back fires because of their higher fire intensity and flame height. Small trees in the sward grow above the grass layer following a simultaneous release from competition, fire and herbivory. Mopane, being a sprouter/coppicing species, is persistent and is able to coppice from the cambium of the stem if the terminal buds have been damaged or, if the stem has also been killed, from the root collar (Rutherford 1981). This persistence, in the face of burning, varies greatly among different height classes because of the vertical release of heat energy during burning. Unlike other disturbances, fire alone, or in combination with other forces, regularly kills mature plants. It is therefore an important agent in structuring communities, since the new openings created provide the potential for vegetation change (Bond and van Wilgen 1996).

Fire is an important phenomenon in the semi-arid savanna areas of southern Africa. Rainfall occurs in the warmer summer months with a dry period of two to eight months duration during which fire is a typical phenomenon at intervals of one to fifty years (Huntley 1982). Succession advances towards an open woodland or shrub savanna climax, but under disturbed conditions (fire, browsing or edaphic) a dense thicket may develop.

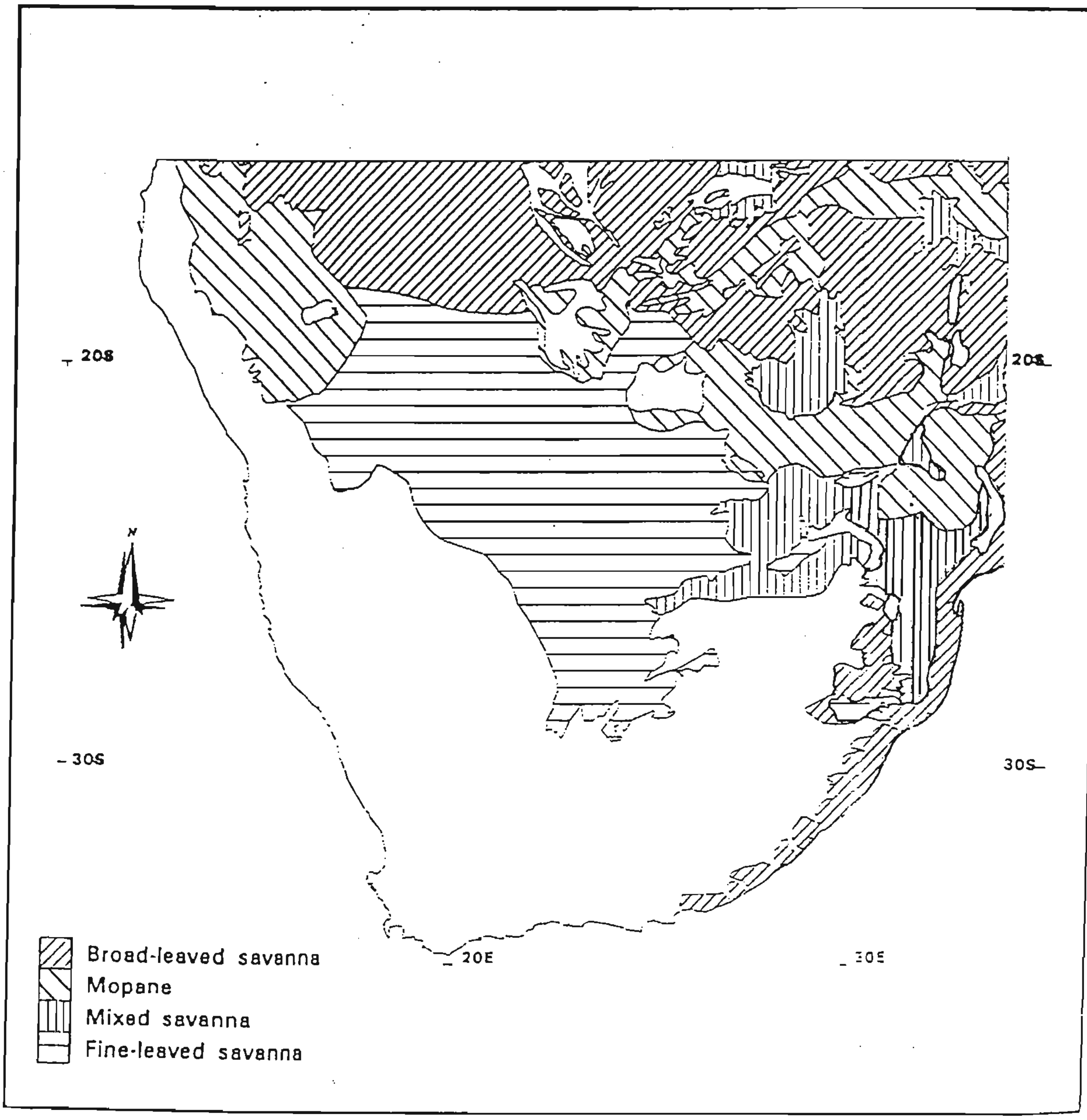

Figure 1.1 The distribution of broad classes of savanna in southern Africa (from Scholes 1997).

The nutritive value of semi-arid savannas is high and, in contrast to the moist savanna areas, can be viewed as sweetveld *ie.* veld which remains palatable and nutritious when mature, and provides forage for a full 12 months (Scott 1947).

Historically the semi-arid savanna areas supported large concentrations of indigenous ungulates (Huntley 1982). Because of the year-round palatability of the savanna grass component, the utilization of these areas for extensive cattle ranching has been widespread. This was the case in the south-eastern lowveld of Zimbabwe, and together with the introduction of large numbers of cattle, the removal of indigenous ungulates and elephants, was the suppression of fire. This simultaneous release of trees from competition, fire and herbivory resulted in the widespread increase in tree density of opportunistic early successional species.

Motivation and objective

It is widely accepted that fire is an essential determinant of savanna structure (Walker 1985), and is an effective method of succession management that has been used by man for centuries (Trollope 1982, Wright and Bailey 1982, Dublin *et al.* 1990, Menaut *et al.* 1990, Silva *et al.* 1991). It has been shown that the exclusion of fire allows for successional development of open savanna to a forest/thicket state (Trapnell 1959, Smith and Goodman 1987), and conversely that fire *per se* can maintain or reduce woody encroachment (West 1971, Trollope 1980, Trollope 1999).

It was with this knowledge of rangeland succession in mind that the previous Director of Malilangwe Conservation Trust, Dr Jeremy Anderson, motivated for a research project to study the effects of fire on mopane (*Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard) woodland. It was perceived that previously open grasslands and savanna areas had been encroached by mopane, and the objective of this study was to gain an understanding of the effects of different seasons of burning and types of fire on mopane woodland. During a cursory visit, and a subsequent data collection period, it was found that mopane encroachment was not as widespread as perceived. Even-aged cohorts of mopane occur on the peripheries of mesic grasslands, while soil physical, chemical and hydrological properties limit the establishment and survival of mopane trees within the mesic grassland areas. Instead, it appears as if mopane stand density has increased within existing stands in the last 30 to 40 years, and encroachment is by microphyllous species such as *Acacia borleae* Burtt Davy and *Dichrostachys cinerea* (L.) Wight Arn.

Chapter 2

Literature review: The major determinants of mopane woodland dynamics in the south-eastern lowveld of Zimbabwe

This chapter deals with the conceptual backdrop to this thesis: Effect of season and type of fire on *Colophospermum mopane* woodland in the south-eastern lowveld of Zimbabwe. A comprehensive synthesis of the global literature pertaining to the following is presented:

1) a review of mopane (*Colophospermum mopane*) physiology and ecology,
2) the major determinants of mopane woodland structure and functioning,
3) fire in semi-arid savanna areas, and
4) the components of the fire regime and how they effect mopane woodland dynamics.

Introduction

"I put this to those studying burning; we are challenged by a most involved process, a series of complex reactions. We must therefore be humble in attempting to apply the interpretations derived from observations and experimentation, even when aided in future by the right feeding in of the right material to the computer." (Phillips 1971). It is with this warning in mind that this literature review is undertaken.

The determinants of the structure and functioning of mopane vegetation are numerous and highly complex, the major factors being climatic and edaphic conditions. Other determinants are human impact, frost, fire, elephants and other browsers, invertebrates, lightning, drought and competition with the herbaceous layer for limited resources. It is widely accepted that fire is a secondary determinant of savanna structure (Walker 1985), and an effective method of succession management that has been used by man for centuries (Trollope 1982, Wright and Bailey 1982, Dublin *et al.* 1990, Menaut *et al.* 1990, Silva *et al.* 1991). It has been shown that the exclusion of fire allows for successional development of open savanna to a forest/thicket state depending on climate and soil factors (Trapnell 1959, Smith and Goodman 1987), and conversely that fire *per* *se* can maintain or reduce woody encroachment (Spinage and Guinness 1971, West 1971, Trollope 1980, Pellew 1983, Bell and Jachmann 1984, Tainton 1999). However, the principles and trends found to be relevant to other savanna tree species may not be relevant to mopane, owing to physiological and ecological factors that make it highly resistant to the effects of fire, very competitive with the grass layer and extremely persistent in semi-arid savanna areas.

The effects of fire regime on mopane vegetation dynamics is still an unknown quantity, and the hypotheses formulated for other semi-arid savanna species still have to be tested specifically for mopane.

Mopane: a review

Introduction

Colophospermum mopane is a widespread and important tree species in sub-tropical southern Africa, occurring between just south of the Tropic of Capricorn and 10° south (Timberlake 1995). It can become locally dominant forming an almost monospecific woodland, in other circumstances it can occur as a component of a more open savanna with numerous other species, or it can occur as an isolated population. Over its whole range it is economically important as fuel and charcoal, for fencing and building material, as the host of a protein-rich human food source (mopane worms), and as valuable browse for domestic and wild animals. Timberlake (1995) stresses the need for an endeavour to understand the ecology of this species, as it is of great importance, especially in the northern areas of southern Africa.

Phytology

Description

It is a shrub or small to large-sized deciduous tree (5-20 m), with an erect narrow crown (van Wyk and van Wyk 1997). It occurs in almost pure stands in hot, low-lying areas, often on alluvial or lime-rich soils and basalt-derived lowlands (Timberlake 1995). Stem diameter is variable, normally 5-80 cm, but can attain 150 cm.

The bark is dark grey or brown, rough, with longitudinal fissures. Leaflets are stalkless, resembling two butterfly wings, with a minute protuberance between the pair, hairless and smell strongly of turpentine when crushed (van Wyk and van Wyk 1997). The root system is generally shallow, 30-120 cm (Thompson 1960). Lateral roots are well developed and a taproot may be present when young but dies back as the tree gets larger (Henning 1976). Fine roots are endomycorrhizal (Hogberg and Piearce 1986).

Inflorescences are greenish-white; wind pollinated, and appear from December to March. The seed pods are light to dark brown, compressed, and have numerous scattered resin glands on the surface (Timberlake 1995).

Life cycle and phenology

Mopane is irregularly deciduous, the leaves turning yellow to red-brown at the start of the dry season. Trees are normally leafless for two to three months at the end of the dry season (September to November). The flush of new leaves coincides with the onset of the rains, or directly thereafter. In most environments this flush of new leaves takes place later than other savanna tree species. Regrowth of leaves is possible if the young leaves are removed soon after the start of the growing season (Guy *et al.* 1979).

Physiology

Mopane is physiologically adapted to xeric and low soil nitrogen and potassium conditions. Stress adaptations differ between areas and appear to be genetically heritable (Prior 1991). It is able to grow at a matric water potential below -15.2 bar (Henning and White 1974) and is also capable of internal osmotic adjustment, involving osmotically active nitrogen compounds in the cell sap. Mopane performance (the product of mean stem diameter by density over all height classes) was found to be correlated with soil nitrogen and phosphorous, exchangeable magnesium and per cent subsoil moisture over a range of soils from southern Africa (Henning 1976).

Seed germination takes place under a wide range of conditions, best being at a water stress of -1.4 bars (Choinski and Tuohy 1991). Seedling growth has been found to lead to a reduction in soil pH due to selective uptake of cations (Smith 1972). Seedlings require freedom from competition, especially from grasses (Sharma *et al.* 1989). Under natural conditions germination is very good, and many seedlings can be found after the first rains. Due to competition and large herbivore selectivity (especially elephants), few survive the first dry season to become saplings (Timberlake 1995). Prior (1991) reports that mopane seedlings are more stress tolerant than those of *Acacia*.

Pests and diseases

Seedlings are prone to damping, and one species of leaf-spot fungus has been reported on mopane in southern Zimbabwe (Piearce 1986).

The mopane worm is the edible larva of the moth *Gonimbrasia belina*, which can cause severe defoliation of trees in some years, but recovery is rapid (van Voorthuizen 1976). Another lepidopteran defoliator is the 'green slug', *Latoia vivida*, which in some years causes large-scale reduction in leaf matter. *Arytaina mopane*, the mopane psyllid, produces an excretory product (lerp) which is reputed to make the leaves more palatable to browsing animals (van Wyk 1972).

Ecology

Distribution

Mopane is a xeric species of the savanna woodland zone of south tropical Africa. It is found mostly on heavier-textured soils in the wide, flat valley bottoms such as the Limpopo, Zambezi, Okavango and Luangwa (Cole 1986). It is indigenous to the semi-arid savanna areas of the south-eastern lowveld of Zimbabwe, with an area of 101 500 km^2 (18.5% of total mopane area) under mopane-dominated vegetation in Zimbabwe (Timberlake 1995).

Altitudinal distribution is from <100 m (Mozambique) to 1200 m (Zimbabwe), and in the Zimbabwe lowveld from 300 to 600 m (Figure 2.1). Within its distribution the annual rainfall ranges from 100-800 mm, with the majority of the population range being found in the 400-700 mm annual rainfall zone. It is intolerant of severe frosts, being restricted by the 5°C mean daily isotherm for July (Henning 1976).

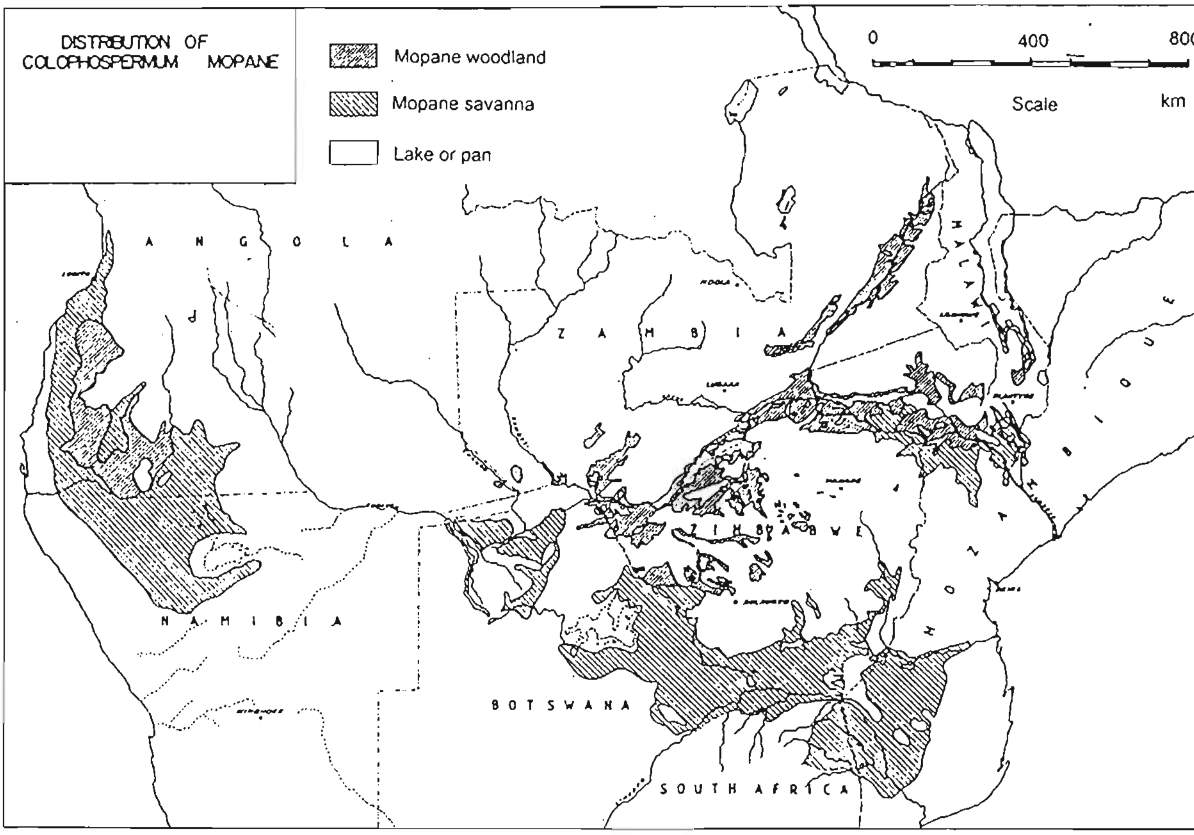

Figure 2.1 Distribution of *Colophospermum mopane* in southern Africa (from Mapaure 1994).

Mopane vegetation distribution is determined by different ecological factors in different areas, with frost incidence, minimum temperatures, rainfall minima/maxima and altitude all contributing. In the south-eastern lowveld of Zimbabwe the land rises from the Mozambique coastal plain to the central plateau, and increased rainfall (soil moisture availability) allows other tree species and vegetation types to dominate (Timberlake 1995). On basalt-derived soils in southern Zimbabwe the mopane vegetation is an early deciduous shrub savanna, whilst on the more alluvial soils it is a dry deciduous tree savanna. The "cathedral mopane" (tall single-stemmed trees) of the northern and western areas of its distribution do not occur in the lowveld.

Mopane-dominated savanna areas are noted for their low alpha-diversity (few associated species). Also, there are a low number of similar associated species (low beta-diversity). Grass cover is generally poor, and often dominated by annuals.

Soils

Mopane generally occurs on clay-rich soils, or soils with a clay layer immediately below the surface. It also establishes on duplex soils and sodic sites, usually as a small tree or shrub, where it endures and expands its range as soil erosion and surface capping increases (Dye 1977). The shallow root system coincides with the zone of maximum moisture retention (Thompson 1960), and mopane is excluded from better soils by deeper-rooted *Acacia* species (Cole 1986). Mopane is thus a strong competitor with the grass layer, as well as with other tree species, where the available soil moisture is retained near the surface. Thompson (1960) notes that factors reducing grass growth will favour mopane on suitable sites, including:

1) low and erratic rainfall in combination with sandy surface soils of low water-retaining capacity,
2) competition for available moisture by massed mopane surface roots, and
3) the occurrence of shallow sandy soils over relatively impervious sodic subsoils.

Short tree and shrub forms are found on the alkaline black clays of the south-eastern lowveld of Zimbabwe (Cole 1986). The tree form is found on more permeable soils. As rainfall increases edaphic factors become more important in its distribution and mopane is confined to physiologically drier sites (Thompson 1965).

Biomass production and tree density

Standing biomass figures vary in response to stand density, soil factors and climatic conditions. For the south-eastern lowveld of Zimbabwe, Kelly and Walker (1976) found that standing above-ground biomass and annual production varied with level of utilisation (Table 2.1).

Table 2.1 Annual production (**A**) and mean standing above-ground biomass estimates (**B**) of mopane woodland in the south-eastern lowveld of Zimbabwe (from Kelly and Walker 1976)

	$t.ha^{-1}$	Component	Utilisation
A.	1.18	FW	mean
	1.58	*, FW	no
	1.49	*, FW	light
	1.66	*, FW	moderate
	1.22	*, FW	high
B.	15.0	FW	no
	15.7	FW	light
	28.1	FW	medium
	15.9	FW	high

* tree+shrub, FW field weight (before drying)

Mopane generally comprises >90% of the total biomass of mopane savanna vegetation (Guy 1981), which is probably a higher proportion than most other individual species contribute to the woodland types in which they are found (Timberlake 1995). Only 3.7% of total mopane biomass is browse (leaf + twig), the rest being mainly wood (Martin 1974).

Equations for the prediction of biomass of mopane from individual stem diameter or crown measurements were developed by Kelly and Walker (1976) for the semi-arid south-eastern lowveld of Zimbabwe, and of leaf dry mass and leaf volume for the Soutpansberg in South Africa by Smit (1994), (Table 2.2).

Table 2.2 Predictive equations for mopane field weight (FW, before drying) biomass (Kelly and Walker 1976), leaf dry mass and leaf volume, (Smit 1994)

Equation
Trees - standing biomass
mass (kg Fw.ha^{-1}) = -2934.8 + 219.1(canopy area, m^2 x dbh, cm)
Shrubs - standing biomass
mass (kg FW.ha^{-1}) = -481.4 + 425.6(canopy volume, m^3)
mass (kg FW.ha^{-1}) = 882.3(canopy volume, m^3) [shrubs<1.5 m]
Annual production - trees, shrubs
production (kg FW.ha^{-1}.yr^{-1}) = -2505.4 + 993.1(height, m) [leaves+twigs]
production (kg FW.ha^{-1}.yr^{-1}) = 175.1 + 71.4(canopy volume, m^3) [leaves+twigs]
Leaf dry mass
leaf dry mass (g) = 0.025 x EXP(0.702 x Ln spatial volume, cm^3) [non-coppicing]
leaf dry mass (g) = 0.174 x EXP(0.558 x Ln spatial volume, cm^3) [coppicing]

Density of trees and/or stems is determined by soil properties, soil depth and the successional status of the stand *ie*. a mature woodland versus a coppicing shrubland. Within mopane shrubland, self-thinning of stems and trees occurs (Scholes 1990), therefore size and density affect survival and size-class dynamics. Mature tree densities, shrublands and coppice densities are given in Table 2.3.

Table 2.3 Mean densities of mopane woodland in the south-eastern lowveld of Zimbabwe (Kelly and Walker 1976)

stems.ha^{-1}	utilisation
956	none
984	light
1 717	medium
850	high

Conclusions

Mopane vegetation is generally a species-poor vegetation type that appears to hold no endemics or threatened species. However, it is a key species in a wide range of landscapes not only as an important wildlife habitat, but also as an economically important renewable resource (Timberlake 1995).

It is a resilient and persistent species occurring over a wide range of ecological conditions, but mainly on heavier eutrophic soils, and lighter soils in low rainfall areas (Timberlake 1995). The following points must be noted with regard to mopane dynamics:

1) it is a shallow-rooted tree species (and therefore competes directly with the grass layer for limited resources such as light, water and nutrients);
2) it can utilise water at a lower matric potential than grass species (it therefore has a competitive advantage);
3) over time it can come to dominate a site, forming extensive mono-specific stands, leading to reduced grass growth, and
4) once established is difficult to remove, having to be manually thinned or intensively controlled with arboricide.

In light of these points, and with an understanding of mopane physiology and ecology, a review of the literature pertaining to the determinants of mopane woodland structure and functioning, and in particular the effects of fire on mopane population dynamics, is now undertaken.

Factors determining mopane woodland structure and functioning

Introduction

The factors determining the structure and functioning of mopane woodland are numerous, and the interactions between them are dynamic and highly complex in most instances. In the available literature there are very few instances of work relating to mopane woodland dynamics specifically.

Because of the stochastic nature of semi-arid savannas, it is intuitive that mopane woodlands are dynamic (albeit less than other savanna types because of their more homogenous nature) and that the species composition, tree density, canopy volume and successional status vary both spatially and temporally. Changes may be brought about by the community itself (autogenic factors), or from other external determinants (allogenic factors).

Autogenic factors

Self-thinning

Self-thinning is a form of density-dependent population regulation. It is not reasonable to assume that population growth, survival and fecundity vary only with time and are independent of population density. The manner in which self-thinning occurs has been labelled the -3/2 self-thinning rule, which predicts that plants which are small or occur at low densities grow without thinning until they reach the -3/2 slope of log(plant weight) versus log(plant density), when size increases at the expense of density (Yoda *et al.* 1963). Schlesinger and Gill (1978) studied most of the aspects of density-dependent thinning in a chaparral shrub *Ceanothus megacarpus*, and found a slope of -1.23. Walter (1971) reported that *Acacia mellifera* thickets became moribund and reverted to open savanna after 50 years of protection from fire in Namibia, although this could not be attributed to density-dependent factors. Other researchers found density-dependent mortality due to intraspecific competition (Riggan et al. 1988, Kenkel 1988). Scholes (1990), studying the regrowth of mopane following clearing, found evidence for self-thinning. However, this phenomenon has not been adequately described for mopane woodlands.

Competition, succession and the Gulliver effect

"Ever since Darwin, competition has been considered to be one of the major forces shaping the morphology and life history of plants and the structure and dynamics of plant communities" (Grace and Tilman 1990).

Competition can be the major factor in determining the changes in plant communities over time, over spatial gradients, and can alter species diversity (Bond and van Wilgen 1996). Vegetation changes over time, and Clements (1916) described succession as an orderly and predictable approach towards a dynamic equilibrium. In response to a cleared area, plants colonise the space released, with pioneer species facilitating the invasion of later species by ameliorating the environment, or being superseded by species with a greater competitive ability. An equilibrium is eventually reached (climax) where, if undisturbed, only top competitors persist. The climax was assumed to be self-sustaining and persistent (Bond and van Wilgen 1996).

The relay floristic model of succession, *ie*. the predictable sequence of species replacement, has greatly influenced ecological thinking. By this approach, predictions of community dynamics are based on competition as the central process. Given the strong competitive abilities of mopane, and its persistence over long periods of time, it is proposed that mopane is a late successional species with great competitive ability. Walker (1980) defined three concepts central to system dynamics, *viz*. stability, resilience and a system's domain of attraction. A stable system is one that changes little in composition and production, in response to perturbation or stress. A resilient system may or may not be stable, but remains attracted towards the equilibrium. A domain of attraction is that region of a system's state-space within which the system is attracted towards an equilibrium. Using these definitions, mopane woodland can be described as a stable, resilient system with a large domain of attraction (a large state-space region within which attraction towards equilibrium takes place). The degree of stability and resilience of mopane vegetation needs to be quantified, as well as further investigation into competition-dependent effects in mopane woodland specifically.

In the savanna systems of southern Africa the dynamics of woody plants are affected by interactions with the grass sward. Grasses are effective at suppressing regeneration of other growth forms because of their rapid growth rates (D'Antonio and Vitousek 1992), production of large quantities of seed and competitive advantage in the soil surface layers. Grasses form highly flammable fuels, but recover quickly after burning. Their meristematic regions are near or below the soil surface, and protected from fire. In the event of fire, standing biomass is removed (much of which is dry and dead).

They are thus important in the regeneration phase - producing what Bond and van Wilgen (1996) termed the 'Gulliver effect' (after Swift's sailor bound helpless by hordes of tiny Lilliputians). Gulliver plants are those which dominate communities as adults, but struggle to emerge from the herbaceous layer as juveniles. The grass layer suppresses Gulliver recruitment by competing with seedlings, slowing the growth of established plants, and by fuelling frequent fires that kill or stunt the survivors so that they fail to escape the danger zone (Bond and van Wilgen 1996). Release from this state takes place when the grass layer is removed - normally by grazing or burning, or if fires are suppressed. When released from this state the Gullivers flourish, they escape the danger zone as they grow, and in turn suppress grass growth as they gain a competitive advantage. This process of increasing tree density accelerates as the density of the grass component is subjected to increasing competition from the tree layer. This can be compounded by the pressure placed on the grass sward by grazing ungulates, especially at high grazer stocking densities (Tainton 1999). It is this scenario that may have taken place in the south-eastern lowveld of Zimbabwe, with the exclusion of fire; removal of indigenous ungulates; and the introduction of large numbers of cattle on extensive cattle ranches. This situation released Gulliver-type tree species that have come to dominate certain vegetation types and encroach into others. Mopane, whose distribution is determined by soil type and condition, has generally increased in density within historical ranges rather than encroaching into previously grassland areas.

Allogenic factors

The allogenic factors determining mopane woodland dynamics fall into three categories:

1) climatic,
2) edaphic, and
3) environmental.

The individual factors within these categories contribute, to various degrees, to the structure and functioning of a particular woodland at any one time.

Climatic factors

The climate under which savanna vegetation occurs is widespread all around the world, in a broad belt north and south of the Tropics. Semi-arid savannas are those in which the annual rainfall is between 300 and 750 mm. The south-eastern lowveld of Zimbabwe has a warm climate, with a mean annual rainfall of approximately 500 mm, concentrated in the summer rainy season

(December to March). Owing to the low and erratic rainfall, and the fact that annual potential evaporation is usually twice rainfall, the growth of savanna trees is restricted by the amount and periodicity of rainfall events. Of all the determinants of vegetation production in the semi-arid savanna areas, water is the most limiting (Snyman 1987). The growth and success of both trees and grasses are thus determined by the amount of water each component can obtain and utilise. A simple, general explanation for the coexistence of trees and grasses over 20% of the Earth is based on the apparent niche differences in tree/grass rooting systems (Walter 1971). The two components are able to coexist because they have different strategies for obtaining moisture. Trees tap deeper subsoil sources of water than grasses, but grasses are more competitive in the soil surface layers. Trees should dominate deep, sandy soils because their deep tap roots would benefit from the deeper infiltration of water, and grasses dominate on shallow soils where they would outcompete trees for surface soil moisture. Owing to its shallow root system, this model may not apply as rigorously to mopane however, as it competes strongly with the grass sward in the surface soil layers. Alternatively tree-grass coexistence may be mediated by disturbance factors such as fire, elephants and drought that prevent tree communities from attaining their full growth potential.

Severe droughts have been recorded in the Zimbabwean lowveld, and these occur approximately every nine to ten years. Tree mortality is widespread, and impacts the vegetation of the more mesic sites dramatically (Timberlake 1995, Tafangenyasha 1997). Walker (1996) points out that high inter-annual variation in rainfall keeps the amount of trees lower than the amount that the average rainfall can sustain. This is because dieback of trees is rapid in a drought, but recovery during wet periods is much slower, limited by both demographic and physiological processes. The amount of trees is therefore determined by the periodicity of dry years.

Tafangenyasha (1997) states that loss rates of trees in the Gona-re-Zhou National Park were probably exacerbated by dry spells between 1977 and 1983 during which a severe drought was experienced. He also notes that the impact of drought on woody species was found to be significantly different between burnt and unburnt sites, with unburnt sites displaying higher levels of damage, but the reasons for this are not clear. This supports Wing and Buss (1970) and Field (1971) who suggest that there is a decrease in browsing pressure by elephants with an increase in rainfall (as increased grass intake takes up higher proportions of the diet), and an increase in tree mortality during drought years.

Edaphic factors

Not only the underlying geology, but also the soils they form, are important determinants of plant production potential and consequently the carrying capacity of savannas (Fritz and Duncan 1994). The edaphic factors relating to mopane are covered earlier in this chapter.

Environmental factors

I have included the vertebrate and invertebrate animals that effect mopane woodlands, as the environmental factors. Man, being part of the environment, is also a factor that determines the dynamics of mopane vegetation. However, this paper does not deal with the widespread impacts of man in mopane-dominated vegetation types. Suffice it to say that in the south-eastern lowveld of Zimbabwe, where extensive cattle and game ranching is practised, there is no threat to any of the mopane-dominated vegetation types. However, over-utilization of mopane woodlands for fuel, charcoal production and building materials does threaten some woodlands in communal areas (Kelly and Walker 1976).

Vertebrates

The vertebrate animals that impact mopane are mainly the browsing ungulates such as kudu (*Tragelaphus strepsiceros* Pallas), eland (*Taurotragus oryx* Pallas), black rhino (*Diceros bicornis* Linnaeus) and African elephant (*Loxodonta africana* Blumenbach). Other vertebrates such as the porcupine (*Hystrix africaeaustralis* Peters) and buffalo (*Syncerus caffer* Sparrman) damage trees, and in so doing create sites for further fire damage. However, of all of these, the elephant has the greatest impact, and will be dealt with.

The African elephant is confined to privately owned wildlife ranches, and the Gona-re-Zhou National Park, in the south-eastern lowveld of Zimbabwe. On privately owned land their numbers are low, with densities of less than 1 elephant every 4 km^2. In the Gona-re-Zhou National Park the density is approximately 1 elephant per km^2. Pienaar *et al.* (1966) concluded that in the Kruger

National Park, 6 000 elephants (1 every 1.9 km^2) was the highest number of elephants that could be carried "if the total destruction of the vulnerable areas near water is not to result". This is because elephants have an impact on savanna ecosystems, and if the population is allowed to exceed a certain density, then these affects may lead to an undesirable change in species and structural diversity.

Trollope *et al.* (1996), compared mopane-dominated landscapes that had been excluded from elephant utilisation, with those that had. They showed that neither fire, nor elephants and fire, had any effect on the density of the woody vegetation. However the interaction of elephants and fire caused a significantly marked reduction in the phytomass of bush in areas with clay soils, irrespective of rainfall. It is suggested that the changes in the woody vegetation indicate a change in structural diversity rather than species diversity. This is in agreement with other researchers, who concluded likewise (van Wyk 1971, Pellew 1983 and Dublin 1995).

The kinds and proportions of forage consumed by elephants varies seasonally, with grasses and herbs being selected in the rainy season, and woody plants in the dry season (Field 1971). Browsing involves breaking off branches, uprooting trees, stripping bark and selective removal of leaves. Where fire has removed the grass component, elephants may push over trees to utilise the remaining leaves. In such areas the recruitment of mopane seedlings may be severely curtailed by the effects of the interaction of fire and browsing. The impact of elephant on post-burn coppice material may also lead to structural change, both in the basal and aerial strata. With low elephant densities the effect on a landscape level will be diffused over a wide area. However, Bell and Jachmann (1984) showed that the distribution of elephants is influenced by burning. Elephant use of woodland burnt early in the dry season is lower than the use of areas burnt later, or not at all. The dry season is the time at which most browsing occurs, and early burning reduces the browsing pressure to a significant extent and reduces the impact of elephants on woodlands. Conversely, unburnt areas will experience increased browsing pressure, leading to an impact on the tree layer.

The combined effects of elephants and fire can lead to a reduction in woody phytomass and the creation of more open habitats. If the objective is to achieve this, then the combined effects of fire and elephants may lead to such a situation.

Fire in semi-arid savanna ecosystems

Introduction

Fire is an important phenomenon in the semi-arid savanna areas. Rainfall occurs in the warmer summer months with a dry period of two to eight months duration, during which fire is a typical phenomenon at intervals of one to fifty years (Huntley 1982). In the south-eastern lowveld of Zimbabwe fire has been suppressed during the last 50 years because of the rationale that the burning of grass is a waste of a valuable fodder source for cattle.

Fire history of semi-arid savanna ecosystems

Evidence of ancient fires is available in the Palaeozoic, Mesozoic and Tertiary Periods (West 1965). Modern evidence shows that southern African savanna areas have been subjected to burning at one time or another, but the frequency with which this took place differs greatly over the sub-region. In the south-eastern lowveld of Zimbabwe, extensive areas of the Gona-re-Zhou National Park have been burnt almost annually by runaway fires from within Zimbabwe and Mozambique. The extent of fire in the past is presumed to have been higher than today, as fire protection controls and the removal of communities out of National Parks has reduced the occurrence and extent of man-induced fires. The savanna biome is adapted to regular and frequent burning, and has many plant species whose evolutionary development accords with community behavioural responses to fire (Bews 1925; Bean 1962).

Natural fires

It has been documented that fires can be started by physical means such as falling boulders (Wicht 1945). Other possible causes of physical induction include earthquakes and earth tremors. There is little evidence of the frequency with which boulders and earth tremors cause fires. It appears that these instances are restricted to mountainous areas where there is abundant flammable plant material.

Lightning is generally considered to be the most significant of the natural causes (excluding man) of veld fires in southern Africa (Scott 1970). Lightning is widely accepted as an ignition source, but the literature shows differing opinions as to the frequency and importance of lightning induced fires in natural ecosystems. Ground lightning flash densities from over 300 lightning counters, were recorded between 1975 and 1978 by the Council for Scientific and Industrial Research (CSIR) in South Africa. Highest densities were found mainly at altitudes over 1 000 m in Lesotho and Natal, and lowest in the southern Afro-montane forest and fynbos. Annual reports for the Kruger National Park testify to the incidence of lightning induced fires during electrical storms. In the lowveld of Zimbabwe, the occurrence of intense electrical storms, such as those experienced in the Kruger and Pilansberg National Parks, are infrequent. It is held therefore that lightning induced fires within the south-eastern lowveld of Zimbabwe are very infrequent (Mr Ray Sparrow, previous owner of Lonestar Ranche, P. Bag 7085, Chiredzi, Zimbabwe). Most lightning induced fires cover relatively small areas under present-day conditions (2.43 km^2 per fire average), although there are modern instances of fires having burnt large areas eg. 780 km^2 of savanna in the Kruger National Park (Pienaar 1968) and 200 km^2 in the Mkwasine area of the Zimbabwe lowveld (Gavin Campbell-Young, Estate Manager, ME, P. Bag 7085, Chiredzi, Zimbabwe). It is assumed however that in pre-colonial times with low human population densities, lightning induced fires could have burnt extensive tracts of country, especially when they occurred under conditions favourable for veld fires.

Fire parameters of semi-arid savanna ecosystems

Productivity is a functional parameter of the semi-arid savanna ecosystem and refers to the rate of production of above ground biomass. The structural parameter of the vegetation (herbaceous and woody components) is the above-ground physiognomy of the community. These two parameters together determine the potential natural fuels of savanna areas and communities (Edwards 1984). Thus, the quantity and quality of fuels available for fires varies widely in relation to climate, last rainfall, season and degree of use by man and animals. Herbaceous layer production of the semi-arid savanna areas is related to the density of the woody tree and shrub layers and to rainfall. Rainfall in the northern regions is almost exclusively a summer phenomenon, while winter precipitation increases southwards. The herbaceous layer is more flammable than the woody layer and dense woody vegetation with a low herbaceous biomass is less prone to fire than a mixed grass-woody vegetation (Edwards 1984). In a savanna area of average rainfall (*ca* 500 $mm.yr^{-1}$) herbaceous layer growth is approximately 1 000 $kg.ha^{-1}.yr^{-1}$ or more (Rutherford 1979). The potential fuel loads are lower in the more arid areas.

Despite the high total biomass, fires in the semi-arid savanna areas are mainly close to the ground, though fires impacting the crown sometimes occur in woody vegetation above 3 to 4 m. This may be attributed to the open distribution and lower flammability of the woody plant material and to low herbaceous biomass and its discontinuous distribution.

Savanna communities are characterised by the lateral discontinuity of the herbaceous layer, Edwards (1984) found, for example: from 640 $kg.ha^{-1}$ under shrubs, to 970 $kg.ha^{-1}$ under trees, and 1 230 $kg.ha^{-1}$ between trees and shrubs. It must be noted, however, that the biomass production of the herbaceous and woody components is dependent on a suite of interacting factors. The combined environmental, species-specific and management factors determine the available natural fuels and fuel load for a specific area.

Factors influencing fire behaviour

The findings presented in this section are taken from Trollope's (1983) work on the control of bush encroachment with fire, unless otherwise stated. The three factors influencing fire behaviour are fuel factors, and atmospheric and physiographic conditions. Fuel load is the most significant factor affecting topkill up to 3 m.

Fuel load

Fine fuels (<6 mm diameter) and heavy fuels (>6 mm diameter) can be distinguished. Combustion is rapid and often complete with fine fuels, whereas usually incomplete in heavy fuels. This fuel is distributed vertically *ie*. ground, surface and aerial fuels. Surface fuels support intense surface fires whose intensity is proportional to the biomass per unit area. Fuel compaction relates to the placement of the individual fuel pieces. Fire intensity is optimised when the fuel is loose enough to allow oxygen to reach the flame front.

Fire intensity is directly proportional to the amount of fuel available for combustion at any given rate of spread of the fire front (Brown and Davis 1973). In semi-arid savanna systems such as the south-eastern lowveld of Zimbabwe, rainfall largely determines the available fuel load at any one time, and the frequency of fires would have been determined by the accumulation of high fuel loads after very wet seasons.

Fuel moisture

The most critical factor regarding fuel load, with respect to fire intensity, is fuel moisture. This is expressed on a dry matter basis, and is critical in determining the intensity of a fire as it affects the ease of ignition, quantity of fuel consumed, combustion rate, rate of spread and flame height. However, Trollope (1983) found that fuel moisture per se only had a significant effect on fire intensity when this value exceeded 45%.

Atmospheric and physiographic conditions

Air temperature

Air temperature has a direct effect on fire intensity. High air temperatures raise the temperature of the fuel, and therefore the lower the amount of heat energy required for ignition. The indirect effects of air temperature are on relative humidity and evaporation. Fire intensity of surface fires increases with higher air temperatures, *ceteris paribus*.

Relative humidity

Relative humidity influences the moisture content, and has a negative effect on fire intensity. High fire intensities have been recorded when humidity is below 30% (Trollope 1983).

Wind

Wind is important because it determines the amount of oxygen available for combustion. Rate of energy release is positively related to the wind speed. Also, wind influences the frequency and extent of spotting (fire-brands landing ahead of the flame front) and pre-heating of the unburnt fuel load.

Slope

Slope changes the flame angle, especially when greater than 15-20°. However, due to the flat topography of most of the semi-arid savanna areas, slope is not a critical consideration.

The effect of fire regime on mopane woodland dynamics

Introduction

Fire is a disturbance factor in semi-arid savanna vegetation. A disturbance has been defined as "any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species" (Begon *et al.* 1990). Fire is a discrete event that opens up space at various scales, at various intervals, depending on the nature of the fuels and the occurrence of conditions conducive to fire (Bond and van Wilgen 1996).

The effect of fire on vegetation depends upon the combined effects of the different components of the fire regime:

1) the type and intensity of the fire, and

2) the season and frequency of burning.

The fire regime experienced by a particular system can strongly influence its vegetation composition and dynamics (Collins and Gibson 1990, Glitzenstein *et al.* 1995).

The effect of type of fire

Savanna trees are sensitive to various types of fire because of the differences in the vertical distribution of the release of heat energy. The most common types of fire in savanna areas are surface fires burning either as head (with the wind) or back (against the wind) fires. Crown fires occur under extreme fire conditions (high fuel load, high temperature, low relative humidity and strong winds), and are rare in semi-arid mopane woodlands. Observations in the Kruger National Park and the Eastern Cape indicate that crown and surface head fires cause the highest topkill of stems and branches, as compared with back fires (Trollope *et al.* 1996). This is because the heat energy is released above the soil surface at levels closer to the terminal buds of the aerial portions of the tree (Trollope 1993). However, there is only limited quantitative data to support these observations. A burning trial at the University of Fort Hare (arid savanna) showed that the phytomass of bush was reduced by 75% in the area burnt as a head fire, in comparison to 42% in the area burnt as a back fire (Trollope 1980).

Head fires are recommended because they cause the least damage to the grass sward, but maximum damage to the woody vegetation (Stocks and Trollope 1993). Conversely, back fires have a slow and low release of heat energy. This may have the potential to kill seeds and seedlings, and impact over the long term, as these fires limit or exclude recruitment of tree species (even those that are fire-resistant as adults).

Trollope *et al.* (1996) state that the repeated application of intense head fires (caused by the ignition procedure, applied in the Kruger National Park, whereby burning blocks were ignited around the perimeter, and the subsequent development of a fire convection column) prevented the recruitment of large trees. Also, by repeating the type of fire applied, a more homogenous response (even-structured stands) was observed.

The effect of fire intensity

If the grass component is drastically altered and reduced, then the attainable fuel load is reduced. A reversal to a pioneer stage may have a marked effect on fuel load (van Wilgen *et al.* 1990). Alternatively, an increase in woody density, accompanied by reduced grass production, could have the same effect on fuel load. Trollope (1983) shows that the effects of fuel load, fuel moisture, relative humidity and wind speed were the most significant factors in determining fire intensity. Observations in the Kruger National Park (Trollope *et al.* 1996) indicate that bush is very resistant to fire alone (mopane even more so than other species). The average mortality for 14 of the most common bush species subjected to 43 fires (ranging in fire intensity from 110 to 6 704 $kJ.s^{-1}.m^{-1}$) was only 1.3%. Generally, the main effect of fire on the woody component in semi-arid savannas is to cause a topkill of stems and branches forcing the plants to coppice from the collar region of the stem. The impact is therefore on vegetation structure rather than on tree mortality.

The effect of fire intensity on the topkill of bush was investigated in the savanna areas of the Kruger National Park (Trollope *et al.* 1995), and it was found that the woody vegetation is not significantly affected by fire alone when the trees and shrubs are taller than 3 m (Figures 2.2 and 2.3).

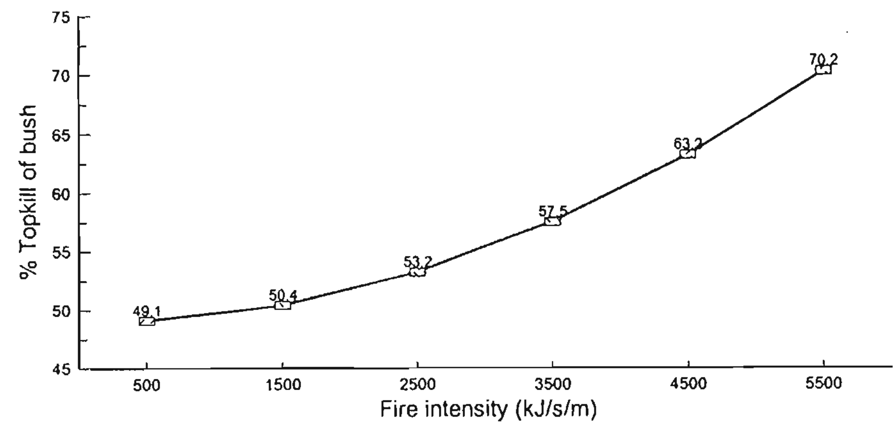

Figure 2.2 Effect of fire intensity on the topkill of bush two metres high in the Kruger National Park, South Africa

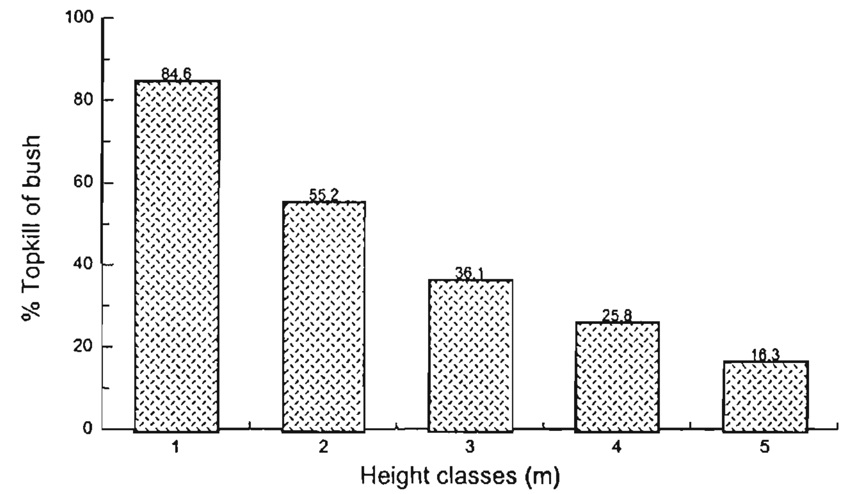

Figure 2.3 Effect of height on the topkill of bush subjected to a fire intensity of 3 000 kJ.s^{-1}.m^{-1} in the Kruger National Park.

The effect of season of burning

The effect of season of burning on tree and shrub vegetation is difficult to quantify because it is confounded with fire intensity. Fire intensities are not determined so much by season, but primarily by fuel load and moisture, and the fire intensity experienced in a particular season may not be unique to that season. However general trends relating to fuel load, temperature and relative humidity can be recognised. In winter the grass layer is dormant, dry, and able to support intense fires, whereas during summer the grass is green and fires are much cooler. West (1965) postulated that trees and shrubs are probably more susceptible to fire at the end of the dry season when the plant reserves are depleted due to the new spring growth. Wade and Johansen (1986) concluded that the seasonal variations in tree physiology or phenology are critically important in determining the susceptibility of trees to fire. I refer to this as the 'phenophase' hypothesis, which postulates that mopane trees differ in their response to fire owing to their potentially variable sensitivity to fire at different phenological stages *ie.* increased susceptibility shortly after leaf expansion, than in winter when the trees are leafless.

Glitzenstein *et al.* (1995), consistent with this phenophase hypothesis, showed that deciduous oak species were least vulnerable to dormant-season burning and most vulnerable to burning in the early growing season. This was shown particularly by seasonal trends in the effect of burning on oak mortality (both topkill and complete kill) and, to a lesser extent, on oak recruitment. Detrimental effects of spring burning on oaks were partly explained by fire behaviour, but there was an important residual effect of burning season, particularly on complete kill. These results are species-specific, applying to oak species. Their results showed few systematic or predictable effects of season or frequency of burning on dynamics of longleaf pine (*Pinus palustris*).

Trollope *et al.* (1995) showed that the 1.3% mortality of bush after fires, had been applied to bush ranging from dormant to actively growing plants. With such a low mortality over such a range of phenological states, it was concluded that the woody vegetation is not sensitive to season of burn in the Kruger National Park.

The effect of frequency of burning

Results relating to the effects of frequency of burning are generally conflicting. Frequency of burning in the Kruger National Park, over 42 years, appears not to have had any significant effect on the density of woody plants (van Wyk 1971). However, frequent burning has a highly significant effect on the physiognomy of tree and shrub communities in savanna areas. Plots with 14 years of annual burning at the Matopos Research Station, Zimbabwe, showed a 70% reduction in woody phytomass by comparison with plots completely excluded from fire (Kennan 1971). In the arid savanna of the Eastern Cape annual burning caused a 65% reduction in the woody phytomass, over an 11 year period (Trollope 1983).

No quantitative data for the effect of frequency of burning on changes in tree and shrub phytomass are available from the long-term burning trials in the Kruger National Park. Visually, however, the difference in woody phytomass between the control plots that are completely protected from fire and the annual, biennial and triennial burning treatments show a dramatic decline in the woody phytomass with an increase in burning (Trollope *et al.* 1996). Any worthwhile investigation into the effects of frequency of fire on mopane woodland density and structure will need to concentrate on the effects over long periods because the event-dependent effects of fire behaviour during a single fire event may show accumulative effects over time. Repeated burning will suppress Gulliver individuals, and in combination with selective browsers such as black rhino and elephant, may result in low recruitment of new individuals into the system. Not only the low height classes, but also the larger trees, will be impacted by more frequent burning. Continued defoliation by annual fires will result in coppicing from aerial and basal regions. Post-burn browsing pressure may lead to removal of this regenerative growth, leading over the long term, to a reduction in plant vigour and a structural change.

Conclusions

It is evident that the factors affecting mopane woodlands are numerous and highly complex. The tree density, physiognomic structure and species diversity of a particular site is determined by a combination of the following: autogenic factors (self-thinning and competition with the grass sward), and allogenic factors (climate, edaphic conditions and environmental factors).

Fire is an environmental factor that is a major determinant of mopane woodland dynamics. If co-occurring with elephant impacts, this combination can be critical in driving vegetation change, even overriding other factors. The reaction by mopane to fire regime (type and intensity of the fire, and season and frequency of burning) is similar to that of other tree and shrub species in southern Africa. Profuse coppicing occurs after high intensity fires and, in conjunction with browsing by elephants, results in a highly significant decrease in the phytomass of the canopy, but very little change in the density of trees. An area lacking in understanding is the degree to which mopane reacts to the different components of the fire regime, especially the type and intensity of fire.

Owing to its ecological distribution, being found on low potential and xeric soils, the opportunity for intense fires is limited. This is further exacerbated by mopane's strong competitive ability, as it is shallow-rooted and is able to utilise water at matric potentials lower than grasses. Therefore, even if tree density is reduced, the areas opened up may not support vigorous grass production. This will still exclude the potential for intense fires, and lead to no long-term change in tree density as a result of fire alone. However, in combination with elephants and drought, the structure of the mopane woodland may well change dramatically. The following flow diagram is proposed for mopane woodland in the south-eastern lowveld of Zimbabwe:

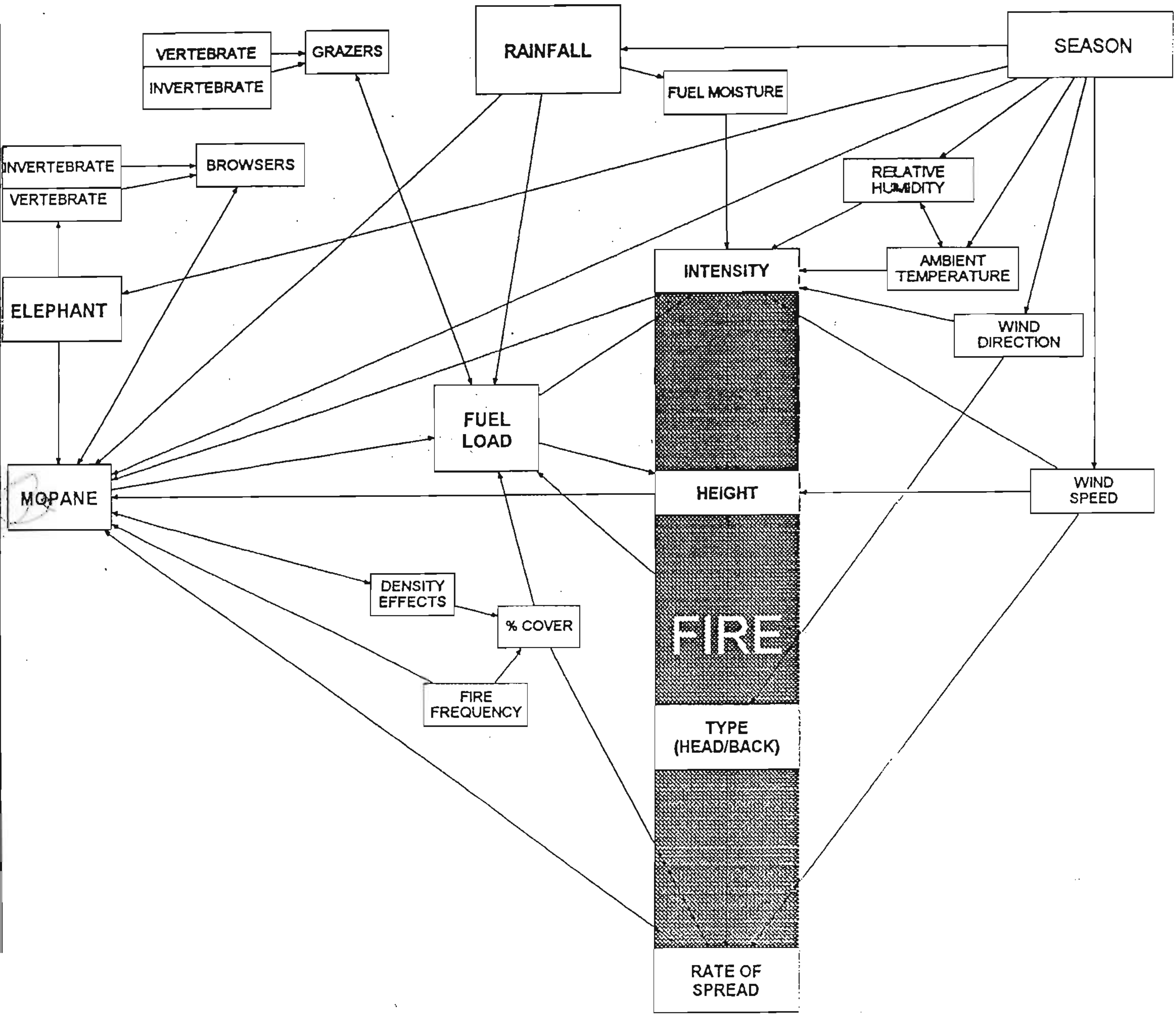

Figure 2.4 Conceptual model of fire dynamics in mopane woodland in the south-eastern lowveld of Zimbabwe (interpret arrows as interactions, with the direction of the arrows determining the dependent/independent components of the interaction/s. Arrows that cross are not linked).

It is concluded that the factors determining mopane woodland structure and functioning are numerous and complex. This suite of factors interact in response to each other, and to a highly variable environment. The available literature does not include much quantitative data, or elucidate principles, relating to the effects of fire regime on the population dynamics of mopane vegetation. It is concluded however that mopane is a strong competitor with the grass layer, is highly adapted to its environment (climatically and edaphically), and is both stable yet resilient where it occurs. Fire, although being a major determinant of mopane population dynamics, does not alter the stand density or species diversity of mopane woodlands, but together with elephant impacts, leads to a change in the structure of the vegetation. This change is generally an opening up of the woodland. The degree of this change will depend on the type and intensity of fires, the frequency and season of burning, and the extent of elephant impact. Further research into the effects of fire on the population dynamics of mopane, and aspects of its physiological response to fire, is necessary for a more accurate and complete approach to mopane woodland management.

The complexity of the factors involved in determining mopane woodland structure and functioning are obvious. The major determinants however are the following:

1) climate (*ie*. rainfall),

2) elephants, and

3) the fire regime.

Key questions and hypotheses

Standing crop dynamics

1) It was hypothesized that owing to the variability in grass sward structure through the year, one standard disc pasture meter calibration equation cannot suffice to predict standing crop for the whole year. Is there one standard equation applicable to all seasons, or are there equations suitable for different seasons because of the varying growth forms of the grass sward through the season? In addition, is the standard disc pasture meter procedure the most accurate to estimate the standing crop of the mopane woodland vegetation?

2) It was hypothesized that standing crop for a particular month is highly dependent on the effective rainfall for the previous month. Can a predictive equation for determining standing crop (for a given month) from standing crop and/or effective rainfall for the previous month, be determined? With this equation, standing crop, and therefore fuel load, can be accurately estimated.

3) It was hypothesized that peak standing crop is positively related to annual rainfall, and can be predicted. Is there a quantifiable relationship between peak standing crop and effective rainfall? With this it will be possible to estimate the potential peak standing crop (fuel load) from the effective rainfall over the season. This peak standing crop figure is the theoretical maximum from which standing crop through the dry season will decline.

4) It was hypothesized that standing crop declines through the dry season as effective rainfall decreases. Can a 'decrease function' for the decline in standing crop through the dry season be described? It is expected that standing crop will decline from peak standing crop as effective rainfall drops. Knowing this decline function will allow the estimation of standing crop for a specific month, given the peak standing crop.

Mopane leaf quantification

1) In order to successfully describe and interpret the effects of fire on mopane woodlands an appropriate quantitative description of individual trees was required. A method to estimate leaf dry mass using tree dimensions was developed by Smit (1994) in mopane veld north of the Soutpansberg in South Africa. However it was hypothesized that the mopane leaf quantification equations for Malilangwe Estate are different to those developed for the Soutpansberg. Is the mopane leaf quantification equation for the south-eastern lowveld of Zimbabwe different to that determined for the Soutpansberg in South Africa? Owing to the differences in the growth forms encountered in the two areas (Malilangwe having shorter, more shrub-type stands), it is expected that the two equations will be different.

Effect of season and type of fire

1) It was hypothesized that the damage to a mopane tree through fire is largely determined by the phenophase of the plant. Trees burnt in the late dry season will be damaged more than those burnt in the early dry season, with those burnt in the mid dry season being impacted least.

2) It was hypothesized that within the same season the damage to a mopane tree is largely determined by the type of fire. Head fires lead to greater damage than back fires. What is the effect of season of burning and type of fire on mopane woodlands in the south-eastern lowveld of Zimbabwe? It was proposed by West (1965) that trees and shrubs are probably more susceptible to fire at the end of the dry season, when plant reserves are depleted after initiating new growth. Because of this phenophase sensitivity, mopane trees burnt in different seasons may differ in their response to fire. The type of fire (back fire or head fire) was investigated as trees are sensitive to various types of fire because of the differences in the vertical distribution of the release of heat energy (Trollope *et al.* 1996). In other savanna areas it has been shown that head fires cause the highest topkill of stems and branches, because the concentration of heat energy is at levels closer to the terminal buds of the tree (Trollope 1980).

I have assumed that the principles and trends described for other semi-arid savanna tree species should give some guidelines as to the possible responses of mopane to the factors influencing it. However, it is my intention to test specific hypotheses in this thesis, in order to gain a better understanding of how mopane woodland responds to different seasons and types of fires. In order to answer the questions posed above, an empirical investigation into the effects of different seasons of burning and types of fire on mopane woodland in the south-eastern lowveld of Zimbabwe was undertaken, incorporating the following:

1) To grasp the present state of understanding and knowledge of the effect of fire on mopane woodlands, a comprehensive literature review of the determinants of mopane woodland dynamics in the south-eastern lowveld of Zimbabwe was undertaken.

2) To record the primary determinants of savanna grass production, monthly rainfall and pan evaporation figures were recorded over the study period.

3) In an attempt to accurately predict standing crop (fuel load) in the mopane woodland areas, a predictive equation for determining standing crop, for a given month, from the previous month's standing crop and effective rainfall, was determined. Also, the determination of the relationship between peak standing crop and rainfall was calculated. Using this relationship to determine peak standing crop, a 'decrease function' for the decline in standing crop as effective rainfall decreases through the dry season (to estimate standing crop as it declines from peak standing crop) was

4) It was realised that the form of the mopane trees occurring in the south-eastern lowveld of Zimbabwe were different to those found in the Soutpansberg of South Africa, and therefore the leaf quantification equations determined by Smit (1995) may be inappropriate. This led to the development of a mopane leaf quantification equation for the south-eastern lowveld of Zimbabwe (to estimate leaf dry mass by measuring the spatial canopy volume of individual trees).

5) The recording of rainfall/evaporation data, the prediction of standing crop (fuel load) over the study period and the derivation of two leaf quantification equations for mopane, were required to undertake the major focus of the study: the investigation and quantification of the effect of fire on mopane woodlands by recording the impact of different seasons of burning and types of fire on tree height, number of stems, maximum canopy diameter and leaf dry mass of mopane trees.

Chapter 3

Study area

The study area refers to Malilangwe Estate (ME), which is a privately owned commercial wildlife operation, managed by the Malilangwe Conservation Trust (MCT). This area was previously known as Lone Star Ranche.

Location

Malilangwe Estate lies approximately 20°58'- 21°15' S and 31°47'- 32°01' E, and covers an area of 40 600 ha. This includes what was previously two wildlife ranches situated in the south-eastern lowveld of Zimbabwe (Figure 3.1). Maranatha Ranch forms the northern section, and is 12 100 ha in size. Lone Star Ranche is the larger southern section, being 28 500 ha in size.

The southern boundary of ME is contiguous with the Gona-re-Zhou National Park, with a twin-cable game fence that allows for the free movement of all game species in and out of the Park. The western boundary borders with the Chiredzi River, ie. Hippo Valley Estates game section, with a short distance running along Matibi II Communal Land. The boundary with the communal land is fenced with a game-proof fence. The eastern boundary is Resettlement Land, also with a game-proof fence having been erected. This fencing extends along the northern boundary (the Triangle/Tanganda tar road).

History of Malilangwe Estate

Before the arrival of white settlers the area was inhabited by small numbers of agro-pastoral Tsonga people, who had settled along the Chiredzi, Nyamasikana and Runde rivers (as well as other smaller tributaries and artesian wells). During 1934 the adjacent Chipinda Pools area was proclaimed the Gona-re-Zhou Game Reserve (the fifth National Park to be established in Rhodesia). This large reserve stretches from the Mabalauta area in the south to the Save river in the north.

Figure 3.1 Malilangwe Estate (in relation to Zimbabwe and Africa).

After World War II areas of land were allocated to returning servicemen by the then Land Settlement Board of the Federation of Rhodesia and Nyasaland. Mr Ray Sparrow was allocated land in the Masvingo District, but applied for an area of land in the lowveld, in exchange for this. This was authorized, and he and his family moved down, in 1949, to what became known as Lone Star Ranche. The ranch was originally 4 000 ha in size, and was situated to the south of the Malilangwe Hills. Over the following 30 years he bought a further 24 500 ha of the surrounding Crown Land, and this was much the same area that is today ME.

From 1949 to 1969 cattle were the sole income from Lone Star Ranche. Even so, the majority of wildlife species (excluding predators) were conserved on the ranch. An indication of the dedication of Mr Sparrow to conserving wild game species, was the measures he took from 1972 onwards to keep buffalo, while pressure was applied by the Veterinary Department to eradicate this species in the lowveld. This matter was eventually decided in court, and Mr Sparrow erected a buffalo-proof fence to retain his population within the Lone Star Ranche. From the early seventies the Sparrow family began running organised hunting safaris on the land. During the 1983 drought nearly 80% of the cattle were lost, but by this stage the trophy hunting operation was well established. By 1985 the last remaining cattle were driven off the land completely. Once these animals were removed predator control was relaxed and the populations of resident species (predators and ungulates) increased. Trophy hunting continued to be the main income until 1987, when photographic safaris began. The severe drought of 1992/93 significantly reduced the numbers of wildlife species however.

In March 1994 the ranch was sold to the Malilangwe Conservation Trust, which is a board of trustees set up to manage funding coming into the country from an American sponsor, for the purpose of conserving wildlife, and extending the benefits of renewable natural resource management into the local communities. Consumptive and non-consumptive wildlife utilisation continues today, with additional programmes for the re-introduction of locally extinct species and research into the functioning and management of the various ecosystems in the area.

Climate

The south-eastern lowveld of Zimbabwe has a warm, arid climate with a distinct wet season (December to March), cool dry season (April to August) and hot dry season (September to November). The mean annual temperature exceeds 18°C (van Rooyen *et al.* 1981). Temperatures are high, with daily maxima above 32°C and peak temperatures often over 45°C. Winters are mild, the lowest recorded temperature being 10°C, and no record of frost exists.

Daily rainfall figures for ME have been recorded since July 1951. These records, as supplied by the Department of Meteorological Services (Harare) in June 1996, and updated monthly since then, were used to examine past rainfall patterns, determine long-term monthly and annual means and medians, and to represent graphically the monthly rainfall for the 1995/96 to 1997/98 seasons. A 5-year running mean technique was used to 'smooth' the long-term annual rainfall figures. This was done to examine possible wet and dry periods. Daily pan evaporation figures were obtained from the Zimbabwe Sugar Association (ZSA) in Chiredzi. These figures were totalled to obtain monthly pan evaporation figures. The long-term mean annual pan evaporation was also supplied by the ZSA (1991).

As at June 1998, ME had a long-term mean and median annual rainfall of 542 and 574 mm respectively (Appendix 1). This describes a negatively skewed distribution, where the occurrence of a number of very low values bias the mean downwards. As is so characteristic of semi-arid savanna areas, annual rainfall is highly unpredictable and variable (standard error about the mean is 180.4 mm). Figure 3.2 presents the annual rainfall from 1951 to 1998.

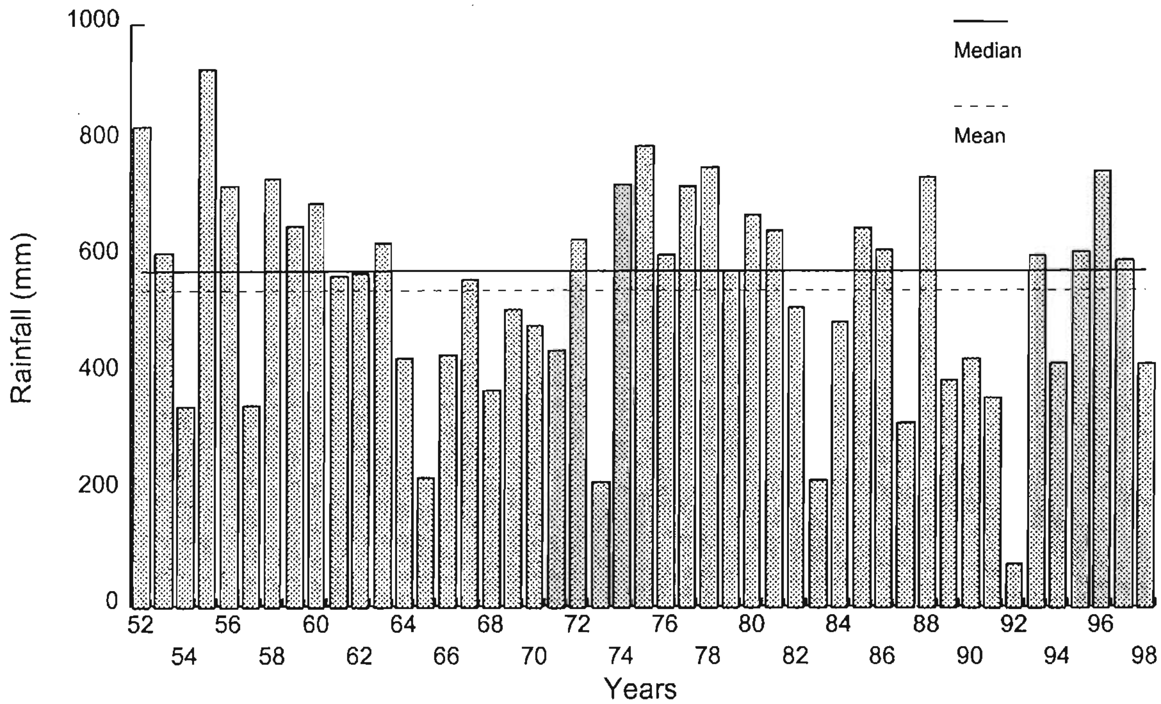

Figure 3.2 Annual rainfall for Malilangwe Estate, from 1951/52 until 1997/98, in relation to the long-term median and mean.

The variability in year-to-year rainfall has been large (up to 30%), and, with the exception of the last two decades, has shown little sustained trend (Hulme 1996). Much of this variation is random. However, within the record, real and significant non-random components are clearly identifiable. Contained within the generally random year-to-year rainfall variability is this underlying non-random component which has varied systematically for over 80 years. This is strong enough to have imparted a degree of regularity to rainfall variations, that cannot be ignored (Preston-Whyte and Tyson 1988). A feature of Southern African rainfall is the apparent cycles of wet and dry periods. Eighteen-year cycles of nine dry and nine wet years occur in the summer rainfall areas of South Africa. A similar wet/dry oscillation is evident for ME (Figures 3.2 and 3.3). Records from 1951 to 1998 show periods of above and below average rainfall. These periods are clearly observed in Figure 3.3, in which a five-year moving-average technique is applied to smooth the data. Above-average periods were 1952-1963 and 1974-1981. Below average periods were 1964-1973 and 1982-1994. No predictions can be made from the data presented in Figures 3.2 or 3.3.

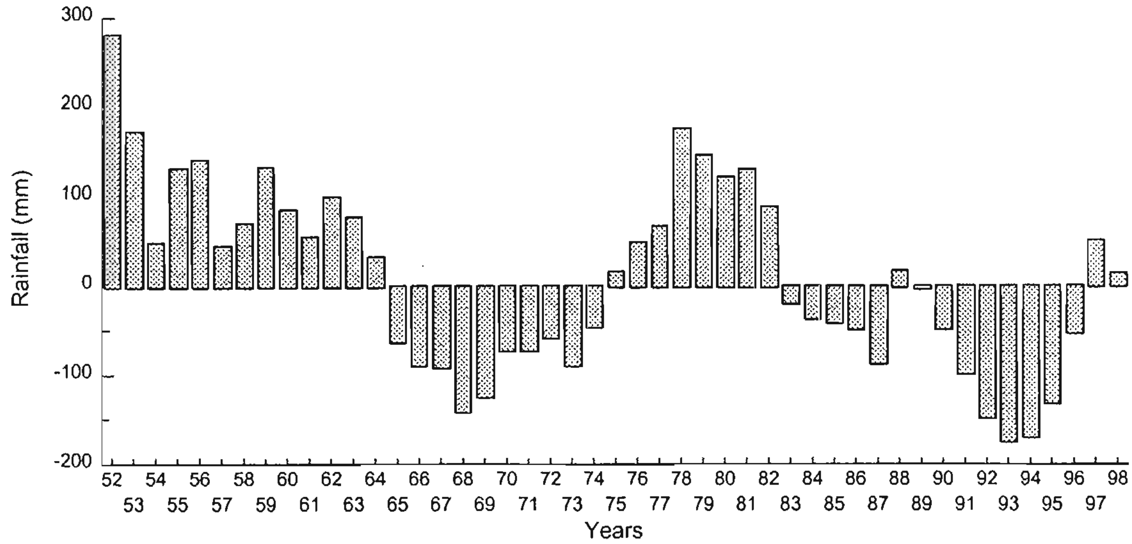

Figure 3.3 Five-year moving-average annual rainfall for Malilangwe Estate, presented as positive or negative deviation about the long-term mean of 542mm.

The 1995/96, 1996/97 and 1997/98 rainfall figures are presented in Table 3.1.

Table 3.1 Long-term (1951-1998) mean and annual rainfall (mm), s.e and CV% figures for Malilangwe Estate, on a monthly basis (Department of Meterological Services, Harare)

Month	**1951-98**	**1995/96**	**1996/97**	**1997/98**
July	6.5	42.5	33.5	8.5
August	4.6	0	6	0
September	12.6	0	4	9.5
October	24.8	0	2.5	17
November	63.7	32	64.5	40.2
December	109.4	82	66.5	70.4
January	116.5	300	167.5	184.3
February	115.1	205	119.5	63
March	44.5	33	72.5	17.9
April	26.8	33	36	3.8
May	10.2	13.5	20	0
June	7.2	5	0	0
Total		746	592.5	414.6
Means	542.0	543.7	544.8	542.0
S.E	180.4			
CV%	33.3			

The 1995/96 season was 37.2% in excess over the long-term mean of 543.7 mm for that season, 1996/97 an 8.8% excess and 1997/98 a 23.5% deficit. The 1995/96 season was the fourth highest rainfall season recorded at Malilangwe. Rains fell late, but when they did fall, 67.7% of the annual total fell in January and February (Figure 3.4). Seven of the twelve other months were below the long-term monthly mean.

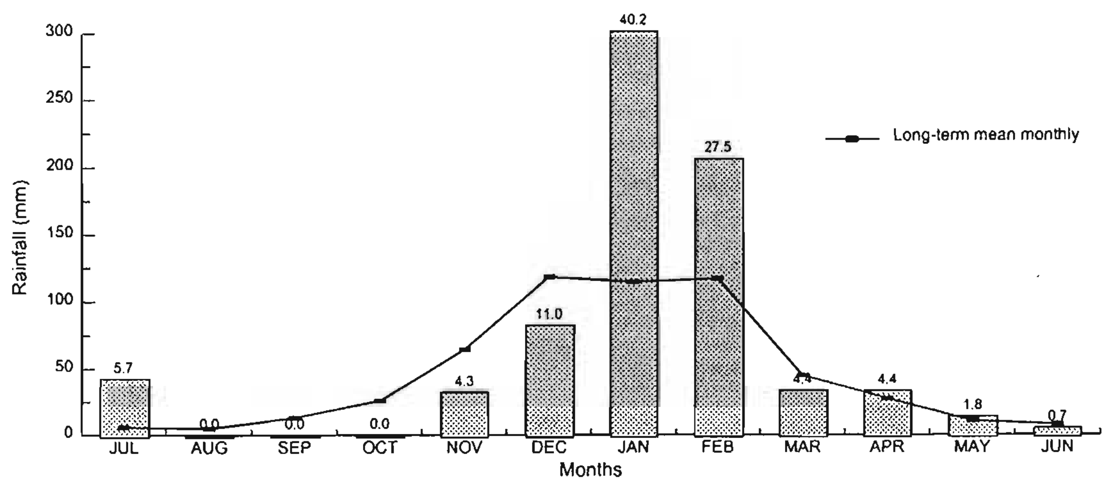

Figure 3.4 Monthly rainfall for Malilangwe Estate for 1995/96 in relation to long-term monthly mean and percentage contribution to annual rainfall.

The 1996/97 rainfall season was characterised by above-average rainfall in eight out of twelve months, and only 48.5% of the annual rain fell in January and February (Figure 3.5).

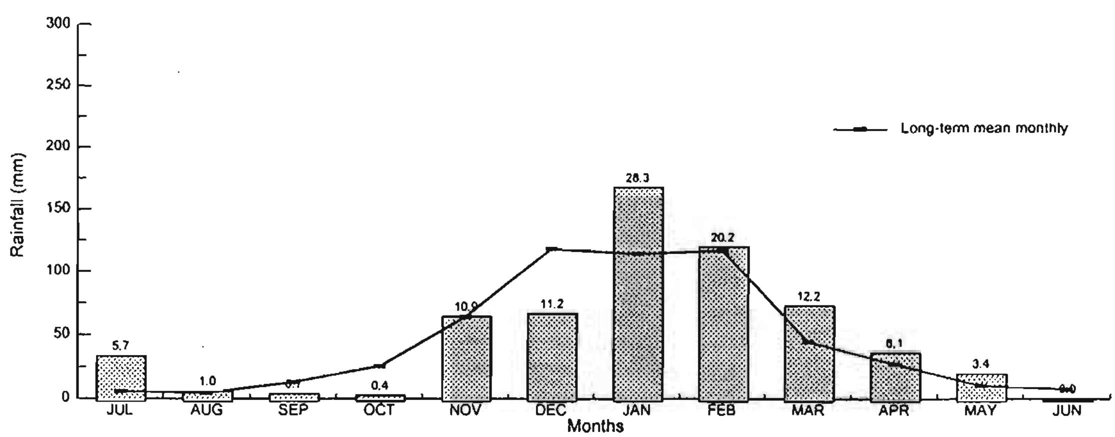

Figure 3.5 Monthly rainfall for Malilangwe Estate for 1996/97 in relation to long-term monthly mean and percentage contribution to annual rainfall.

This pattern started in July 1996, with uncharacteristically high falls, and continued into the wet season. Two weeks of early rains in November 1996 resulted in early grass growth and wet conditions that made burning impossible.

The 1997/98 season had only two months with above-average rainfall. December, January and February accounted for 76.6% of the annual rainfall, with January alone contributing 44.5% of the annual total (Figure 3.6).

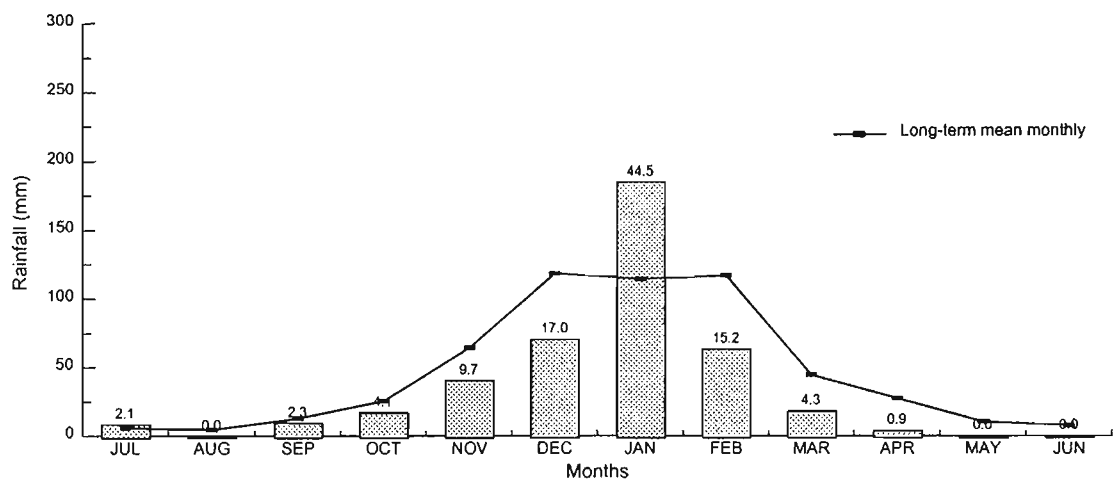

Figure 3.6 Monthly rainfall for Malilangwe Estate for 1997/98 in relation to long-term monthly mean and percentage contribution to annual rainfall.

The average annual rainfall is considerably lower than the world average of 860 mm. Over most of the country annual pan evaporation ranges between 1 100 mm and 3 000 mm, with ME being estimated as 1 900 mm (Zimbabwe Sugar Association 1991).This is well in excess of the annual rainfall, as well as that recorded on a monthly basis (Figure 3.7). January 1998 was the only month during the study period in which rainfall exceeded pan evaporation.

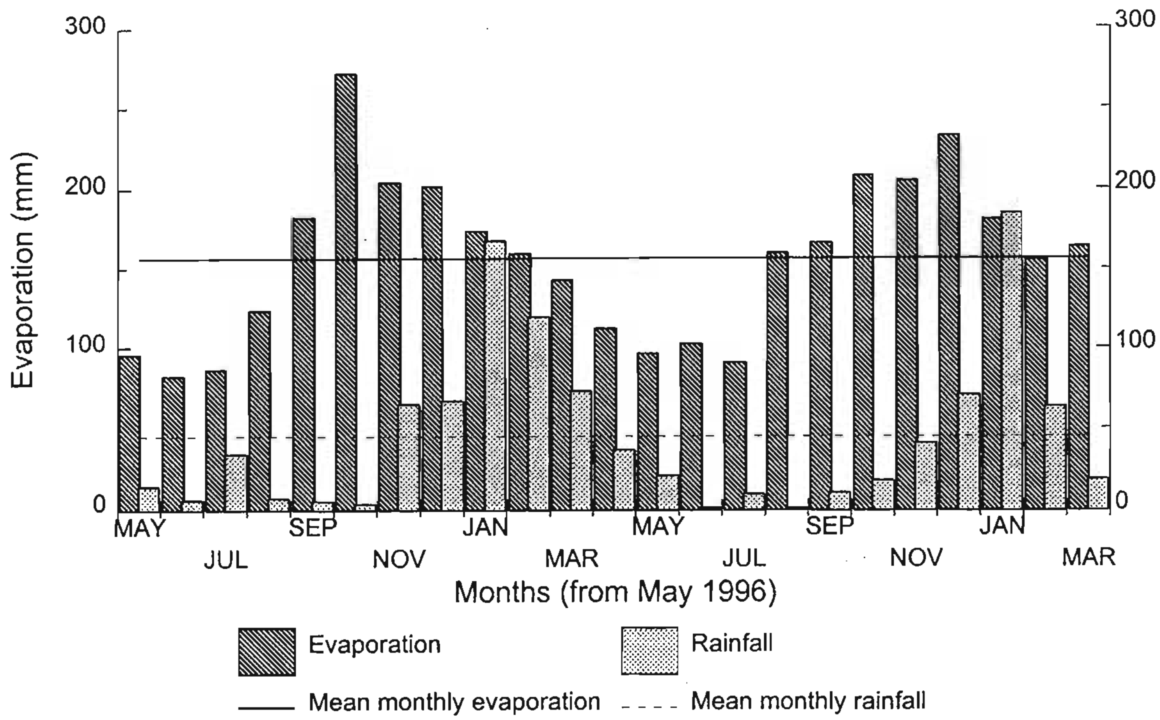

Figure 3.7 Monthly pan evaporation and rainfall for Malilangwe Estate, in relation to mean monthly pan evaporation and rainfall.

From this figure it is clear that ME is in a continuous situation of moisture deficit, both on a monthly and annual basis.

The rainfall records for ME Headquarters are assumed to be representative of the rainfall occurring at the treatment blocks, which is approximately 9 km distant. No rain gauges are located at the nearest game scout picket, and the purchase and installation of one or more rain gauges within the study site was regarded as too costly and unnecessary.

The factors influencing the rainfall patterns, under the influence of the South East Trade Winds which penetrate inland from the Mozambique Channel, appear regional rather than local (Booth 1991). Therefore the spatial variation in rainfall over the treatment blocks, within the study site, is considered to be not great enough to influence treatments. The temporal scale is also important when considering the population dynamics and life-class interactions within a community, especially when the species under consideration is adapted to low soil moisture conditions.

November to March is considered to be the rainy season, as approximately 82% of the annual rain falls within this period (Figure 3.8). However, the majority of this falls in turn during the three months December to February (62%).

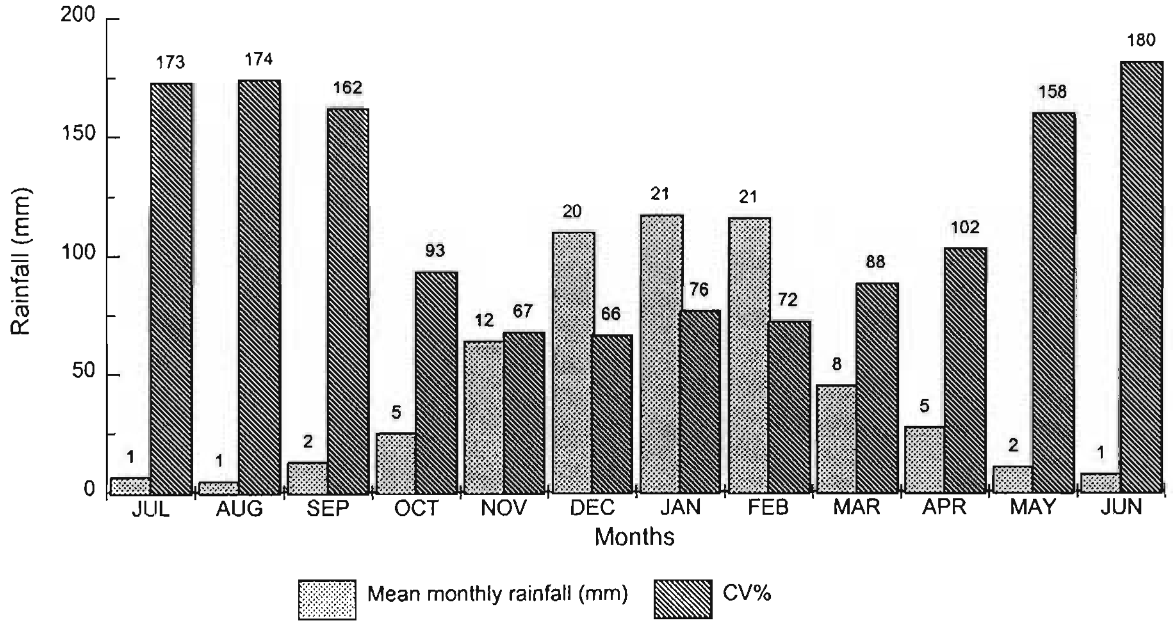

Figure 3.8 Long-term mean monthly rainfall, percentage contribution to long-term mean annual rainfall and CV%'s for Malilangwe Estate.

Average monthly rainfall for December, January and February is very similar. The point to note though is the fact that January rainfall is more variable than either December or February. The months with the least variability are November, December and February. In contrast, the low rainfall (drier) months are highly variable and unpredictable (CV%'s over 135%).

During most years the arid and semi-arid savannas of the south of Zimbabwe (below 600 mm) are characterized by a mid-season "drought". High rainfall is experienced at the start of the season, whereafter there is a period of lower rainfall during the middle of the wet season, often January. This contributes to the high variability of January rainfall.

A winter period of "guti" rain (soft drizzle) is characteristic of the south eastern lowveld of Zimbabwe. The 1995/96 season had a marked winter rainfall period (Figure 3.4), and this resulted in extended grass production and high fuel loads. The same occurred in the 1996/97 season.

Soils and geology

The Malilangwe Range dominates the central and northern areas of ME, consisting of Stormberg sandstone, cut by many faults, and resulting in a broken rocky landscape. North of this range, the area is dominated by paragneiss with numerous dolerite intrusions. Most of the area south of this sandstone range is covered by basaltic soils, and extends into the Gona-re-Zhou National Park. The soils near the Malilangwe Range are of low base status (dystrophic sandy soils), derived from the sandstone. The soils of the basalt plains are deep, heavy clays (vertisols), having a high base status (eutrophic).

The main river systems in the area are the Chiredzi, Runde (previously the Lundi) Nyamasikana and Mahande rivers. To the south of the Nyamasikana gorge, and overlying the basalt derived soils are palaeo-delta deposits comprising mesotrophic red sandy loam soils. Lastly, two narrow, well weathered, alluvial belts exist along the incised Chiredzi and Runde rivers. These rivers flow strongly during the rainy season, but are dry during the dry season. A large dam has been constructed on the Nyamasikana river, as well as other smaller weirs and reservoirs on the tributaries leading from the hills into the basalt plains.

Vegetation

The area falls within the Mopane vegetation of the Sudano-Zambezian Region (Werger and Coetzee 1978). This corresponds to Acocks (1988) veld type 15 (Mopane veld). The area is a deciduous savanna, and the vegetation has been recently described by Stalmans (1994). A list of vegetation communities is presented in Table 3.2. Nomenclature of species follows van Wyk and van Wyk (1997).

Table 3.2 The different vegetation communities of Malilangwe Estate (after Stalmans 1994)

Vegetation community
Coleochloa - Danthaniopsis
Brachystegia glaucescens- Androstachys johnstonii
Julbernardia globiflora - Diospyros usumbarensis
Newtonia hildebrandtii - Gyrocarpus americanus
Colophospermum mopane - Grewia spp.
Colophospermum mopane - Combretum apiculatum
Colophospermum mopane - Heteropogon contortus
Colophospermum mopane - Brachiaria eruciformis
Croton megalobotrys - Phyllanthus reticulatus
Eriochloa - Echinochloa
Sporobolus iocladus - Chloris gayana
Acacia tortilis - Grewia spp.
Acacia nigrescens - Combretum imberbe
Combretum imberbe - Setaria sphacelata
Acacia borleae - Brachiaria deflexa
Kirkea acuminata - Acacia erubescens
Albizia sp. - Dalbergia melanoxylon
Androstachys johnsonii - Mundulca sericea

The sandstone outcrops are dominated by miombo vegetation that is dominated by *Julbernardia globiflora* and *Brachystegia glaucescens* (approximately 10% of the area). Belts along the major rivers consist mainly of *Loncocarpus capassa, Acacia nigrescens*, *Acacia borleae* and *Combretum imberbe* (approximately 10% of the area). *Acacia tortilis* and *Grewia* spp. dominate the small areas which were cleared for habitation by the Tsonga people, and along the Chiredzi and Nyamasikana rivers (approximately 8% of the area) where tsetse clearing took place (1959-1964).

Away from the Malilangwe Range, *Colophospermum mopane* is the most common and widespread woody species in the study area (approximately 72% of the area). Two mopane-dominated communities were identified on the basalt plains by Stalmans (1994):

1) on better drained stony soils a *Colophospermum mopane-Heteropogon contortus* community occurs, with associated species such as *Sclerocarya birrea* and *Pterocarpus brenanii* being present, and

2) nearer the Chiredzi and Runde Rivers clay percentage increases dramatically and drainage is impeded. A *Colophospermum mopane-Brachiaria eruciformis* community was identified on these heavier soils, but the trees are stunted and occur as dense stands. Both in cover and bulk of the grass layer *Panicum maximum* and *Urochloa mosambicensis* form the largest component (Stalmans

1994). The treatment blocks were chosen in these mopane-dominated communities.

This vegetation type is structurally varied, ranging from shrublands to taller closed woodlands. Mopane woodland dominates the low-lying areas, particularly in the southern and northern areas. Other tree species in these vegetation types are *Dalbergia melanoxylon, Acacia nigrescens, Sclerocarya birrea, Grewia* spp. and *Combretum apiculatum.* Grasses include *Urochloa mosambicensis, Cenchrus ciliaris, Heteropogon contortus, Aristida adscensionis* and *Enneapogon cenchroides*. The grass component is dominated by Increaser species, with very low percentage abundance of Decreaser species (Stalmans 1994).

Fire History

Pre-settlement fire history is vague, but the occurrence of periodic fires through the area is accepted, as the fire history of the adjoining Gona-re-Zhou National Park and Mozambique bear testimony to the regular burning of large tracts of mopane woodland. With the introduction of cattle however, the removal of forage through fire was avoided at all costs, and fire exclusion was actively implemented. This, along with the reduction in standing crop through removal by cattle, led to approximately 50 years of no burning, or very low intensity burns.

After the formation of Malilangwe Estate fire was introduced as part of the management programme, albeit on a small and exploratory scale, because of the inhibition of management staff. However isolated fires entered through the eastern boundary fence from Government Resettlement Land , and burned small areas. Together with management burning, the following areas were burnt: 1994 (2 430 ha or 6%), 1995 (9 340 ha or 23%), 1996 (1 625 ha or 4%) and 1997 (4 060 ha or 10%). The non-management fires occurred as head fires moving from the eastern boundary in a westerly direction, while management burns were carried out within management blocks (back fires were implemented along the boundaries, and head fires implemented thereafter from the windward boundaries). These management and non-management fires burned through mopane-dominated vegetation types, as well as small river course vegetation (more open grassland areas).

Chapter 4

Standing crop production in response to effective rainfall

Introduction

Technically the term grass biomass refers specifically to living grass material, and standing crop to living and dead material. For the purposes of this study, standing crop is synonymous with fuel load, as it is the grass layer which forms the greatest proportion of available fuel for burning. The accurate estimation of standing crop was therefore regarded as fundamental to determining the potential fuel load of the mopane woodlands of ME.

The objectives of this exercise were:

1) To successfully calibrate the disc pasture meter over a number of months,
2) determine whether derived regression equations were significantly different,
3) to monitor monthly standing crop and effective rainfall, and
4) to investigate the relationship between what I termed effective rainfall (ER - calculated by dividing monthly rainfall by monthly pan evaporation) and standing crop.

Procedure

Experimental design

The study of standing crop production in response to effective rainfall and the relationship between peak standing crop and rainfall was carried out in two of the control treatment blocks. These sites are representative of the mopane-dominated areas, and are situated within the same vegetation type as the burning treatments. During the study period these blocks were not burnt at all, and had been burnt in 1995 as part of the management burning programme. The age of the grass sward in these two areas was therefore approximately one year at the outset of the study, and had recovered fully from the previous years burn.

1) Disc pasture meter calibration

Standard procedure (Bransby and Tainton 1977)

In an effort to ensure accuracy and applicability to the study area, a bi-monthly calibration approach was used to develop a predictive equation for estimating standing crop using a standard disc pasture meter (Bransby and Tainton 1977). Two areas were chosen (one in each of the control blocks) that were representative of the mopane woodlands of the treatment blocks (the same vegetation type with respect to species composition and structure). Fifty disc meter readings (25 per area) were taken, and the respective grass material harvested from beneath the disc for drying. Drying was carried out at the ZSA laboratory, at 60°C until constant mass was reached, and the samples then weighed. For each calibration, a scatterplot was used to determine the relationship between disc height and dry matter. Linear regression analysis was then applied with disc pasture meter reading (cm) as the independent variable, and standing crop (g) as the dependent variable.

Revised procedure (Trollope and Potgieter 1986)

In addition to the method described above, the revised procedure described by Trollope and Potgieter (1986) was also carried out. This method included the following:

1) Calibration was carried out using a square, 4 m^2, quadrat.
2) Thirty sample points were selected, covering the seven major vegetation communities found on ME, and one quadrat sampled per sample point.
3) Within each quadrat nine disc readings were taken, giving a mean settling height.
4) All herbaceous material was harvested from within each quadrat.
5) The 30 harvested grass samples were dried at the ZSA at 60 °C until constant mass was reached, and the samples then weighed.

The 30 points were located in the vegetation communities presented in Table 4.1. Within each vegetation community, sample sites were chosen that covered widely different potential fuel loads, so as to obtain as wide a range of regression points as possible.

Table 4.1 The seven vegetation communities of Malilangwe Estate in which calibration data were collected for the revised procedure (adapted from Stalmans 1994)

Number	Vegetation community
1	*Colophospermum mopane - Grewia spp.*
2	*Colophospermum mopane - Combretum apiculatum*
3	*Colophospermum mopane - Heteropogon contortus*
4	*Colophospermum mopane - Brachiaria eruciformis*
5	*Acacia nigrescens - Combretum imberbe*
6	*Combretum imberbe - Setaria sphacelata*
7	*Julbernardia globiflora - Diospyros usambarensis*

Due to financial cut-backs by the Zimbabwean Department of Agriculture, the facilities at the ZSA were no longer available after October 1997, and the bi-monthly standard calibration could not be continued. The months for which standard calibration equations were developed were: June, August, October and December 1996; and February, June, August and October 1997. The revised procedure was only carried out once: February 1997.

2) Covariance analysis of regression equations

To establish whether there is a significant difference between the eight calibration equations, covariance analysis was used to test for the homogeneity of regression coefficients and intercepts. Hereafter pair-wise multiple comparisons were carried out among pairs of regression coefficients and intercepts, in order to determine which months are different from which others. To test the influence of season on the calibration equation, the effect of effective rainfall and standing crop on the slope estimates was carried out.

3) Monitoring of monthly standing crop

The recording of standing crop was carried out on a monthly basis from June 1996 to March 1998. The method developed by Bransby and Tainton (1977) was used, as it was considered to be a favourable, robust and quick technique. This measurement was obtained using a standard disc pasture meter, in the two representative control areas. Four transects, each containing 50 recordings (one every five paces), were carried out in each area. This gave a total of 400 points in the two areas.

4) The relationship between effective rainfall and standing crop

Monthly rainfall was believed to be too simple and inadequate a measure of the moisture available to the grass sward for production, because of the losses that take place through evaporation, evapotranspiration and run-off. Without having to take intensive soil moisture readings on a monthly basis, and divide incoming rainfall into its various components, it was decided to use rather an effective rainfall (ER) figure. This ER figure, albeit robust, was determined on a monthly basis, using the respective monthly rainfall and pan evaporation figures, being calculated as the ratio of monthly rainfall divided by monthly pan evaporation.

Standing crop was monitored on a monthly basis over the study period. The relationship between ER and standing crop was then investigated. Linear regression analysis was applied with ER as the independent variable, and standing crop ($kg.ha^{-1}$) as the dependent variable. The variable 'previous month' (standing crop for the preceding month) was then added in an attempt to elucidate more fully the relationship between standing crop and ER. This was done because the standing crop recorded in any particular month is largely dependent on that which exists the previous month, as well as the effective rainfall for that month.

Results

1) Disc pasture meter calibration

Standard procedure (Bransby and Tainton 1977)

The linear regression equations for the eight months are presented in Table 4.2.

Table 4.2 Linear regression values for eight months, including lower and upper 95% confidence limits (for each month degrees of freedom = 49)

Month	Intercept	Slope	R^2	F prob.
Jun 96	11.25	2.12	0.72	<0.001
Aug 96	28.33	3.69	0.39	<0.001
Oct 96	50.23	2.03	0.42	<0.001
Dec 96	33.12	2.63	0.40	<0.001
Feb 97	32.27	3.31	0.41	<0.001
Jun 97	33.64	2.34	0.58	<0.001
Aug 97	24.84	3.28	0.51	<0.001
Oct 97	29.42	3.02	0.46	<0.001

	Intercept		Slope	
	Lower 95%	Upper 95%	Lower 95%	Upper 95%
Jun 96	7.57	14.94	1.75	2.50
Aug 96	13.24	43.41	2.38	4.99
Oct 96	42.51	57.95	1.36	2.71
Dec 96	22.35	43.88	1.72	3.54
Feb 97	21.22	43.32	2.19	4.43
Jun 97	27.38	39.90	1.77	2.92
Aug 97	15.95	33.74	2.37	4.19
Oct 97	21.21	37.64	2.09	3.94

The linear regression equations were all highly significant (F prob. <0.001), with adjusted R^2 values between 39% and 72%. Figures 4.1 and 4.2 present these intercept and slope data.

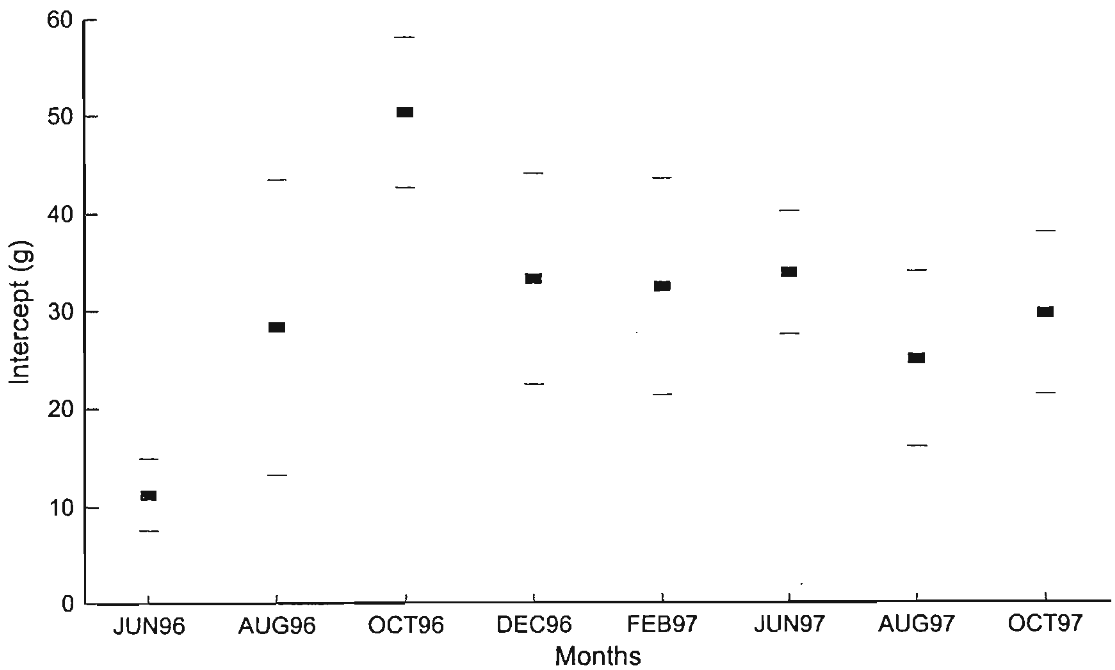

Figure 4.1 Intercept estimates (with 95% confidence limits) for eight regression equations.

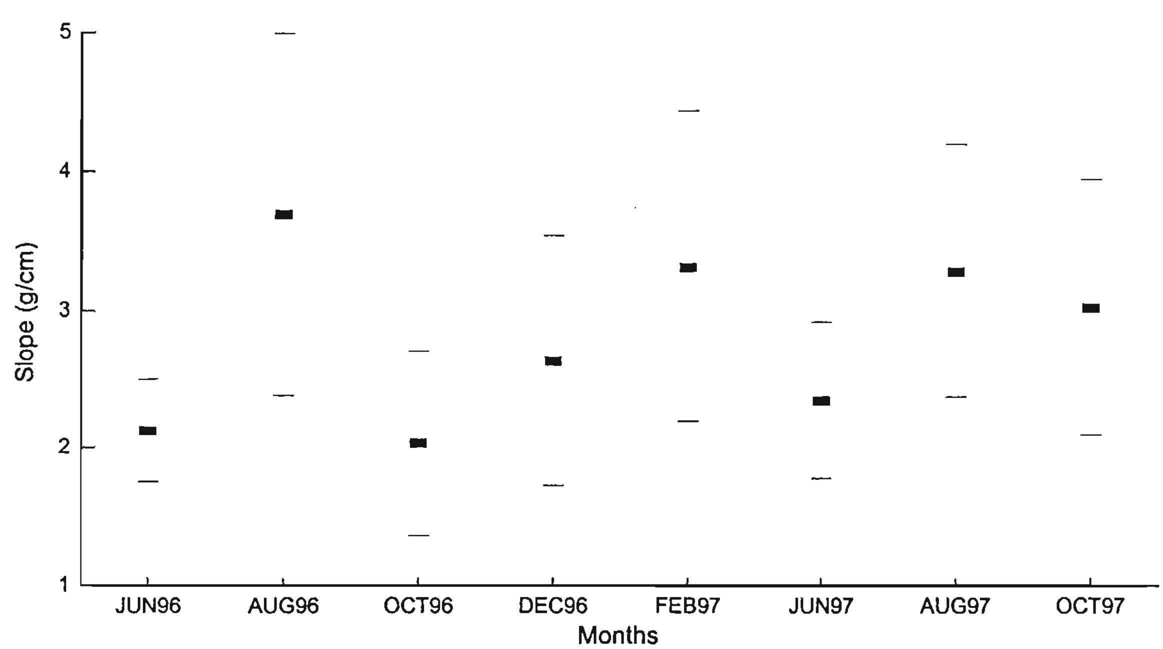

Figure 4.2 Slope estimates (with 95% confidence limits) for eight regression equations.

From the linear regression equations, it is obvious that both the intercepts and slopes of some months are significantly different to others, and that there is inconsistency in the trends of slopes and intercepts for the different months.

Revised procedure (Trollope and Potgieter 1986)

Regression analyses were conducted with the dependent variable standing crop ($kg.ha^{-1}$) and the independent variable (disc height). The independent variable was then subjected to logarithmic (ln x), square (x^2), square root ($x^{0.5}$) and reciprocal (1/x) transformations. Five points were found to be resulting in an appreciable reduction in the coefficient of determination. These points all had a high degree of lodged grass material, and because of this were unrepresentative, and these points were therefore excluded. The linear regression equations are presented in Table 4.3.

Table 4.3 The linear regression between disc height (cm), transformations of disc height, and standing crop ($kg.ha^{-1}$), (degrees of freedom for each analysis = 24)

Transformation	n	R^2	Intercept	Slope
x	25	0.88	376	197
ln (x)	25	0.85	-74	1 190
x^2	25	0.79	980	9
$x^{0.5}$	25	0.90	- 850	1 081
1/x	25	0.54	2 629	-2 467

R^2 = coefficient of determination

It was found that the square root transformation of the independent variable resulted in the best fit of the linear regression, for which the coefficient of determination was highly significant ($R^2 = 0.90$, $P<0.01$). The linear regression equation derived using the revised procedure is thus:

$$\mathbf{Y = -849.95 + 1081(X)}$$

where: Y= estimated standing crop ($kg.ha^{-1}$)

X = square root of disc height (cm)

The linear regression for the square root of disc height and standing crop is presented in Figure 4.3.

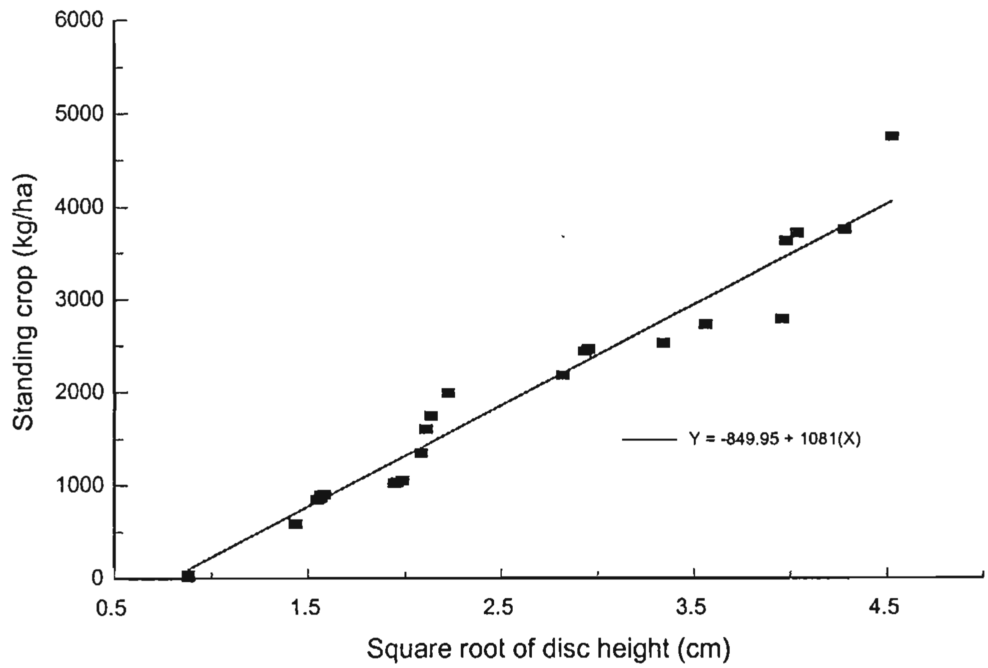

Figure 4.3 Calibration equation for revised procedure (Trollope and Potgieter 1986) covering seven vegetation types on Malilangwe Estate.

2) Covariance analysis of regression equations

The analysis of covariance carried out on the eight regression equations, gave the following results (Table 4.4).

Table 4.4 Covariance analysis results for intercept and slope

Intercept	Slope
F = 2.20	F = 15.60
F (7,384) = 2.04	F (7,391) = 2.04

On the basis of these tests, at the 95% confidence level, one concludes that the intercepts and slopes for the eight regression equations are significantly different. The multiple pair-wise comparisons between months was carried out for intercept, and then slope estimates.

Table 4.5 Intercept and slope t-test probabilities (read columns as comparisons between months)

Intercept

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97
Jun 96							
Aug 96	0.004						
Oct 96	<0.001	<0.001					
Dec 96	<0.001	0.480	0.012				
Feb 97	<0.001	0.557	0.008	0.903			
Jun 97	<0.001	0.394	0.008	0.936	0.831		
Aug 97	0.028	0.602	<0.001	0.234	0.280	0.170	
Oct 97	0.006	0.877	0.003	0.613	0.694	0.534	0.525

Slope

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97
Jun 96							
Aug 96	0.005						
Oct 96	0.873	0.004					
Dec 96	0.372	0.070	0.304				
Feb 97	0.059	0.552	0.046	0.299			
Jun 97	0.683	0.016	0.576	0.612	0.124		
Aug 97	0.065	0.522	0.050	0.318	0.968	0.134	
Oct 97	0.212	0.352	0.175	0.602	0.706	0.347	0.732

A more easily understood representation of Table 4.5 is presented in Table 4.6.

Table 4.6 Intercept and slope t-test probabilities (read columns as comparisons, months without letters in common are significantly different at the 95% level)

Intercept

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97	Oct 97
Jun 96	A							
Aug 96	B	B						
Oct 96	B	C	C					
Dec 96	B	B	D	D				
Feb 97	B	B	D	D	D			
Jun 97	B	B	D	D	D	D		
Aug 97	B	B	D	D	D	D	D	
Oct 97	B	B	D	D	D	D	D	D

Slope

	Jun 96	Aug 96	Oct 96	Dec 96	Feb 97	Jun 97	Aug 97	Oct 97
Jun 96	A							
Aug 96	B	B						
Oct 96	A	C	C					
Dec 96	A	B	C	C				
Feb 97	A	B	D	C	C			
Jun 97	A	C	C	C	C	C		
Aug 97	A	B	D	C	C	C	C	
Oct 97	A	B	C	C	C	C	C	C

The multiple comparisons between intercepts shows that the first three equations (Jun, Aug and Oct 1996) are significantly different to each other, and the other equations. The remaining five intercepts are not significantly different from each other, but are all different from the first three. The intercept estimate aids in defining the regression line, and may in fact be a sample statistic prone to misleading interpretations (Zar 1984). In this situation for example, discussion of the intercepts may require extrapolation of the regression lines far below the range of disc heights sampled.

The multiple comparisons between slopes are more complex. As with the investigation of intercepts, the five latter months are not significantly different to each other. However, the first three months have a number of significant and non significant relationships with other slope estimates. Using Table 4.5 to aid in examining these relationships, it was concluded that the derivation of a single combined regression equation was unacceptable. as the interrelatedness of slope and intercept coefficients made it difficult to identify a group, or groups, of similar months.

One would expect there to be an effect of season (dry versus wet) on calibration equations for the pasture disc meter. To test the effect of season, linear regression was applied with effective rainfall and standing crop as the independent variable, and the slope estimate as the dependent variable. The standing crop figures used were the dry mass samples from the calibration clipping quadrats. These two variables were chosen as they are two of the most easily obtainable variables available to the landowner. The results of the linear regression analyses are presented in Table 4.7.

Table 4.7 Linear regression values for effective rainfall and standing crop, over eight months (degrees of freedom = 7)

Variable	Intercept	Slope	R^2	P.
Effective rainfall	2.56	0.5200	0.10	0.23
Standing crop	2.05	0.0004	0.07	0.49

From these analyses it is clear that neither effective rainfall nor standing crop are significant in determining the slope coefficients over the eight months of calibration.

An attempt was made to develop a single combined regression equation for determining standing crop. The regression values for this equation are presented in Table 4.8.

Table 4.8 Regression values for common calibration equations using untransformed and transformed independent variables (degrees of freedom = 49)

Regression	Intercept	Slope	R^2	Sig (95%)
Untransformed	29.68	2.90	0.42	<0.001
Transformed	2.76	18.87	0.47	<0.001

The square root transformation of the independent variable led to an increase in the R^2 value, but only by 5%. The common calibration equation can be represented by Figure 4.4.

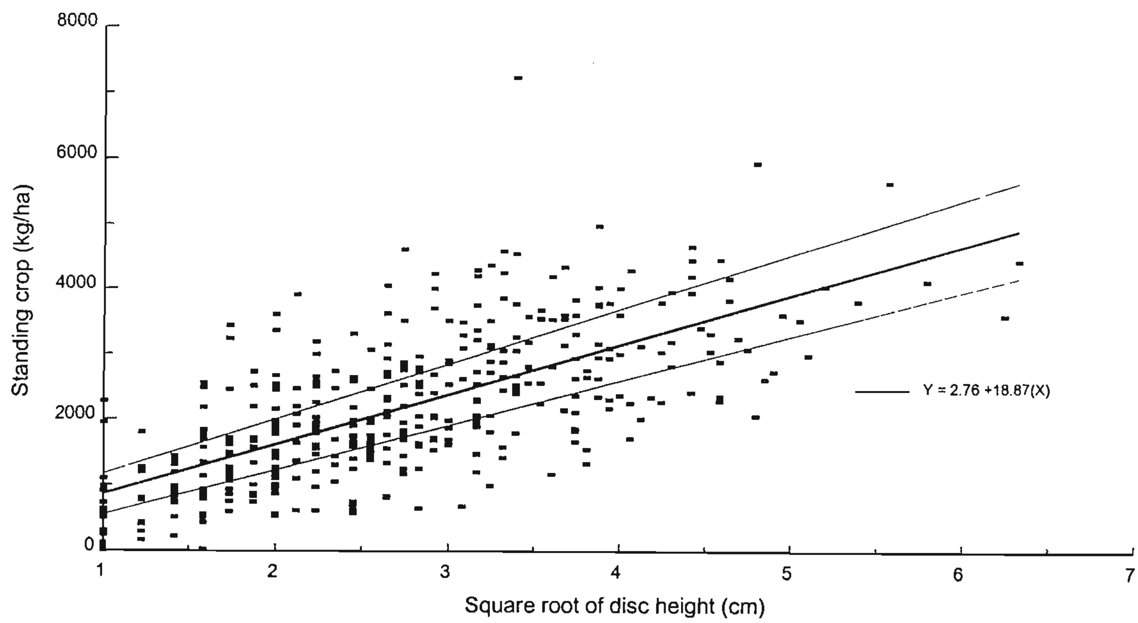

Figure 4.4 Common calibration equation for Malilangwe Estate, showing 95% confidence limits.

The range in variability for a specific disc height is up to 4 000 kg.ha^{-1}. This is exceptionally high, and cannot justify the use of a single equation.

3) Monitoring of monthly standing crop

Standing crop (kg.ha^{-1}), monthly rainfall (mm) and effective rainfall were recorded on a monthly basis from June 1996 to March 1998. These data are presented in Table 4.9. Burning took place as follows: mid dry season (MDS) in September 1996, early dry season (EDS) in June 1997 and late dry season (LDS) in November 1997.

Table 4.9 Monthly rainfall, effective rainfall and standing crop estimates (bold=burn month)

Month	Rainfall (mm)	Effective rainfall	Standing crop (kg.ha^{-1})
Jun 96	5	0.061	913.10
Jul 96	34	0.388	1011.25
Aug 96	6	0.049	1587.37
Sep 96	**4**	**0.022**	**1591.43**
Oct 96	3	0.009	703.14
Nov 96	65	0.316	753.69
Dec 96	67	0.330	1326.18
Jan 97	168	0.965	1385.16
Feb 97	120	0.751	1906.32
Mar 97	73	0.509	1558.21
Apr 97	36	0.321	1802.25
May 97	20	0.186	1543.49
Jun 97	**0**	**0.000**	**1070.28**
Jul 97	9	0.094	1008.75
Aug 97	0	0.000	1106.91
Sep 97	10	0.057	1077.39
Oct 97	17	0.082	1033.42
Nov 97	**40**	**0.196**	**931.36**
Dec 97	70	0.303	1245.97
Jan 98	184	1.020	1643.68
Feb 98	63	0.406	2506.24
Mar 98	18	0.109	1569.94

These data are presented in Figure 4.5.

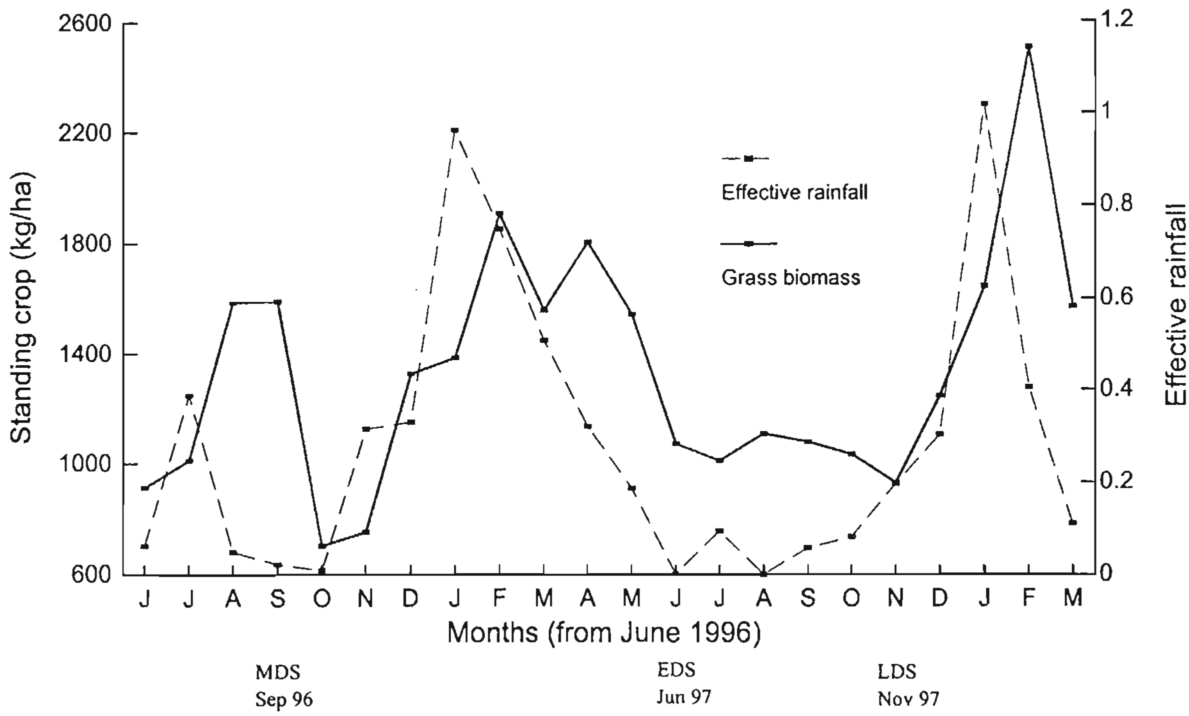

Figure 4.5 Standing crop and effective rainfall plotted over the study period (burns: MDS mid dry season, EDS early dry season, LDS late dry season).

4) Relationship between effective rainfall and standing crop

The regression analysis for standing crop, as determined by effective rainfall from the previous month, is highly significant.

Table 4.10 Multiple regression values for standing crop as the dependent variable, and previous month's effective rainfall (ER) as the independent variable

Adjusted R^2	0.73			
Sig.	<0.001			
Variable	**Estimate**	**P prob.**	**Lower 95%**	**Upper 95%**
Intercept	999.88	<0.001	858.16	1141.59
ER	1214.63	<0.001	872.86	1556.41

The equation for determining standing crop is:

$$\textbf{Standing crop (kg.ha}^{-1}\textbf{)} = \textbf{999.88} + \textbf{1214.63(ER)}$$

This regression is presented in Figure 4.6.

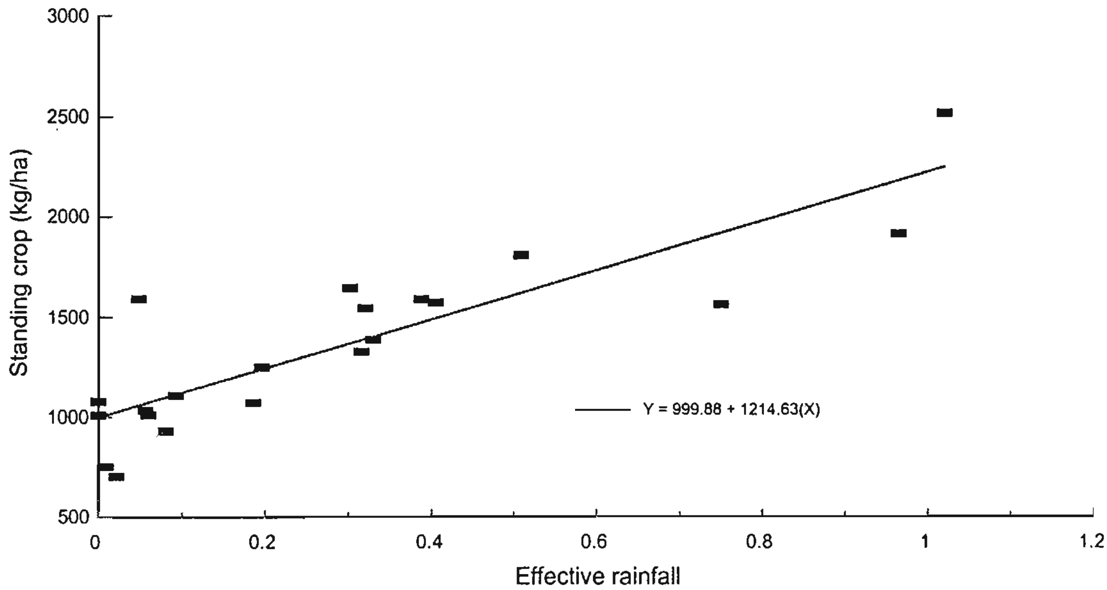

Figure 4.6 Linear regression for determining standing crop from previous month's effective rainfall

Discussion

Disc pasture meter calibration

The calibration of the disc pasture meter was carried out, and eight separate calibration equations were determined. However in five of the eight calibrations the settling height of the disc accounted for less than 50% of the variability in the standing crop of grass. The R^2 values varied between 39% and 72%, illustrating clearly the variability between months. This variability is characteristic of the low basal cover of the grass sward in the mopane woodlands, and the lack of precision represented by the high variation is accepted. The results are accepted as accurate owing to the large number of samples (50), this number of sampling events being representative of the sampling population. In order to increase the degree of variability accounted for by the falling disc, Trollope and Potgieter (1986) developed a revised procedure for calibrating the disc pasture meter for grass swards that have a very low basal cover. This revised procedure showed that disc height accounted for more than 90% of the variation in the standing crop of grass (Trollope and Potgieter 1986). This approach was carried out once on ME, over seven of the major vegetation types. As with the findings by Trollope and Potgieter (1986), more than 90% of the variation in standing crop was accounted for by disc height. This is very encouraging, but was developed over a wide range of vegetation types. It was felt that the sampling population represented by this approach was too broad *ie.* covered unrepresentative vegetation types with different grass species compositions and sward structures to those found in the mopane woodland areas. In light of this, and the fact that a large sampling population (50) was sampled using the standard procedure, the calibration equations developed for the standard disc pasture meter procedure were chosen. Their inherent imprecision is acknowledged as being representative of the variation in the grass sward, but the accuracy and specificity of the equations to the mopane woodlands being investigated, is viewed as being greater than that of the equations developed for the revised procedure.

There were significant differences between the intercept and slope estimates for each of the standard calibration equations. The degree of variability for each equation was itself highly variable (as shown by the 95% confidence limits). The June 1996 and June 1997 variability was very low, and similar. However the August 1996 variability was extremely high. The reason for the high variability of this calibration may be the effect of the extremely high rainfall for July 1996. This rainfall resulted in unseasonal grass growth. The response of particular grass species may have been different to the normal grass growth experienced during the growing season months. Although there were significant differences between the regression equations for different months (Table 4.2), it was extremely difficult to separate any group, or groups, of months as being distinctly different to all others, because of the number of significant and non significant relationships between slope and intercept values. After examining the multiple comparisons between intercept and slope estimates, it was decided that the development of a single common regression equation, that will suffice over all months and seasons, was not possible (Figure 4.5). Although being applicable in monospecific planted pasture situations, the efficacy and applicability of the use of the pasture disc meter for multispecific veld conditions is less extensive (Danckwerts and Trollope 1980). The basic requirement of any method of estimating grass biomass is that the method be capable of sampling adequately across the spatial heterogeneity in vegetation, as well as seasonal conditions and different operators (Friedel *et al.* 1988). This study shows conclusively that for highly heterogenous grass swards, that vary spatially and temporally, the use of the standard disc pasture meter procedure, as described by Tainton and Bransby (1977), is questionable. Unfortunately the pasture disc meter has been used since 1994 for annual estimation of grass yield on ME, and the standard calibration equation developed by Trollope and Potgieter (1986) for the Kruger National Park, has been used to determine the standing crop. In light of this study the following approach is recommended: the procedure described by Trollope and Potgieter (1986) should be followed, but (1) specific calibration equations should be developed for individual vegetation types, and (2) that the effect of season on the calibration equations be considered. This approach overcomes the problem of spatial variation within the grass sward, but does not imply that one regression equation will suffice over different seasons. It is felt that it will be necessary to calibrate the disc pasture meter annually, before the estimation of standing crop is carried out. This is highly recommended if management is striving to implement research findings regarding the effect of fire on savanna vegetation on Malilangwe Estate.

Relationship between effective rainfall and standing crop

The regression analysis for standing crop, as determined by the effective rainfall from the previous month, was highly significant. Using effective rainfall (monthly rainfall divided by monthly pan evaporation) from the previous month, standing crop can be estimated using the standing crop equation. This is a valuable tool for the land manager, as potential fuel loads and grazing capacities can be estimated.

Chapter 5

The relationship between peak standing crop and rainfall, and the development of a decrease function of standing crop

Introduction

From chapter four it is evident that the estimation of standing crop at time (t+1 month) is largely dependent on the effective rainfall at time (t). This allows one to estimate standing crop for the coming month (if given the present months rainfall) or the existing standing crop (given last months rainfall). This equation is however limited to monthly rainfall figures in the range 1-250 mm. At levels higher than this upper limit (the maximum recorded monthly rainfall), the estimation of standing crop is not possible, as this range is beyond that of the monthly rainfall figures sampled. To overcome this, and to develop a start-point for the decline function of standing crop from the end of the growing season, it was decided to investigate the relationship between annual peak standing crop and annual rainfall. However, the study period at ME gave only one season of peak standing crop (PSC) recording, which was inadequate. It was therefore necessary to utilise data from other mopane-dominated areas, with similar soils and climates.

Procedure

Peak standing crop in relation to rainfall

The following annual peak standing crop and respective annual rainfall figures were sourced.

Table 5.1 Source, number of years and area from which data on peak standing crop were sourced

Source	Number of years	Area
Walters	1	Malilangwe Estate
Stalmans (pers. comm.)	3	Malilangwe Estate
Kelly (1977)	2	Gona-re-Zhou National Park (Zimbabwe)
Zambatis (pers. comm.)	9	Landscapes 22, 23 and 24 of Kruger National Park

Nine years of records are available for each of the three landscapes in the Kruger National Park. These landscapes are (after Gertenbach 1983):

22) *Combretum* spp./*Colophospermum mopane* rugged veld,

23) *Colophospermum mopane* shrubveld on basalt, and

24) *Colophospermum mopane* shrubveld on gabbro.

Linear regression analysis was applied with annual rainfall (mm) as the independent variable and peak standing crop (kg.ha^{-1}) as the dependent variable. The range of independent values (rainfall) for the south-eastern lowveld (ME and Gona-re-Zhou) were extremely limiting, leading to an inappropriate and poor regression result. On the basis of these findings, the south-eastern Zimbabwe values were not considered for any further analyses.

From the initial regression analyses the slope estimates were compared. No significant differences were found between the three Kruger National Park slope estimates. Hereafter regression analysis was repeated, but with a constant slope estimate being used. From these results, two regression equations were derived.

The decrease function of standing crop from PSC

The monthly standing crop figures for ME, from February 1997 (PSC) to November 1997, were plotted (Figure 4.4). This showed an initial decrease in standing crop from February (month 0) to March. There was then an increase in April, after which there was a sharp decrease until July. After midwinter rainfall in July ("guti") there was an increase in August, after which there was another decrease until November (month 9). Non-linear regression analysis was applied with month as the independent variable and standing crop ($kg.ha^{-1}$) as the dependent variable.

Results

Peak standing crop in relation to annual rainfall

The results of linear regression analysis for three landscapes in the Kruger National Park and south-eastern Zimbabwe are presented in Table 5.2.

Table 5.2 Linear regression values for three landscapes in the Kruger National Park (KNP22, KNP23, KNP24) and south-eastern Zimbabwe (SEZ), including lower and upper 95% confidence limits (degrees of freedom: KNP22 = 8, KNP23 = 8, KNP24 = 8, SEZ = 5)

Area	Intercept	Slope	R^2	P.
KNP22	460.5	2.62	0.07	0.245
KNP23	1153.3	4.61	0.43	0.033
KNP24	959.4	3.57	0.27	0.089
SEZ	1272.9	1.04	0.23	0.797

	Intercept Lower 95%	Upper 95%	Slope Lower 95%	Upper 95%
KNP22	-1688.8	2609.9	-2.3	7.5
KNP23	-575.9	2882.5	-0.5	8.7
KNP24	-798.7	2717.6	-0.7	7.9
SEZ	-5099.0	7644.9	-9.5	11.5

At the 5% level, only the KNP23 regression equation is significant. KNP24 is significant at the 10% level. The high F probability and lower/upper 95% confidence limits for the SEZ regression analysis are an indication of the inappropriateness of the regression equation. This is clear from Figure 5.1.

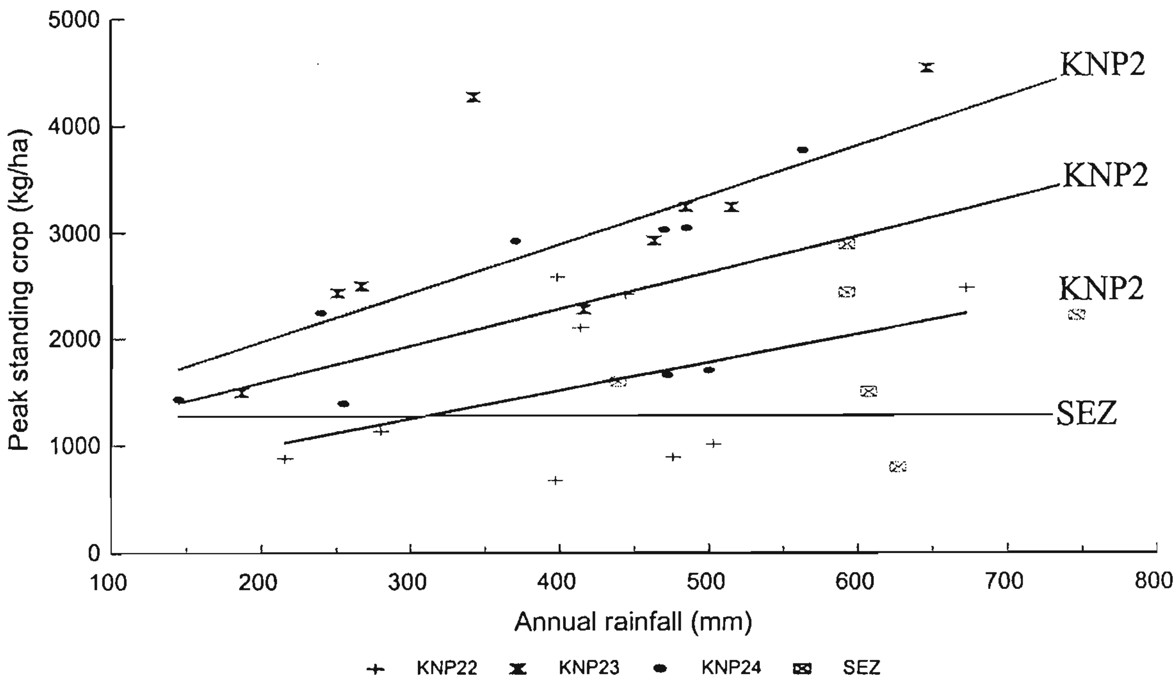

Figure 5.1 Scatterplot of peak standing crop ($kg.ha^{-1}$) and annual rainfall (mm) for three landscapes in the Kruger National Park (KNP22, KNP23, KNP24) and south-eastern Zimbabwe (SEZ).

From this figure it is clear that the data for SEZ do not cover a wide enough range of rainfall variation. Four of the six points are extremely close to the 600 mm rainfall level. This results in a very poor data set with which to attempt linear regression analysis. In light of this, it was decided to ignore the SEZ values (due to their narrow independent value range), and continue further analyses with the Kruger National Park landscapes only. It must be noted at this stage that landscape 23 (*Colophospermum mopane* shrubveld on basalt) is the most similar, of the three landscapes, to the treatment blocks on ME, as the climate, soils and vegetation communities of these blocks are very similar to those found in landscapes 23 and 24.

The slope coefficients (with 95% confidence limits) for the three landscapes are displayed in Figure 5.2.

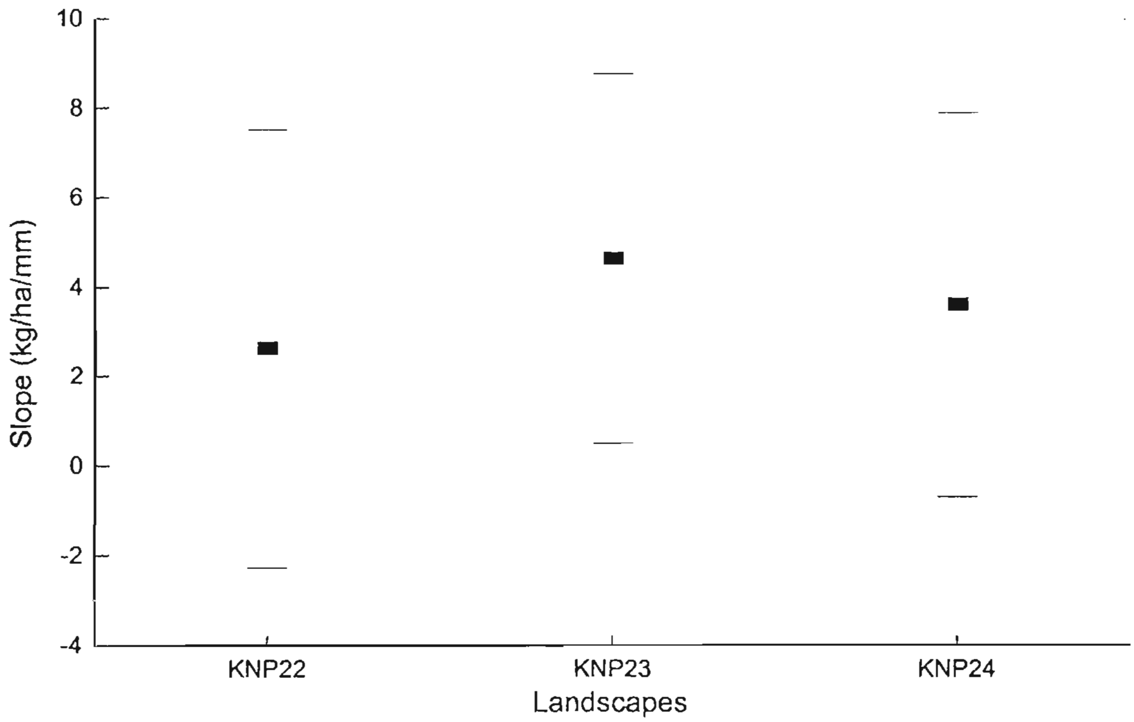

Figure 5.2 Slope coefficients for linear regression equations of three landscapes in the Kruger National Park.

It is clear that there is no significant difference between the slopes of any of the three landscapes. This led to the regression analysis of the three landscapes being repeated, with a 'common' slope and individual intercepts being determined.

Table 5.3 Regression analysis values for three landscapes in the Kruger National Park, incorporating a 'common' slope and individual intercepts (degrees of freedom = 26)

Adjusted R^2	0.51
F prob.	<0.001

Variable	Estimate	s.e.	t prob.
Slope	3.67	1.04	0.002
KNP22	17	500	0.973
KNP23	1524	339	<0.001
KNP24	919	340	0.014

Multiple comparisons between the three intercept estimates gave the following results.

Table 5.4 Intercept t probabilities (read columns as comparisons between landscapes)

Intercept		
	KNP22	KNP23
KNP22		
KNP23	<0.001	
KNP24	0.014	0.087

A more easily understood representation of Table 5.4 is presented in Table 5.5.

Table 5.5 Intercept t probabilities (read columns as comparisons between landscapes, months without letters in common are significantly different at the 95% level)

Intercept		
	KNP22	KNP23
KNP22	A	
KNP23	B	B
KNP24	B	B

This indicates that the intercept estimates for landscape 23 and 24, although non-significantly different to each other, are significantly different to landscape 22. From this the following two regression equations can be derived.

Table 5.6 Regression analysis values for landscape 22 and landscape (23/24)

(degrees of freedom: 22 = 8, 23/24 = 17)

Landscape	Intercept	Slope	s.e.	t prob.
22	17	3.67	500	0.973
23/24	1205	3.67	340	0.008

The regression analysis results for landscape 22 indicates that the linear relationship between PSC and rainfall is inadequate (t prob. = 0.973). This equation is therefore unacceptable, and the combined equation for landscape 23/24 is the only equation that can be used to estimate PSC from annual rainfall.

The regression equation for these landscapes is:

Landscape (23/24): PSC = 1205 + 3.67(Annual rainfall)

This equation was assumed to be applicable to the treatment blocks on ME, because of their similarity.

The decrease function of standing crop from PSC

On ME peak standing crop was achieved in February. Over the study period, only one recording of the decline in standing crop from peak standing crop at the end of the growing season, was possible. The results for the non-linear regression analysis applied to months from peak standing crop as the independent variable, and standing crop as the dependent variable, are presented in Table 5.7.

Table 5.7 Non-linear regression analysis results (degrees of freedom = 9)

F prob. =	0.002
R^2 =	0.79
s.e. =	166

Variable	**Estimate**	**s.e.**
R	0.826	0.119
B	1203	387
A	715	432
Equation	$Y = A + B(R^x)$	

(Where Y=standing crop, R=rate of exponential increase, B=range between the asymptote and the value when x=0, A=the asymptote, and x=month after peak standing crop).

The equation to estimate standing crop for a particular month, after peak standing crop has been reached, is:

Standing crop (month x) = 715 + 1203 (0.826^x)

The exponential relationship between standing crop (kg.ha^{-1}) and months from peak standing crop is presented in Figure 5.3.

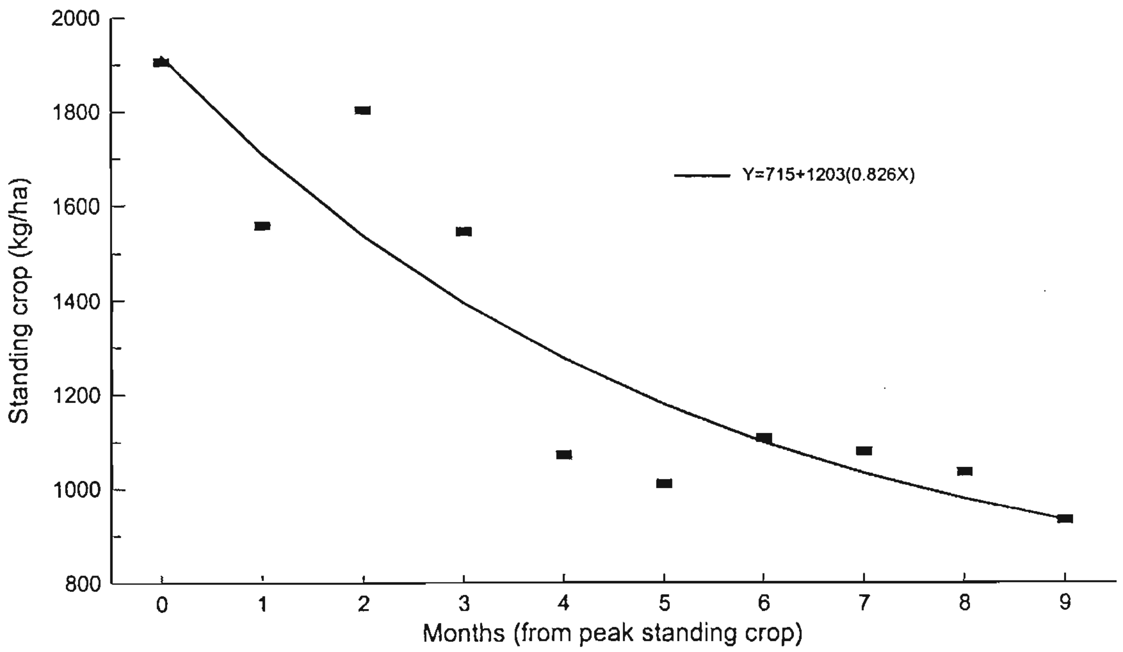

Figure 5.3 The exponential relationship between standing crop and months from peak standing crop.

Discussion

The monthly monitoring of standing crop and effective rainfall shows that there is a distinct lag-effect between effective rainfall and change in standing crop. The resolution of this study (monthly intervals) indicates that the lag period is one month. However, the response by the grass sward to changes in soil moisture (especially during the early and mid growing season) is in most cases shorter than one month. The effective change in standing crop may very well be shorter than one month after a rainfall event. The monitoring interval of the grass sward by a land manager will very seldom be less than one month, and the results are therefore considered acceptable. The effect of effective rainfall, from the previous month, on standing crop was found to be highly significant ($R^2 = 0.73$, $P<0.001$). The standing crop for a particular month can be estimated by using the effective rainfall from the previous month. The standing crop values recorded for the treatment areas were not indicative of the expected standing crop values within a given year.

Intuitively, standing crop declines from peak standing crop (February/March) through the dry season. This is as a result of increasing dormancy of the grass plants, removal by grazing ungulates and termites, flattening by animal movement, and decreasing rainfall. The earlier the burning takes place the higher the expected fuel load *i.e* mid dry season burns should have a higher fuel load than late dry season burns, because of the decline in standing crop as the dry season progresses. The paradoxical situation in the recorded fuel load values, where the early dry season burns had the highest fuel load, and mid dry season the lowest (Table 7.5), can be explained by the increased effective rainfall in July, September and October 1997, which led to an increase in standing crop from August 1997. This resulted in the late dry season treatments having higher than normal fuel loads. The very high mid dry season fuel loads were as a result of the exceptionally high June and July 1996 rains (Figure 4.4). This high effective rainfall led to fuel loads higher than one would expect for the middle of the dry season. These fuel load and fire intensity figures were not recorded within the same season, and therefore inferences from the mid dry season head and back fires (being from the previous year) must be treated with caution.

Chapter 6

A leaf quantification equation for mopane trees in the south-eastern lowveld of Zimbabwe

Introduction

At the outset of the study it was recognized that the successful description and interpretation of the effects of fire on mopane woodlands would require an appropriate quantitative description of tree populations. The number, ecological status (dead, living or coppicing) and structure of sampled individuals (during base-line and monitoring exercises) would be the fundamental parameters with which to compare and study the effects of different seasons of burning and types of fire. The approach needed to be rapid, robust and account for a large proportion of the variation in leaf dry mass.

The approach adopted by Smit (1994) was accepted as a comprehensive and repeatable method whereby tree dimension measurements could be obtained, and from these an accurate estimate of leaf dry mass determined. To test the significance of treatment effects (season and type of fire) the accurate estimation of tree-leaf dry mass was critical.

Procedure

The technique followed a regression analysis approach, whereby the relationship between the spatial volume of a tree and its true leaf dry mass was determined. The leaf quantification technique of Smit (1994) was developed for coppicing and non-coppicing trees in the Soutpansberg area of the Northern Province of South Africa. It was felt however that the tree structure in the aforementioned study area differs to that found on ME in Zimbabwe, owing to different soils and rainfall. It was therefore decided to determine two alternative leaf quantification equations for the south-eastern lowveld of Zimbabwe specifically, one for coppicing and one for non-coppicing individuals.

Two areas were chosen in which to harvest mopane trees, each being approximately five hectares in size. The first area had been burnt the previous year and coppicing was prevalent on the majority of trees. The second area had not been burnt within recent history, and contained non-coppicing individuals. Thirty mopane trees from each of the areas, representative of the mopane woodlands occurring on the basalt-derived soils and ranging in size, were selected for harvesting.

Before harvesting commenced, the dimensions of each tree was measured. Hereafter the trees were felled, and all leaves hand-picked. The leaf samples were air-dried for three days before being sent to the ZSA, where they were oven-dried at 60°C until constant mass, and then weighed. Regression analysis was applied with true leaf dry mass as the dependent variable and calculated spatial volume as the independent variable. The spatial volume of each tree was calculated using the procedure presented by Smit (1994). This procedure involves the estimation of five tree dimensions:

(A) tree height (height of top foliage),
(B) height of maximum canopy diameter,
(C) height of first leaves,
(D) maximum canopy diameter, and
(E) base diameter of foliage at height (C), as well as the calculation of two more
(F) (A-B), and
(G) (B-C).

Smit (1994) elucidates on the calculation of tree canopy volume, regardless of its shape or size, using the dimension measurements above and the volume formulae of an ellipsoid, right circular cone, frustum of right circular cone or a right circular cylinder. Tree canopy volume can then be calculated using these shapes, and two tree segments (Smit 1994). All trees were assumed to be symmetric. This was done for both coppicing and non-coppicing trees. The formulae for calculating tree canopy volume are presented on pages 10 and 11 of Smit (1994).

Results

The summary of the data for the 30 coppicing and non-coppicing trees are presented in Table 6.1.

Table 6.1 Minimum, maximum, mean and s.e. tree dimension values for coppicing and non-coppicing trees

	Number of Stems	Stem diameter (cm at 25 cm)	Tree height (cm)
Coppicing			
Min.	1	3	75
Max.	12	22	410
Mean	4.43	9.8	225
s.e.	3.44	4.5	97.6
Non-coppicing			
Min.	1	1	80
Max.	3	12	475
Mean	1.13	6.4	281
s.e.	0.43	2.5	91.7

The linear regression analysis for coppicing trees was highly significant (Table 6.2).

Table 6.2 Linear regression values for coppicing trees, with spatial volume (cm^3) as the independent variable and leaf dry mass (g) as the dependent variable (degrees of freedom = 29)

Adjusted R^2	0.83
Prob.	<0.001

Variable	Estimate	F. prob.	Lower 95%	Upper 95%
Intercept	133.07	<0.001	88.52	177.61
Spatial Volume	0.00024	<0.001	0.0002	0.00029

The scatter-plot and linear regression line are presented in Figure 6.1.

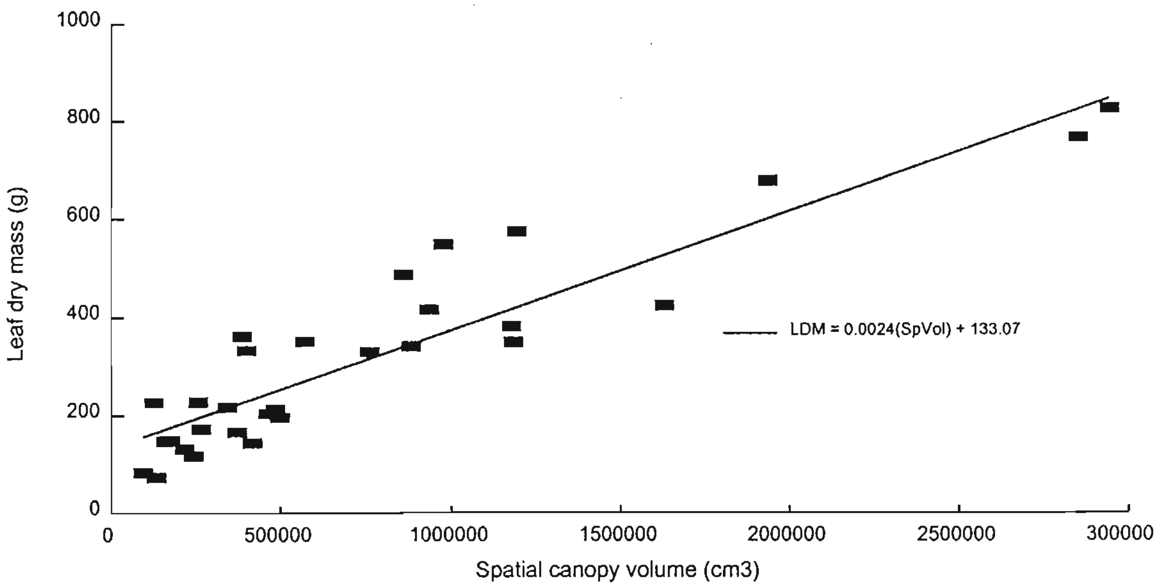

Figure 6.1 Scatter-plot and linear regression of leaf dry mass (g) and spatial canopy volume (cm^3) for coppicing trees.

The regression analysis for non-coppicing trees was also highly significant (Table 6.3).

Table 6.3 Linear regression values for non-coppicing trees, with spatial volume (cm^3) as the independent variable and leaf dry mass (g) as the dependent variable (degrees of freedom = 29)

Adjusted R^2	0.87			
Prob.	<0.001			
Variable	Estimate	F. prob.	Lower 95%	Upper 95%
Intercept	101.97	<0.001	24.08	179.85
Spatial Volume	0.00032	<0.001	0.00027	0.00037

The scatter-plot and linear regression line for non-coppicing trees is presented in Figure 6.2.

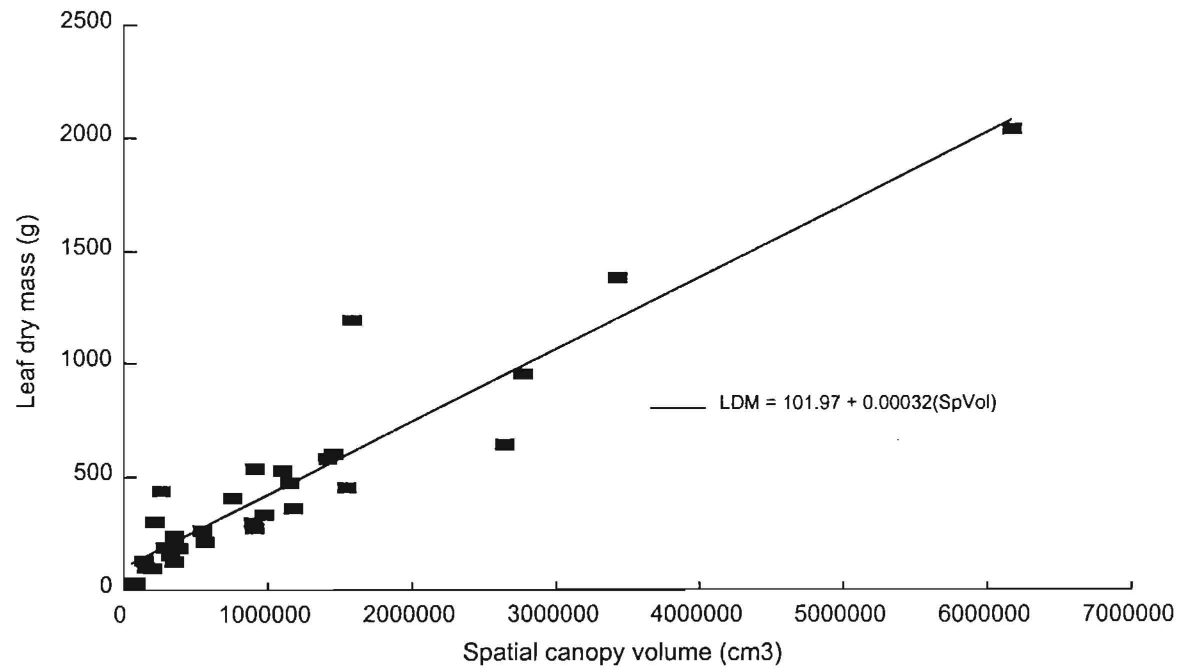

Figure 6.2 Scatter-plot and linear regression of leaf dry mass (g) and spatial canopy volume (cm^3) for non-coppicing trees.

Discussion

Two leaf quantification equations (coppicing and non-coppicing) for mopane, in the south-eastern lowveld of Zimbabwe, were developed to estimate leaf dry mass ($kg.ha^{-1}$) from spatial canopy volume (cm^3). Both analyses were highly significant (Table 6.2 and 6.3), coppicing trees ($R^2 = 0.83$, $P<0.001$) and non-coppicing trees ($R^2 = 0.87$, $P<0.001$). These equations were found to be highly similar to equations developed by Smit (1994) for mopane veld north of the Soutpansberg in South Africa. In Figure 6.3 it can be seen that for coppicing trees there is a significant difference between the leaf dry mass estimates, from the respective equations, at canopy volumes below $5.9x10^6$ cm^3 (*ie.* 15.6 $ln(cm^3)$ on the x-axis). At these canopy volumes, the Soutpansberg equation gives significantly higher leaf dry mass estimates.

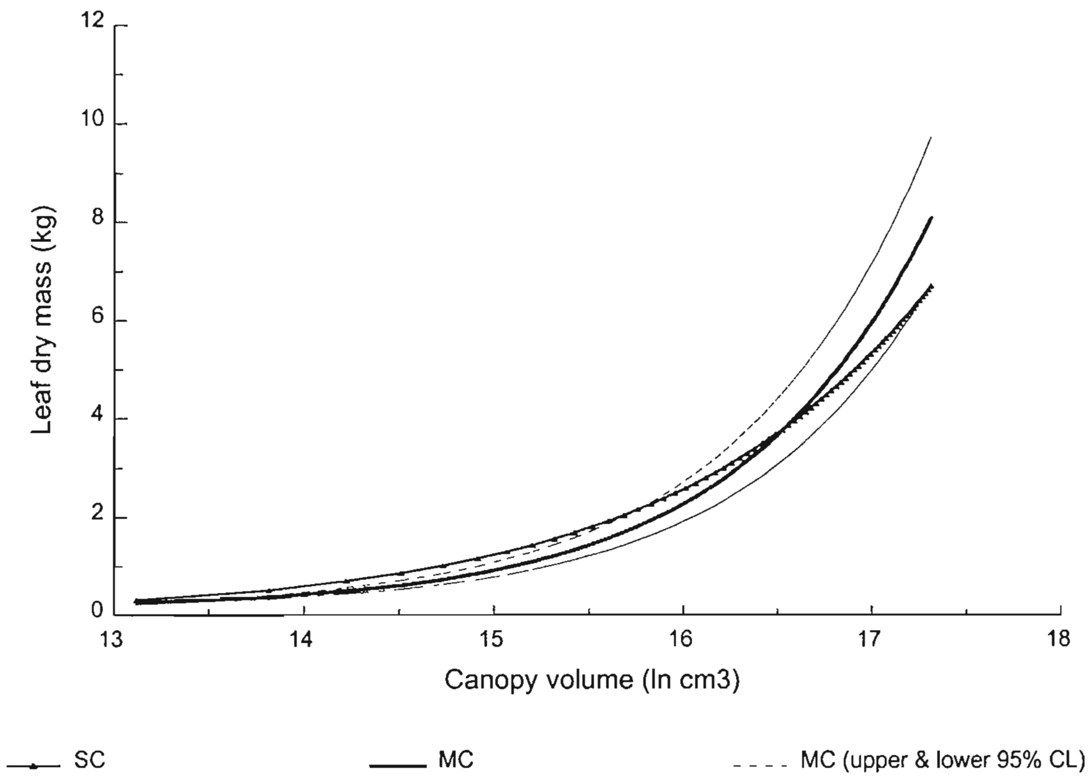

Figure 6.3 Linear regression equation lines of the relationship between tree canopy volume and leaf dry mass of coppicing trees for Soutpansberg (SC) and Malilangwe Estate (MC), as well as the 95% confidence limits (CL) for MC.

From Figure 6.4 it can be seen that for non-coppicing trees there is a significant difference between the two estimates at canopy volumes greater than 1.2×10^6 cm^3 (*ie.* 14.0 ln(cm^3) on the x-axis). At these canopy volumes, the Soutpansberg equation gives significantly lower leaf dry mass estimates.

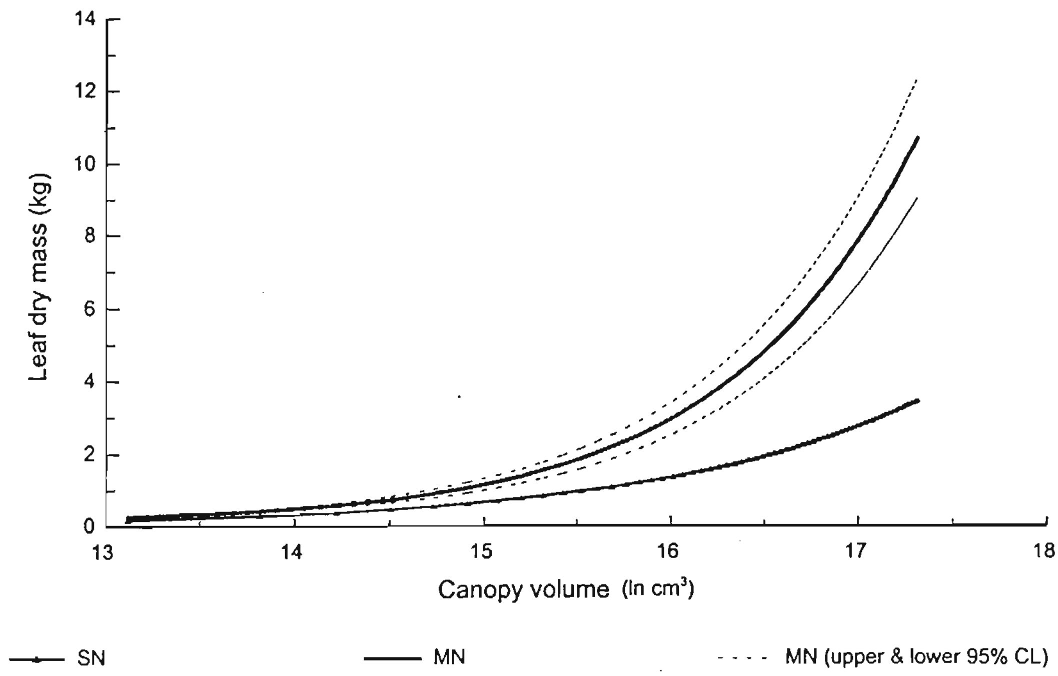

Figure 6.4 Linear regression equation lines of the relationship between tree canopy volume and leaf dry mass of non-coppicing trees for Soutpansberg (SN) and Malilangwe Estate (MN), as well as the 95% confidence limits (CL) for MN.

The Soutpansberg equation gives significantly lower leaf dry mass estimates. This can be explained by the difference in tree sizes harvested for determining the leaf quantification equations in the two areas *i.e* the average height of harvested trees on ME was only 2.4 m, whereas in the Soutpansberg the trees were up to 7 m in height (Smit 1994). Larger trees have increasingly fewer leaves per unit canopy volume, and this explains the higher leaf dry mass for a given non-coppicing tree canopy volume on ME, than that for the Soutpansberg. However, the trees harvested for the leaf quantification study on ME are representative of the woodlands found there, and the equations are specific for that region.

Chapter 7

Effect of season of burning and type of fire on mopane woodland

Introduction

It is accepted that climate and soils may set the limits for plant growth, but that fire and herbivory determine vegetation patterns in the region. Fire sometimes competes with, sometimes replaces and sometimes facilitates herbivory (Bond 1997). The impact of fire can be described at different scales: individual plants (fire responses to burning), plant populations (how burning influences community ecology) and vegetation patterns (landscape and subcontinental level). In this study the effect of season of burning and type of fire is investigated at the individual tree level, as well as the population (woodland) level.

Fire affects tree populations in the following manner (review in Chapter 2):

1) tree seedlings may be killed by fire (whereas larger individuals may survive),
2) burning of the canopy causes topkill,
3) coppicing takes place from the base or from surviving buds (the degree of topkill and coppicing increases with increasing flame height and fire intensity),
4) the architecture of large trees (> 3 m) is unaffected by burning (unless damage occurs through a crown fire or to the trunk bark), and
5) fire changes the structure of the canopy and/or the number of stems.

It was postulated by West (1965) that trees and shrubs are probably more susceptible to fire at the end of the dry season, when plant reserves are depleted after initial spring growth. Because of this phenophase sensitivity, mopane trees burnt in different seasons may differ in their response to fire. The type of fire (back fire or head fire) was investigated because trees are sensitive to various types of fire owing to the differences in the vertical distribution of the release of heat energy. It has been shown that head fires cause the greatest topkill of stems and branches (Trollope *et. al.* 1996), because the concentration of heat energy is at levels closer to the terminal buds of the tree.

Objectives

The objectives of this study were to investigate the following seven parameters, in terms of the effect of season of burning and type of fire on them:

1) the species composition of the treatment areas,
2) the fire parameters and fire intensities of the burning treatments,
3) effect of treatment on stem diameter,
4) effect of treatment on percentage topkill,
5) effect of treatment on tree density,
6) structural response of individuals to burning treatments
   - change in tree height
   - change in number of stems
   - change in maximum canopy diameter (MCD), and
7) effect of treatment on leaf dry mass (LDM).

Procedure

Treatment blocks and treatment areas

Experimental burning took place in three seasons: early dry season (E), mid dry season (M) and late dry season (L). Two types of fire were implemented: head fire (H) and back fire (B), with three replications set up for each treatment. Six controls were also set up (C).

Malilangwe Estate is divided by a network of roads and tracks. These roads, as well as some river courses, are used as the boundaries of the 127 management blocks. In the mopane-dominated vegetation communities, on the basalt plains, six management blocks were chosen as treatment blocks, and treatments allocated as follows: to accommodate the three replications, two treatment blocks were allocated for each of the three season treatments (E,M and L). Within each of these blocks, three treatment areas were then chosen. These treatment areas were chosen in areas where mopane is the dominant species and where soil properties and elevation are similar. Season of burning and type of fire treatments were identified as follows:

Table 7.1 Season of burning (E early, M mid. L late dry season) and type of fire treatment allocations (H head, B back fire), including size of treatment burn and year of last burn

Early	Mid	Late	Controls	
(812 ha)	(815 ha)	(406 ha)		
EB1 - EB3	MB1 - MB3	LB1 - LB3	C1 - C6	
EH1 - EH3	MH1 - MH3	LH1 - LH3		
Last Burn				
EB 1995	MB pre-1994	LB 1997	C1	1994
EH pre-1994	MH 1995	LH 1997	C2/3/4	1995
			C5	pre-1994
			C6	1995

Permanent transects

Ten permanent transects were laid out in each treatment area. Control transects were laid out in similar vegetation, but in areas allocated not to be burned. Five transects were placed in each of the six control areas.

Transects were placed at least 15 m from the road, and 20 m apart. The starting point (a tree) of each transect was marked with yellow paint, and an aluminium disc nailed to it. A 50 m tape was then laid out from this point, and the compass bearing for the transect taken. Another disc was placed at the end of the transect. This allowed for the accurate monitoring of individual trees over time, within a 100 m^2 transect. Transect start-points were recorded using a GPS (Appendix 2).

Data collection

This included the following:

1) Base-line data

Data for the early (E) and mid (M) dry season treatments, as well as the control (C96) treatment were collected in May 1996. The base-line data for the late (L) dry season treatment were collected in May 1997.

The following parameters were recorded for each individual tree encountered:

1) species,

2) status (living or dead),

3) number of stems per individual (counted, but cognisance taken of the fact that underground root stocks may give rise to numerous stems i.e one individual with many stems),

4) the presence or absence of topkill (the occurrence of topkill may be as a result of damage to the extremities of the plant due to drought, and was recorded as such. Effect of topkill on mopane woodland was only considered with regard to damage by fire),

5) spatial canopy volume (the spatial canopy volume of each individual was estimated using five measured, and two derived, dimensions: **(A)** tree height (of living leaf material), **(B)** height of maximum canopy diameter, **(C)** height of first leaves, **(D)** maximum canopy diameter, **(E)** base diameter of the foliage at height **(C)**, **(F)** height of tree crown (**A-B**), and **(G)** height of tree base (**B-C**)),

6) the presence/absence of coppice stems,

7) the number of (a) aerial and (b) coppice stems, and

8) the height to which coppice stems have grown.

This approach was used in Chapter 6 to determine a leaf quantification equation applicable to mopane in the south-eastern lowveld of Zimbabwe. Using these equations (one for non-coppicing individuals and one for coppicing individuals), the estimation of leaf dry mass (LDM) of individual trees was possible. Leaf dry mass is an indicator of competitive ability with herbaceous vegetation for moisture because it is a descriptor of the evapotranspiration potential of the tree. Therefore, it was felt that effects of season of burning and type of fire on mopane would be best interpreted by the change in the competitive ability of the individual or population *i.e* change in leaf dry mass. This is by implication an indirect measure of the plant's competitive ability, and should be viewed more as an indicator of potential change in competitive ability. The mean relationship between leaf volume and leaf dry mass for mopane is 1:0.519 (Smit 1994).

2) Fire intensity data

During the two days prior to burning the following parameters were recorded:

i) fuel load (100 disc pasture meter readings per area)

ii) fuel moisture (25 $1m^2$ grass samples cut, dried and weighed per area)

During the burning of each area, the following parameters were recorded five times during the burning event:

i) ambient temperature (°C)

ii) relative humidity (%, with a whirling psychrometer)

iii) wind speed ($m.s^{-1}$, with a wind anemometer or talcum powder drift speed)

iv) rate of spread ($m.s^{-1}$, time taken for flame front to cover distance between two poles 5 m apart).

A fire intensity formula was developed by Byram (1959) to estimate fire intensity of surface head and back fires. The formula for predicting fire intensity is:

$$\mathbf{I = H*w*r}$$

Where: I = fire intensity ($kJ.s^{-1}.m^{-1}$)
H = heat yield ($kJ.kg^{-1}$)
w = mass of available fuel ($kg.m^{-2}$)
r = rate of spread of the fire front ($m.s^{-1}$)

For the burning treatments fire intensity was estimated using the heat yield values (Byram 1959) and the fuel load and rate of spread values collected.

3) Burning

Early dry season burns were carried out in June 1997, mid dry season burns in September 1996 and late dry season burns in November 1997. Each treatment block was burnt in a day. Burning began when environmental conditions were most conducive to achieving intense and effective fires. Roads were used as fire-breaks, with a back fire put in first to act as a further protective measure. Once this back fire was in place, a head fire was set along the windward side of the block. By using this approach, the safety of the burning exercise, as well as the objective of achieving both head and back fires was met. Control areas were not burnt.

4) End-of-season data

The same individuals that were recorded during base-line data collection, were monitored to ascertain plant responses to treatments. Early and mid dry season (E and M), as well as control (C97) areas were monitored in May 1997, and late dry season (L) and control (C98) areas in April 1998.

The change in any particular parameter was determined by calculating the absolute difference between the base-line and end-of-season values. Comparisons between burning treatments and controls, as well as across treatments, were carried out. Due to the temporal variation inherent in the data (as a result of different years and times of treatment application) the following changes and comparisons against controls for the three treatment seasons were possible (Table 7.2).

Table 7.2 Collection of data for different seasons of burning

(E early, M mid, L late dry season, and C control)

	Early	**Mid**	**Late**
Base-line	E96	M96	L97
End-of-season	E98	M97	L98
Control	C98-C96	C97-C96	C98-C97

5) Analysis of data

Analysis of variance (Genstat 5.41) was carried out to test for the effects of season of burning, type of fire and height class on fire intensity, stem diameter and percentage topkill. Analysis of covariance (Genstat 5.41) was carried out to test for the effects of the same variables on the changes in tree density, as well as an attempt to accommodate the influence of initial tree density. For these analyses comparisons were made across treatments *i.e* tests between the three seasons of burning (early, mid and late dry season), two types of fire (head and back fire) and four height classes, including interactions. Owing to the unbalanced nature of the data set (*i.e* an unequal number of replications between controls and treatments) conventional analysis of variance techniques could not be employed. The residual maximum likelihood (REML) method was used (Genstat 5.41) where the estimation of variance components is possible. The

REML algorithm estimates the treatment effects and variance components in a linear mixed model (i.e a linear model with both fixed and random effects). Unlike regression, it can account for more than one source of variation in the data. This approach was taken to test for significant differences between seasons and types of fire, for each of the three parameters. REML analysis was undertaken to test for significant differences between seasons and types of fire for changes in tree height, number of stems, maximum canopy diameter and leaf dry mass. Comparisons across seasons, and against the control treatments were carried out. It is assumed that the control treatments, owing to them not being burnt, are an effective control, and comparisons between burning treatments and control treatments would give an accurate analysis of burning treatment effects.

Note

The environmental conditions, burning parameters, fire intensities and percentage occurrence of mopane in the treatment areas are presented. These give an insight into the potential damage, and therefore potential change, that the burning treatments incurred. The effect of season of burning and type of fire on stem diameter (at 25 cm above ground level) and percentage topkill are also presented. These parameters were only measured in April 1998, not having been measured during the base-line collection period, and therefore no analysis of change is possible. However, differences were investigated for the sake of completeness.

It must be remembered that the results gained from the tests for significant differences between season of burn and type of fire, for stem diameter and percentage topkill cannot be taken as true effects of treatments. The "once-off" nature of the treatment applications do not allow for long-term prediction or appreciation of past treatments. Significant differences in stem diameter or percentage topkill may reflect the inherent variation in the population, rather than variation due to treatments. However if the percentage topkill in the control areas was significantly lower than in the treatment areas, then the extent of topkill in the treatment areas could well be ascribed to treatment effects.

Results

1) Species composition of treatment areas

The treatment areas were all dominated by mopane (Table 7.3).

Table 7.3 Mean percentage occurrence of mopane per treatment area

Treatment	% Mopane
Early Back	85.6
Early Head	69.4
Mid Back	87.8
Mid Head	82.2
Late Back	63.6
Late Head	64.4
Controls	77.4
Overall	75.8

Other woody species that occured in the treatment areas are listed (Table 7.4):

Table 7.4 Additional tree species occurring in the treatment areas of Malilangwe Estate

Combretum imberbe	*Pterocarpus brenanii*
Combretum apiculatum	*Peltophorum africanum*
Lonchocarpus capassa	*Dichrostachys cinerea*
Newtonia hildebrandtii	*Dalbergia melanoxylon*
Grewia bicolor	*Grewia flavescens*
Dovyalis longispina	*Grewia villosa*
Ormocarpum trichocarpum	*Flueggea virrosa*
Acacia nigrescens	*Balanites aegyptiaca*
Lannea schweinfurthii	*Rhus dentata*

2) Fire parameters and fire intensities of burning treatments

The fire parameters, and fire intensities, of the treatment burns are presented in Table 7.5.

Table 7.5 Mean (±S.E.) of fuel load, rate of spread and fire intensity, and heat yield values (Byram 1959) for season of burning and type of fire treatments in mopane woodlands (degrees of freedom = 2 for each treatment)

Treatment	Fuel load ($kg.m^{-2}$)	Rate of spread ($m.s^{-1}$)	Heat yield ($kJ.kg^{-1}$)	Fire intensity ($kJ.s^{-1}.m^{-1}$)
Early Back	0.23 (0.01)	0.04 (0.05)	17 781	153 (176.7)
Early Head	0.23 (0.02)	0.49 (0.56)	16 890	1833 (2019.8)
Mid Back	0.11 (0.01)	0.02 (0.01)	17 781	30 (15.3)
Mid Head	0.11 (0.01)	0.41 (0.36)	16 890	378 (63.1)
Late Back	0.20 (0.01)	0.06 (0.05)	17 781	236 (158.3)
Late Head	0.24 (0.01)	0.40 (0.37)	16 890	1585 (1408.9)

Table 7.6 (a) Analysis of variance of season of burning and type of fire on fire intensities of the treatment areas

Variate: Fire intensity

Source of variation	d.f.	S.s.	M.s.	V.r.	F pr.
Season	2	2256964	1128482	1.11	0.363
Type	1	5700826	5700826	5.58	0.036
Season.Type	2	1443081	721540	0.71	0.513
Residual	12	12250275	1020856		
Total	17	21651146			

(b) LSD-tests

Type	Mean	Comparisons LSD(0.05) 1037.8
Head fire	1265	a
Back fire	140	b

(Read comparisons down columns, types of fire with letters in common are not significantly different)

It is evident that the fire intensities of the treatment burns implemented in different seasons were not significantly different (Table 7.6). The effect of type of fire was significant however, with head fires being more intense than back fires, over all seasons. This difference was very large, with head fires being almost ten times more intense than back fires.

3) Effect of treatment on stem diameter

Table 7.7 Analysis of variance of season of burning and type of fire on stem diameter (cm) of the treatment areas

Variate: Stem diameter

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Season	3	185.24	61.75	10.6	<0.001
Type	2	2.14	1.07	0.18	0.833
Height class	3	2305.48	768.5	132.0	<0.001
Season.Type	1	23.25	23.25	3.99	0.05
Season.Height class	9	138.2	15.36	2.64	0.01
Type.Height class	6	0.93	0.15	0.03	1.00
Season.Type. Height class	3	98.06	32.69	5.61	0.002
Residual	68	395.98	5.82		
Total	95	3149.27			

There were no significant differences between type of fire for stem diameter at 25 cm. The other two main effects, season and height class, were highly significant. The interaction effects were all significant at the 5% level, except the type-height class interaction. The interactions are presented in Figures 7.1 and 7.2.

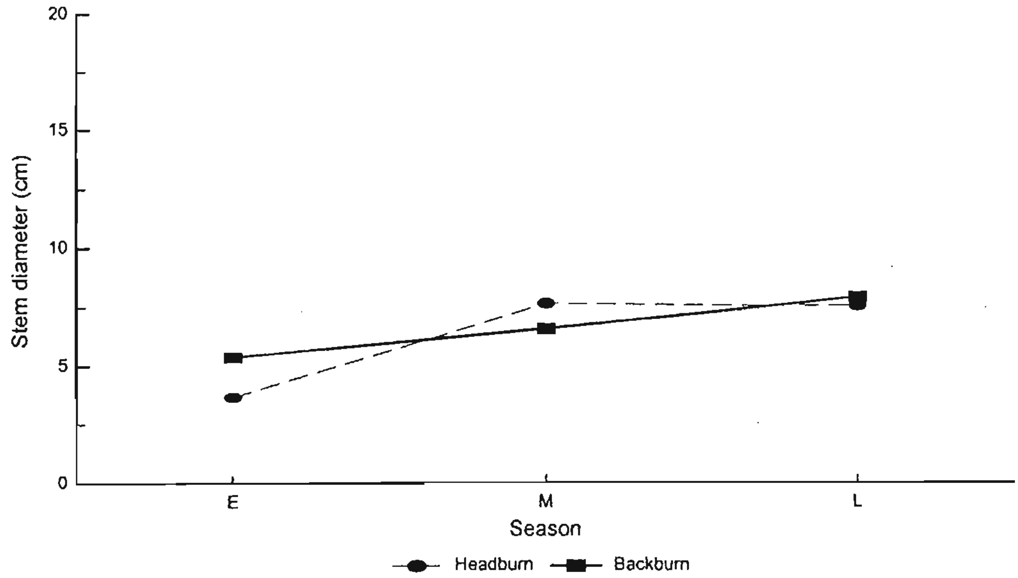

Figure 7.1 Mean stem diameter (cm) at 25 cm above ground level, for season and type of fire, for (E) early, (M) mid, and (L) late dry season burns.

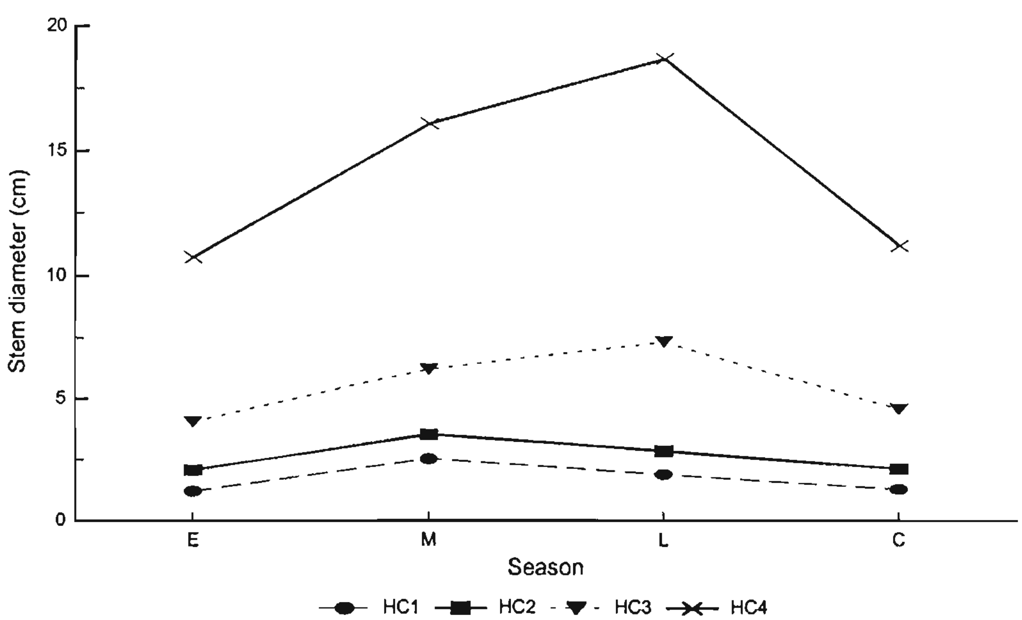

Figure 7.2 Mean stem diameter (cm) at 25 cm above ground level, for season and height class (HC), for (E) early, (M) mid, (L) late dry season burns and (C) control; HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

The season-type-height class interaction is highly significant, indicating that the third order interaction of the three variables is more significant than the second order interactions. The interaction effects give insight into the direction and/or magnitude of levels of season, type and height class as they affect each other at respective levels of the other. The stem diameter of trees headburnt in the early and mid dry season are smaller than those backburnt in the same seasons. The stem diameter of trees headburnt in mid dry season are greater than trees in backburnt areas. This might indicate that head fires in the early and late dry seasons (the two seasons with the highest fire intensities, Table 7.4 b) impacted the trees in such a manner that increase in stem diameter was reduced.

The effect of season of burning on stem diameter is more pronounced on larger trees (Figure 7.2). Trees in areas burnt during the mid and late dry seasons had greater stem diameters than trees burnt in the early dry season, or not at all. This trend was similar for all height classes.

4) Effect of treatment on percentage topkill

Analysis of variance of treatment effects are presented in Table 7.8.

Table 7.8 (a) Analysis of variance of season of burning and type of fire on percentage topkill of the treatment areas

Variate: Percentage Topkill

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Season	2	2853.3	1426.7	4.21	0.021
Type	1	1345.1	1345.1	3.97	0.052
Height class	3	58186.5	19395.5	57.17	<0.001
Season.Type	2	446.2	223.1	0.66	0.523
Season.Height class	6	2927.3	487.9	1.44	0.220
Type.Height class	3	1339.3	446.4	1.32	0.280
Season.Type.Height class	6	788.5	131.4	0.39	0.883
Residual	48	16283.2	339.2		
Total	71	84169.4			

(b) Means and 95% Confidence Limits for percentage topkill of season of burn, type of fire and height class

Season

	Early	Mid	Late
Upper	53.8	59.0	69.0
Mean	**43.0**	**48.2**	**58.2**
Lower	32.3	37.5	47.5

Type

	Back fire	Head fire
Upper	54.27	62.87
Mean	**45.50**	**54.10**
Lower	36.73	45.33

Height class

	HC1	HC2	HC3	HC4
Upper	86.2	88.1	56.3	18.1
Mean	**73.8**	**75.7**	**43.9**	**5.7**
Lower	61.4	63.3	31.5	-6.7

Height classes
HC1 0-50 cm
HC2 51-150 cm
HC3 151-350 cm
HC4 >351 cm

These results are presented graphically in Figures 7.3 to 7.5.

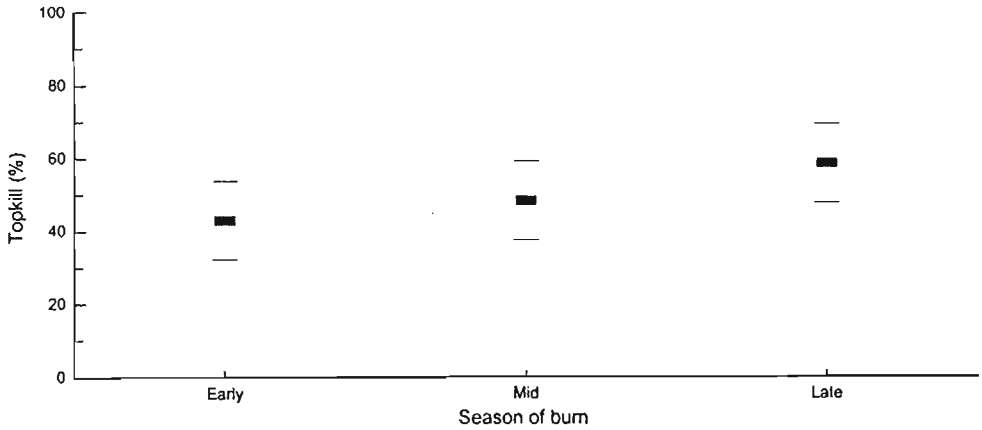

Figure 7.3 Mean percentage topkill for season of burning (±95% Confidence Limits).

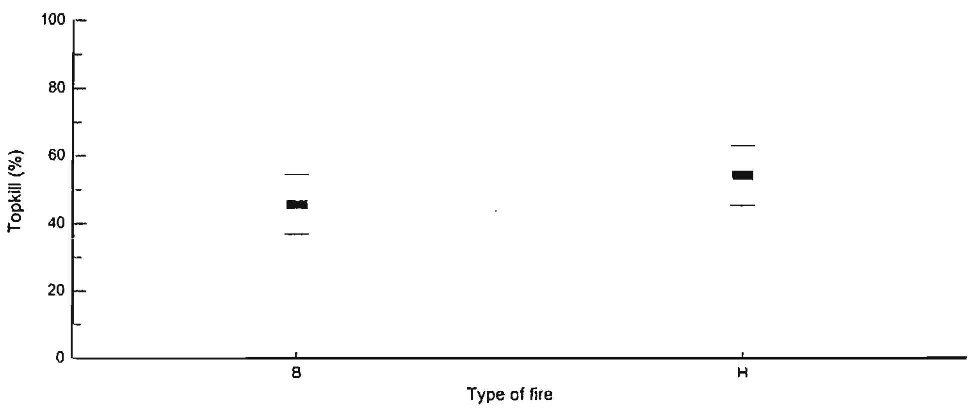

Figure 7.4 Mean percentage topkill for type of fire (±95% Confidence Limits).

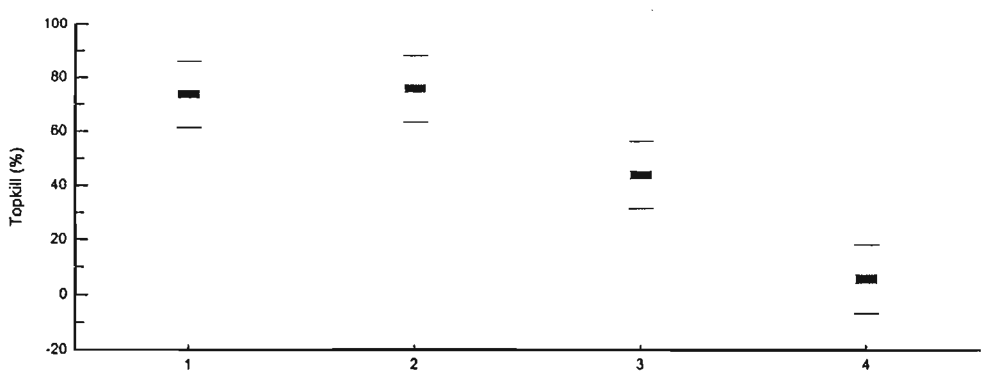

Figure 7.5 Mean percentage topkill for height classes (±95% Confidence Limits), HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

From the analysis of variance it is evident that there are significant differences between the three seasons of burning, between head and back burns and between height classes (Table 7.8a). Percentage topkill after late dry season burns is significantly higher than topkill after early dry season burns, by an average of 15.2%. There is no significant difference between mid and late dry season burns (Table 7.8 b). Topkill in areas burnt as a head fire experienced significantly higher levels of topkill, at the 6% level, with head fires having on average 8.6% more topkill (Figure 7.4). Height class 3 and 4 (43.9% and 5.7%) experienced significantly less topkill than height classes 1 and 2 (73.8% and 75.7%), while height class 2 was not significantly different to class 1. Height classes 2, 3 and 4 are significantly different to each other (Figure 7.5). The interaction effects are all non significant.

5) Effect of treatment on tree density

The population response to burning is presented as the change in population density *i.e* the absolute change in the number of individuals, on a per hectare basis. This is presented in Table 7.9.

Table 7.9 Mean initial population density, mean change in number of individuals and mean percentage change for the burning treatments on Malilangwe Estate

Treatment	Mean initial density (ha^{-1})	Mean change (ha^{-1})	Mean percentage change (%)
Early Back	4750.0	216.7	4.6
Early Head	3500.0	316.7	9.1
Mid Back	4141.7	66.7	1.6
Mid Head	4683.3	91.7	2.0
Late Back	2683.2	33.3	1.2
Late Head	2458.3	266.7	10.9

All burning treatments showed a nett recruitment of individuals, rather than a nett loss of individuals. Covariance analysis (Genstat 5.41) was carried out in an attempt to factor out the influence of initial population density, and thereafter determine whether season of burning, type of fire and height class had an effect on tree density.

Table 7.10 Analysis of covariance of season of burning, type of fire and height class on change in tree density (initial population density as covariate)

Variate: Change in tree density

Source of variation	d.f.	S.S.	M.S.	F.	P.
Season	2	4.34E+06	2.17E+06	1.93	0.157
Type	1	1.17E+04	1.17E+04	0.01	0.919
Height class	3	4.94E+07	1.64E+07	14.63	<0.001
Season.Type	2	1.36E+05	6.79E+04	0.06	0.941
Season.Height class	6	1.64E+07	2.73E+06	2.42	0.040
Type.Height class	3	3.98E+06	1.32E+06	1.18	0.328
Season.Type Height class	6	6.61E+06	1.10E+06	0.98	0.450
Covariate	1	2.47E+06	2.47E+06	2.20	0.415
Residual	47	5.29E+07	1.13E+06		
Total	71	1.75E+08			

There is no significant difference between the burning treatments (season or type of fire). The only significant main effect was height class. Burning had no impact on the recruitment or loss of individuals after one burning event, irrespective of season of burn or type of fire. The season-height class interaction was significant (Figure 7.6).

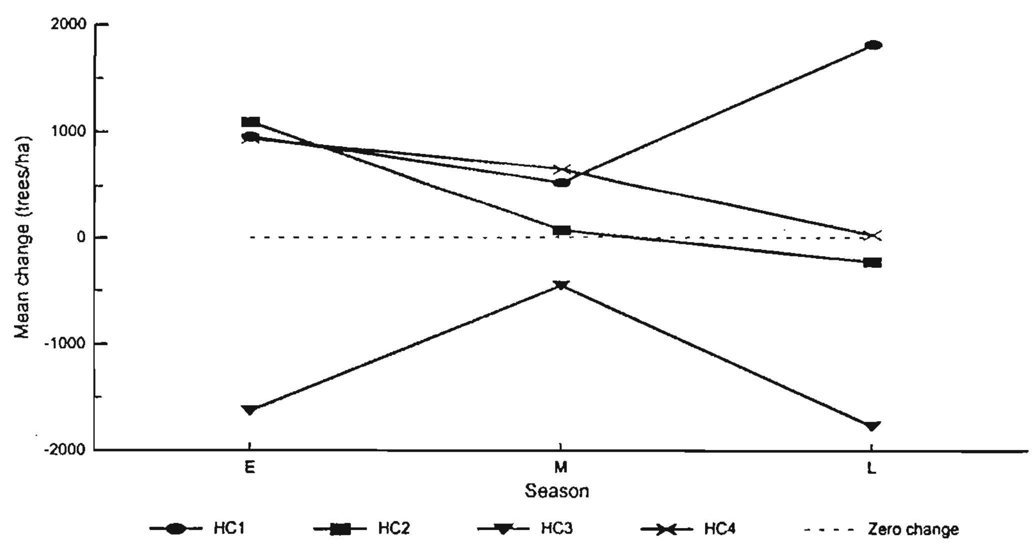

Figure 7.6 Mean change in density of trees, for season of burning and height class, for (E) early, (M) mid, and (L) late dry season burns; HC1=0-50 cm, HC2=51-150 cm, HC3=151-350 cm and HC4>351 cm.

For all seasons of burning, there was an increase in the number of individuals in height classes one and four (Figure 7.6). In height class one, high intensity burns (late dry season) led to the largest increase in individuals, whereas early and mid dry season burns led to smaller increases in tree density. In height class two only early and mid dry season burns led to an increase in tree density, whereas late dry season burns led to a decrease in tree density. For all seasons of burning height class three experienced a decrease in tree density. Late and early dry season burns (the two highest intensity burns) led to the largest decrease, while mid dry season burns did not experience such dramatic decreases in tree density. For all seasons of burning height class four experienced an increase in tree density, with late dry season burns having very little change, but mid and early dry season burns increasing. Height class one (0-50 cm) and three (151-350 cm) are impacted most by fire, height class two (51-150 cm) and four (>351 cm) less markedly. Late dry season burns led to the largest increase in height class one, but the largest decrease in height class three. Mid dry season burns led to the least change in these two height classes, while early dry season burns showed the same trends as late dry season burns.

6) Structural response of individuals to season of burn and type of fire

The change in the following three parameters were chosen as being of ecological and physiological value, and therefore good indicators of effects of season and type of fire on mopane woodland:

1) change in tree height,
2) change in the number of stems, and
3) change in the maximum canopy diameter.

For each parameter the base-line and end-of-season data were used to calculate the change in the particular parameter under investigation. Analysis of this change was then undertaken to determine whether season of burning, type of fire or interactions thereof were significant.

1) Change in tree height

Results of REML analysis are presented in Table 7.11.

Table 7.11 (a) Wald test for treatment effects, degrees of freedom and significance of change in tree height (cm)

Term	Wald statistic	d.f.	Significance
Treatment	46.9	2	P<0.001

(b) Mean change in tree height (cm), including 95% Confidence Limits

Early			
	Control	Early Back	Early Head
Upper	39.14	32.43	17.48
Mean	**18.07**	**11.36**	**-3.590**
Lower	-3.000	-9.710	-24.66
Mid			
	Control	Mid Back	Mid Head
Upper	27.14	14.11	11.67
Mean	**7.271**	**-5.759**	**-8.203**
Lower	-12.60	-25.63	-28.07
Late			
	Control	Late Back	Late Head
Upper	19.12	0.220	-6.060
Mean	**11.61**	**-7.290**	**-13.57**
Lower	4.100	-14.80	-21.08

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	0.62	P>0.5
Control vs. Early Head	2.01	P<0.05
Control vs. Mid Back	1.29	P<0.2
Control vs. Mid Head	1.53	P<0.2
Control vs. Late Back	4.92	P<0.001
Control vs. Late Head	6.57	P<0.001
Early Back vs. Early Head	1.39	P<0.2
Mid Back vs. Mid Head	0.24	P>0.5
Late Back vs. Late Head	1.64	P<0.2

These results are graphically presented in Figures 7.7 to 7.10.

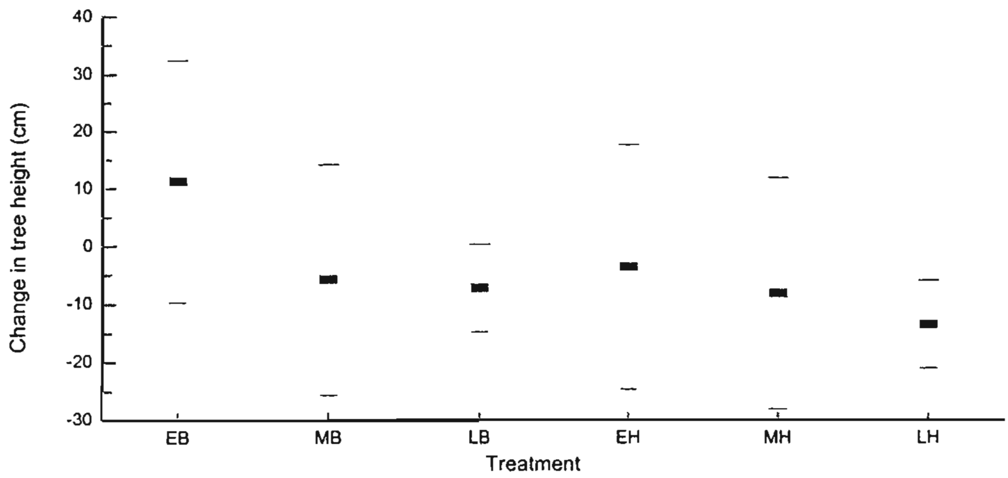

Figure 7.7 Mean change in tree height (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late and B back fire, H head fire) and length of monitoring periods (Figure 4.4).

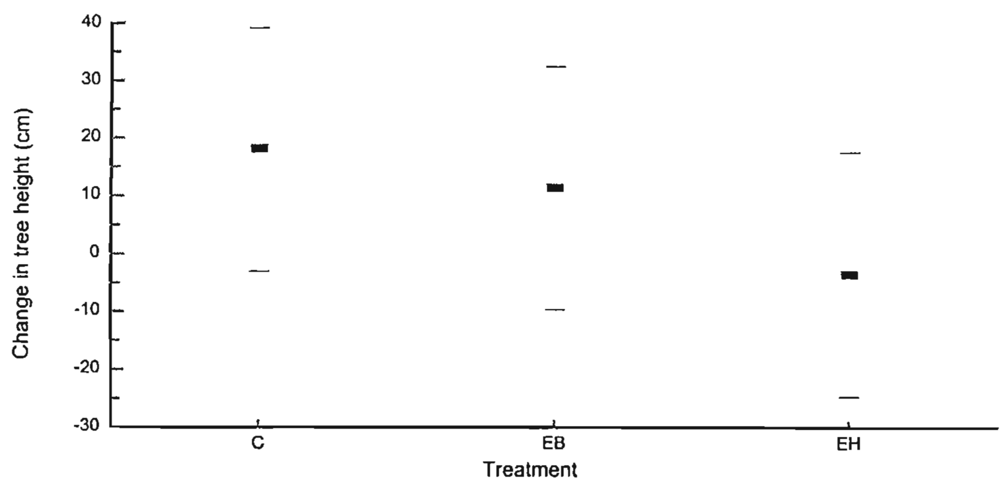

Figure 7.8 Mean change in tree height for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

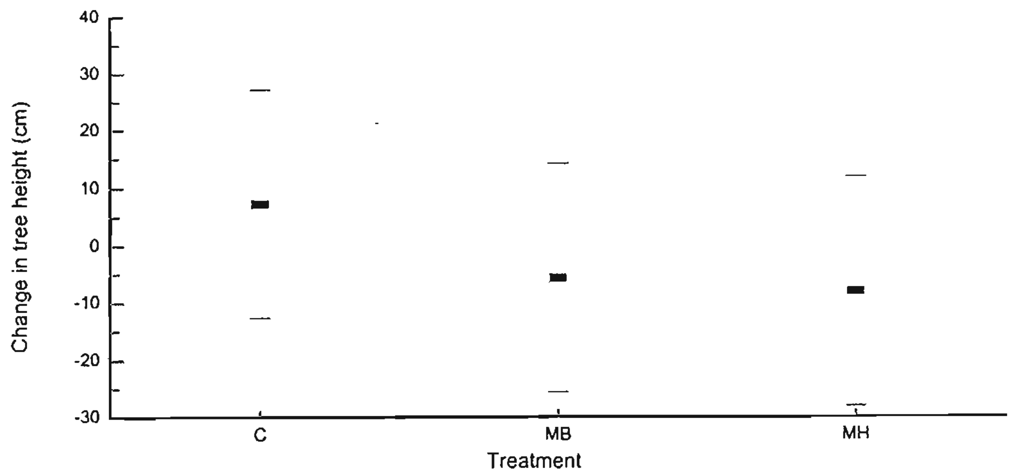

Figure 7.9 Mean change in tree height for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

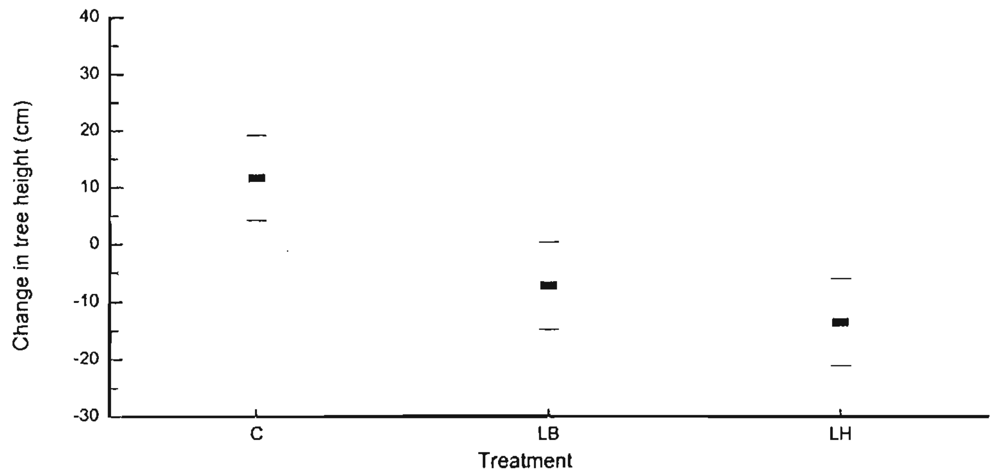

Figure 7.10 Mean change in tree height for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The change in tree height for treatments was significant ($P < 0.001$). For all seasons there was a mean increase in tree height in the control areas. In contrast to this, only the early back fires led to an increase in tree height (Table 7.11b). Early head fires resulted in a significant reduction in tree height, while early back fires were not significantly different. This can be attributed to the very high fire intensities attained during the early dry season head fires (Table 7.5). There was no significant difference between the mid dry season burns and the control, nor between the two types of fire. Notably however, the mid season burning treatments both led to a reduction in tree height, even though low fire intensities were recorded. For late dry season burns there was no significant difference between the two types, but trees in the control area showed a significant increase in height, whereas the treatment trees were reduced in height.

2) Change in number of stems

Results of REML analysis are presented in Table 7.12.

Table 7.12 (a) Wald test for treatment effects, degrees of freedom and significance of change in number of stems per tree

Term	Wald statistic	d.f.	Significance
Treatment	159.2	2	P<0.001

(b) Mean change in number of stems per tree, including 95% Confidence Limits

Early	Control	Early Back	Early Head
Upper	0.562	1.468	2.186
Mean	**-0.098**	**0.808**	**1.526**
Lower	-0.758	0.148	0.866

Mid	Control	Mid Back	Mid Head
Upper	1.023	3.799	3.554
Mean	**0.133**	**2.909**	**2.664**
Lower	-0.757	2.019	1.774

Late	Control	Late Back	Late Head
Upper	0.178	2.073	2.474
Mean	**-0.222**	**1.673**	**2.074**
Lower	-0.622	1.273	1.674

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	-2.69	P<0.01
Control vs. Early Head	-4.83	P<0.001
Control vs. Mid Back	-6.10	P<0.001
Control vs. Mid Head	-5.56	P<0.001
Control vs. Late Back	-9.27	P<0.001
Control vs. Late Head	-11.23	P<0.001
Early Back vs. Early Head	-2.13	P<0.05
Mid Back vs. Mid Head	0.54	P>0.5
Late Back vs. Late Head	-1.97	P<0.05

These results are presented in Figures 7.11 to 7.14.

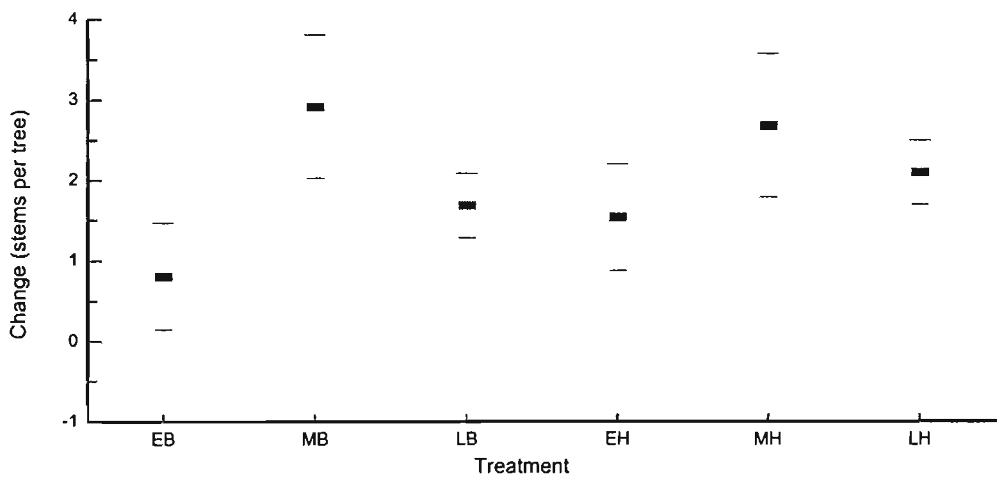

Figure 7.11 Mean change in number of stems per tree (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

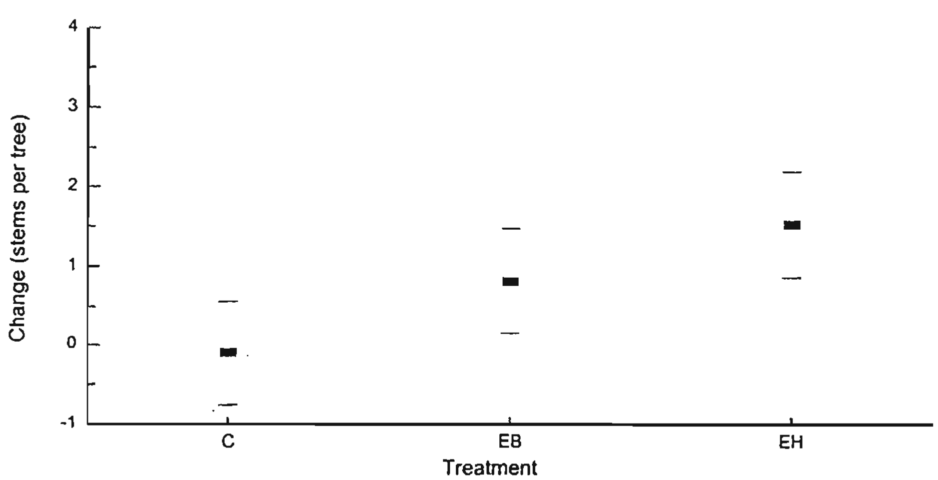

Figure 7.12 Mean change in number of stems per tree for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

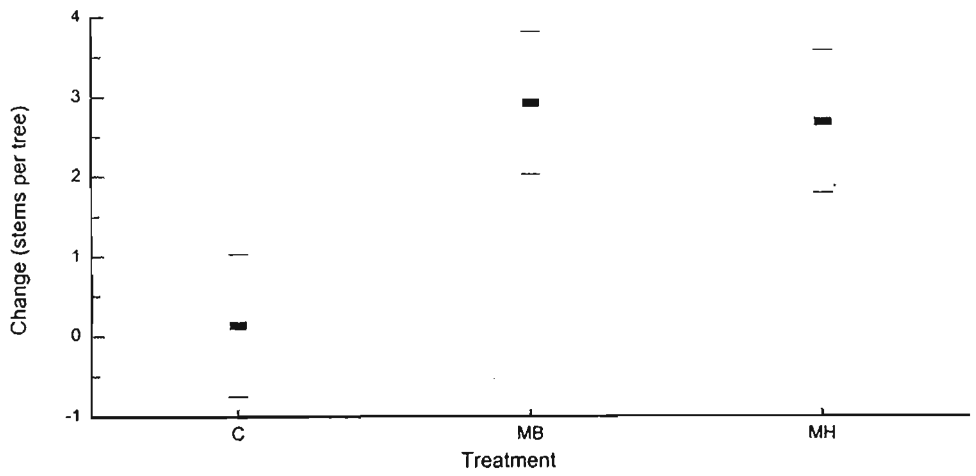

Figure 7.13 Mean change in number of stems per tree for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

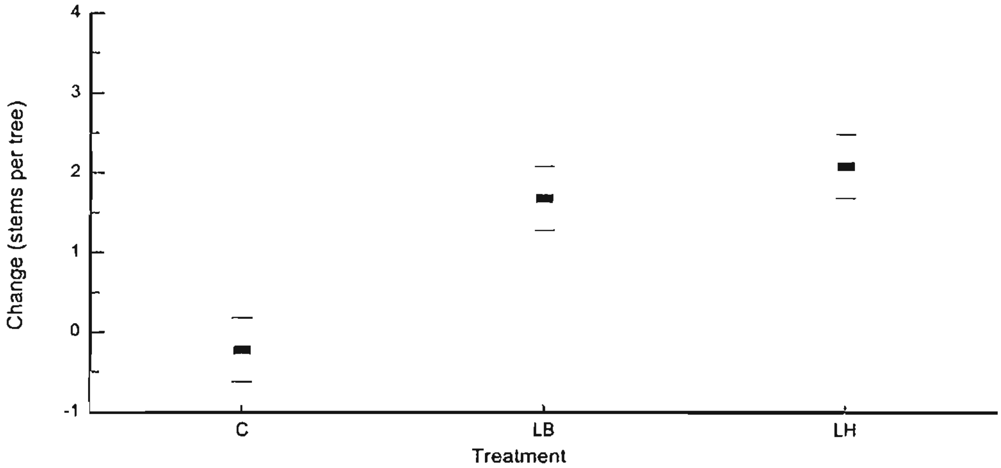

Figure 7.14 Mean change in number of stems per tree for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The effect of treatment was significant ($P<0.001$). In comparison with the control treatment, all burning treatments had a significantly greater increase in number of stems per tree. For early and late dry season treatments the control area showed a reduction in the number of stems. Both head and back fires in the early dry season led to a significant increase in the number of stems, whereas the control area had a reduction in the number of stems. This result also applied to the mid and late dry season burns. Early head fires had a significantly greater increase in number of stems than back fires, this being in response to the higher fire intensities attained by the head fires. For mid dry season burns there was no significant difference between types of fire. Late dry season head fires also had a significantly greater number of stems, than trees in back fire treatments. For late dry season burns there was a significantly greater number of stems as a result of coppicing in response to head fires, than back fires. Mid season back and head fires led to the largest increase in the number of stems, whereas early dry season burns had the lowest increase in stems (Figure 7.10). This trend (Figure 7.11) would indicate that, for intense fires, head fires lead to a greater increase in coppicing stems than do back fires, but that high intensity fires (early and late dry season) lead to a smaller increase in number of stems than low intensity fires (mid dry season).

3) Change in maximum canopy diameter

Results of REML analysis are presented in Table 7.13.

Table 7.13 (a) Wald test for treatment effects, degrees of freedom and significance of change in maximum canopy diameter (cm)

Term	Wald statistic	d.f.	Significance
Treatment	42.4	2	P<0.001

(b) Mean change in maximum canopy diameter (cm), including 95% Confidence Limits

Early	Control	Early Back	Early Head
Upper	30.57	11.92	8.05
Mean	**15.91**	**-2.743**	**-6.61**
Lower	1.249	-17.40	-21.3
Mid	Control	Mid Back	Mid Head
Upper	18.8	-6.64	-12.45
Mean	**5.34**	**-20.1**	**-25.94**
Lower	-8.15	-33.6	-39.43
Late	Control	Late Back	Late Head
Upper	17.77	0.279	-4.23
Mean	**10.45**	**-7.041**	**-11.5**
Lower	3.134	-14.36	-18.9

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	2.49	P<0.02
Control vs. Early Head	3.01	P<0.01
Control vs. Mid Back	3.70	P<0.001
Control vs. Mid Head	4.55	P<0.001
Control vs. Late Back	4.68	P<0.001
Control vs. Late Head	5.89	P<0.001
Early Back vs. Early Head	0.52	P>0.5
Mid Back vs. Mid Head	0.84	P<0.5
Late Back vs. Late Head	1.21	P<0.3

These results are graphically presented in Figures 7.15 to 7.18.

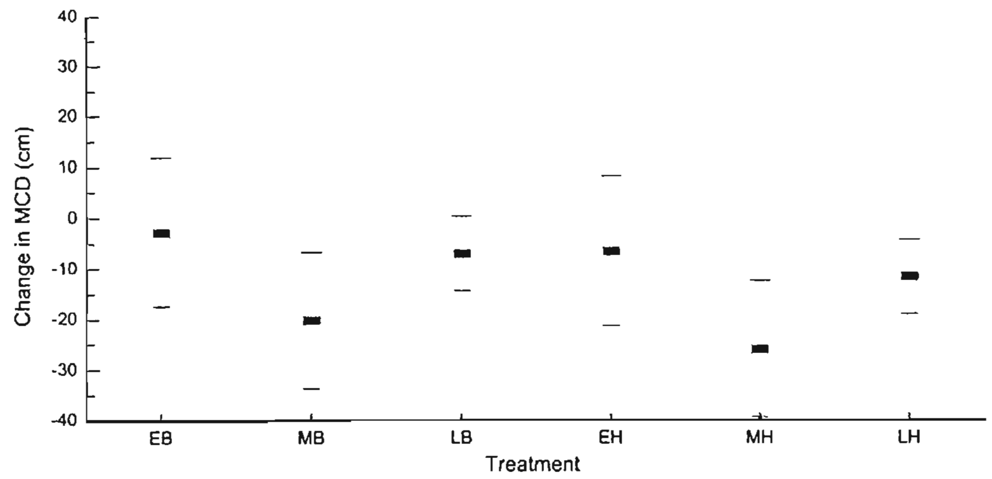

Figure 7.15 Mean change in maximum canopy diameter (MCD) (including 95% Confidence Limits) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

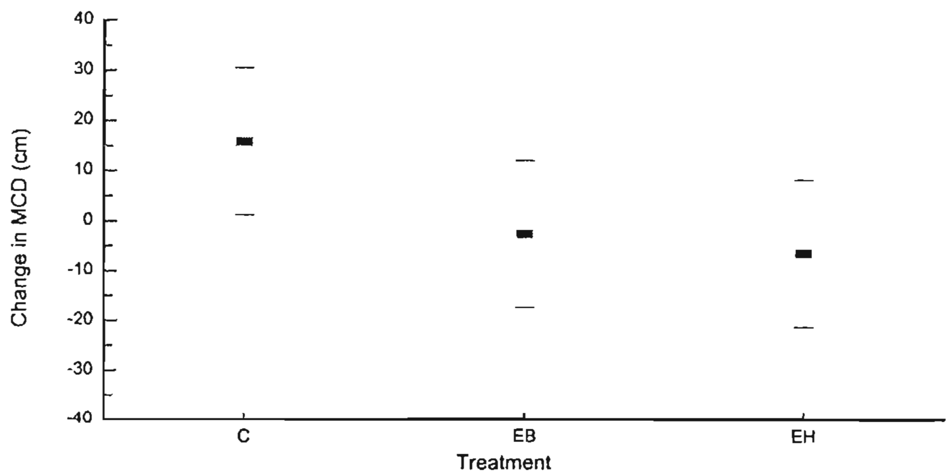

Figure 7.16 Mean change in maximum canopy diameter (MCD) for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

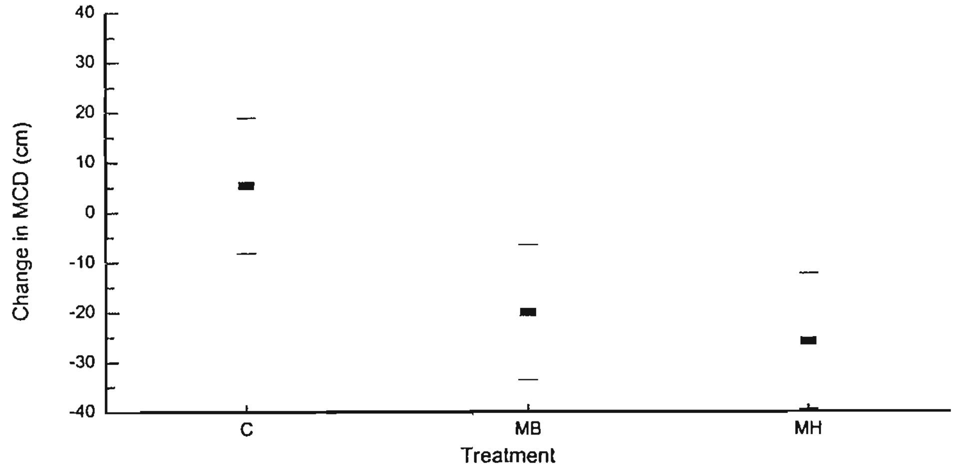

Figure 7.17 Mean change in maximum canopy diameter (MCD) for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

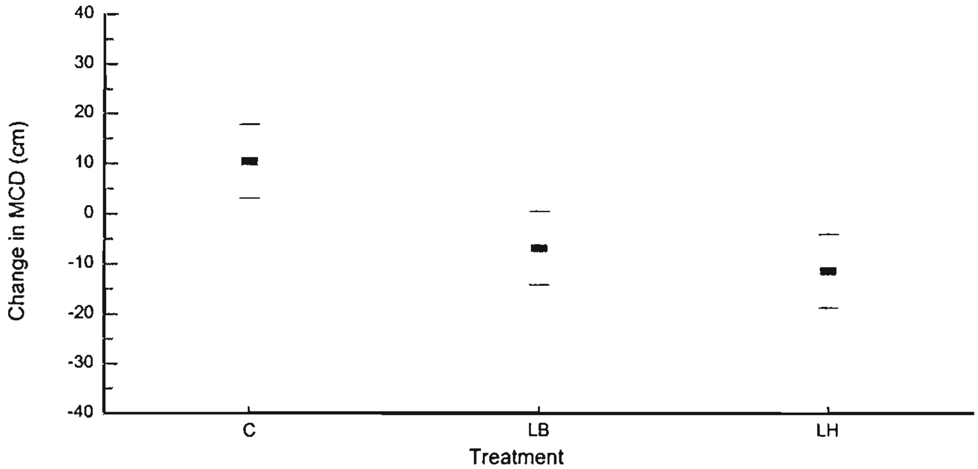

Figure 7.18 Mean change in maximum canopy diameter (MCD) for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

Treatment effects were significant ($P<0.001$). Early dry season burns led to a significant reduction in MCD, whereas the control area had an increase in MCD. The same trend was found for mid and late dry season burns. There were no significant differences between head and back fires for any season. For both head and back fires, the mid dry season treatment led to a significantly greater reduction in MCD than either early or late burns (Figure 7.14).

7) Effect of treatment on leaf dry mass

The equations developed in Chapter 5, for estimating leaf dry mass of mopane individuals using the estimated spatial canopy volume, were used to calculate the leaf dry mass of mopane individuals.

Results of REML analysis are presented in Table 7.14.

Table 7.14 (a) Wald test for treatment effects, degrees of freedom and significance of change in leaf dry mass (kg)

Term	Wald statistic	d.f.	Significance
Treatment	57.3	2	P<0.001

(b) Mean change in leaf dry mass (kg) including 95% Confidence Limits

Early			
	Control	Early Back	Early Head
Upper	0.345	-0.02	-0.03
Mean	**0.195**	**-0.17**	**-0.18**
Lower	0.045	-0.32	-0.33
Mid			
	Control	Mid Back	Mid Head
Upper	0.174	-0.08	-0.08
Mean	**0.014**	**-0.24**	**-0.24**
Lower	-0.146	-0.40	-0.40
Late			
	Control	Late Back	Late Head
Upper	0.3598	-0.0246	-0.2759
Mean	**0.1798**	**-0.2046**	**-0.4559**
Lower	-0.0002	-0.3846	-0.6359

(c) t-tests and significance of test results

Test	t-value	Significance
Control vs. Early Back	4.67	P<0.001
Control vs. Early Head	4.83	P<0.001
Control vs. Mid Back	3.11	P<0.01
Control vs. Mid Head	3.11	P<0.01
Control vs. Late Back	4.15	P<0.001
Control vs. Late Head	6.86	P<0.001
Early Back vs. Early Head	-0.004	P>0.5
Mid Back vs. Mid Head	2.85	P<0.01
Late Back vs. Late Head	2.71	P<0.01

These results are graphically presented in Figures 7.19 to 7.22.

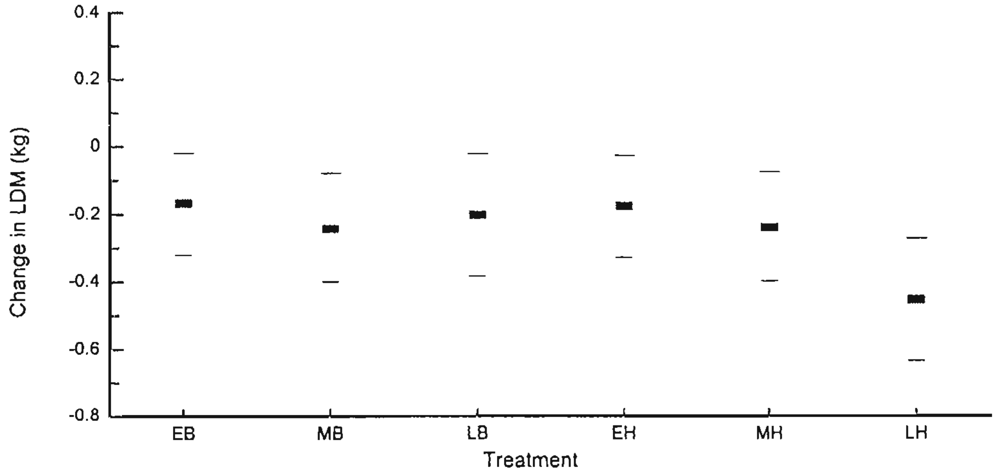

Figure 7.19 Mean change in leaf dry mass (LDM) (± standard error of the difference) for season of burning and type of fire, noting the different burning events (E early, M mid, L late, B back and H head fires) and length of monitoring periods (Figure 4.4).

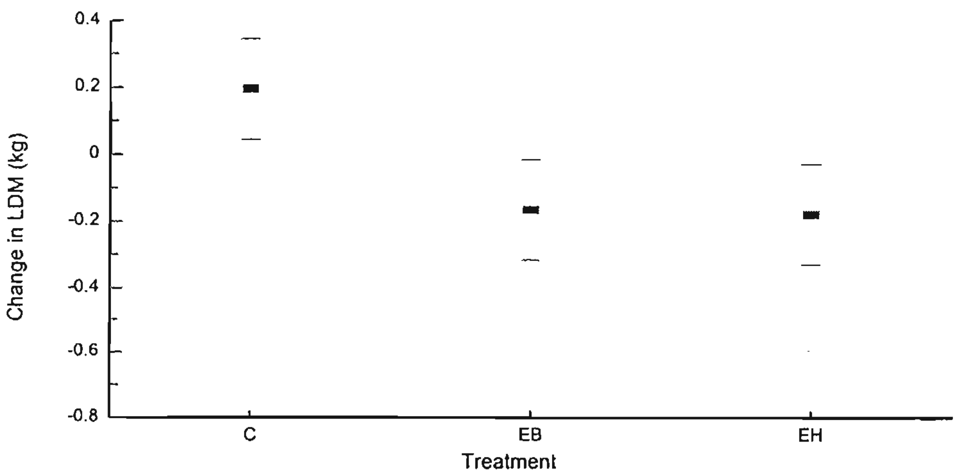

Figure 7.20 Mean change in leaf dry mass (LDM) for early (E) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

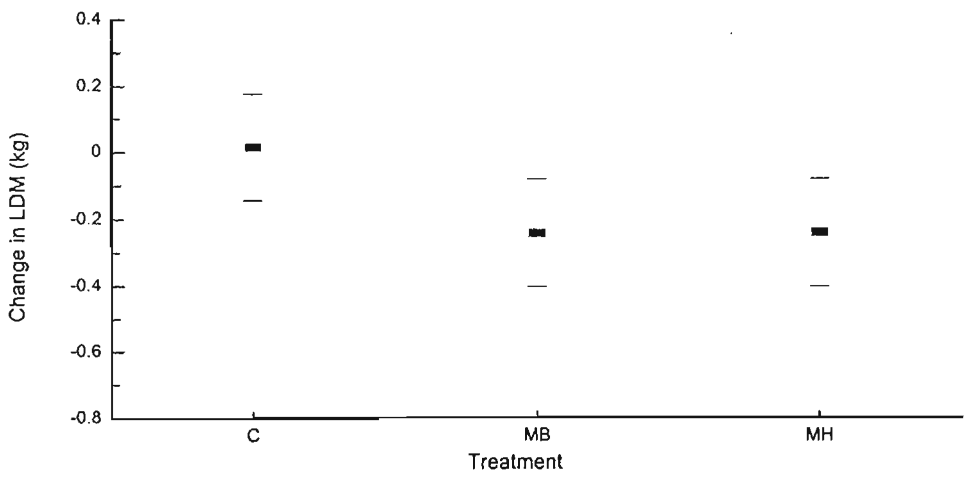

Figure 7.21 Mean change in leaf dry mass (LDM) for mid (M) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

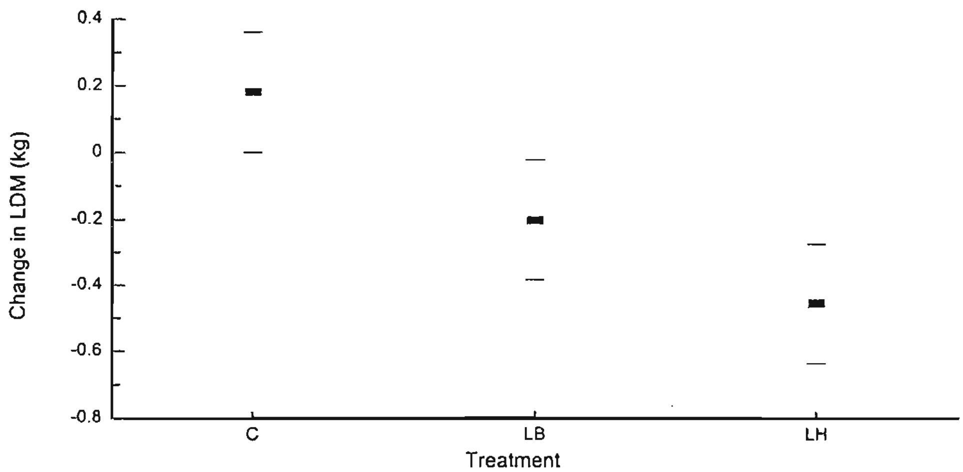

Figure 7.22 Mean change in leaf dry mass (LDM) for late (L) dry season head (H) and back (B) burns and control (C) treatments (± 95% Confidence Limits).

The treatment effects were significant ($P<0.001$). All burning treatments resulted in a reduction in leaf dry mass, whereas control areas had an increase in LDM. There were no differences between the early, mid and late dry season back fire treatments. The late dry season back fires led to a significant decrease in LDM, compared to mid and early dry season treatments. Early, mid and late dry season burns (both back and head fires) were significantly different to the controls (Figures 7.20 to 7.22).

Discussion

There were no significant differences between fire intensities experienced in the three seasons of burning (Table 7.6). Head fires, in all seasons, were significantly more intense than back fires ($P<0.05$). This agrees with many other findings showing that, in general, savanna head fires are more intense than back fires (Trollope and Tainton 1986 and Trollope *et al.* 1996).

It is unfortunate that the analysis of the change in stem diameter (*i.e* post-burn compared with pre-burn) was not possible. The possible effect of burning treatments on stem diameter was therefore not possible, and the variability in stem diameter that is apparent in Figure 7.2 cannot be attributed to treatment effects. However it is not conceivable that changes in stem diameter will occur after only one burning treatment, but would require extended periods of treatment application.

The late dry season treatment led to the highest percentage topkill (58.2%), and was significantly higher than the early dry season treatment. This is in accordance with the fire intensity trend, where late dry season burns were more intense than the mid and early burns. This contrasts with the findings of West (1965) and Wade and Johansen (1986), who postulated that seasonal variations in tree physiology (phenophase) are critically important in determining the susceptibility of trees to fire. There are a number of covarying factors that contribute to determining the susceptibility of trees to fire. For a given fuel load, under early and late dry season conditions respectively, they predict that the percentage topkill after late dry season burns will be greater because of the difference in tree phenophase. However the variation in the susceptibility of a tree to fire is not only determined by the variation in tree phenophase, but by the environmental and specific tree conditions that occur. These covarying factors are extraneous to the tree, being determined primarily by the climate and nature of the standing crop (fuel). These factors include ambient temperature, relative humidity, wind speed, fuel load, fuel moisture and moisture content of the tree branch extremities, which together largely determine the degree of damage to the tree by fire. Head fires led to significantly more topkill, than back fires (Figure 7.4). This finding corroborates findings by other researchers (Trollope 1980, Stocks and Trollope 1993 and Trollope *et al.* 1996). Height classes one and two experienced the greatest topkill, 73.8% and 75.7% respectively (Figure 7.5). Damage to height class three and four was significantly lower (43.9% and 5.7% respectively). Trollope *et al.* (1995) found the same trend for the effect of height on topkill of bush subjected to a fire intensity of 3 000 $kJ.s^{-1}.m^{-1}$ (Figure 1.3). This fire intensity is higher than that experienced in this study, and therefore the percentage topkill was higher.

Fire does not significantly change the stand density within mopane woodlands. The same results were found for mopane in the Kruger National Park by Tainton *et al* (1991) and Trollope *et al.* (1996), for *Acacia spp* species in Hluhluwe Game Reserve (Macdonald 1980), in the Sengwa Wildlife Research Area (Guy 1981), for *Acacia spp* in the eastern Cape (Trollope 1974), and *Pinus palustris* woodlands in the southeastern United States (Glitzenstein *et al.* 1995). These findings repudiate the claims made by Scott (1966) that fire reduces bush density by killing seedlings of trees and shrubs. They also contrast with the high levels of mortality reported by Trapnell (1959) for *Brachystegia-Julbernardia* woodlands in northern Rhodesia, where percentage mortality in late-, early- and protected plots was 17.4%, 7% and 4.2% respectively. However these figures were from woodlands in which fire-sensitive species predominate, and where mopane did not occur. As with other savanna tree species however, mopane is very resistant to fire alone (Trollope *et al.* 1996), and may be particularly tolerant of fires regardless of when they occur. Nett recruitment of individuals took place in all treatment areas, as well as controls (mean change in density for burning treatments 4.9%). This change is almost twice as high as the increase in stand density reported by Guy (1981) of 2.5% for a two year period. This difference can be explained by the differences in elephant density: the two areas being of similar size (approximately 380 km^2), but the elephant density in the Sengwa Wildlife research Area being twice as high as that found on Malilangwe Estate.

This finding, that limited recruitment took place even in burnt areas, contradicts the assumption made by Lewis (1991) that the occurrence of fire would increase seedling mortality, as well as the finding by Macdonald (1980) that fire reduced post-fire seedlings.

Norton-Griffiths (1979) elucidates upon the synergistic relationship between elephants and fire, whereby elephants open up bush thickets and encourage the growth of grass within them, which fuels more intense fires that lead to a decrease in cover density (Buechner and Dawkins 1961). For mopane woodlands however this relationship is much weaker. Owing to its occurrence on shallow, xeric soils unfavourable to many grass species, the grass layer is generally scant, and high fuel loads such as those found in Murchison Falls National Park (Buechner and Dawkins 1961) are not attained (specific fuel loads are not given, but with annual rainfall of over 1 000 mm and a tropical climate, as well as descriptions of the grass sward, it is assumed that fuel loads are a lot greater). Therefore, even when elephants do open up bush thickets, the increase in grass production may not be sufficient to support fires of the intensity needed to kill mopane trees. This suggests that fire may have the same influence as herbivory *i.e* limiting the rate at which density increases. This agrees with the findings by Dublin (1986) that annual seedling mortality by elephants and fire were 4% respectively. It also suggests that there is no increase in herbivory in burnt areas, and that there is no interactive effect of fire and browsing in reducing mopane tree density in burnt areas. However this contrasts with later findings by Dublin (1995) that browsers showed a distinct preference for seedlings in burnt plots. If large browsers such as elephant, black rhino, eland; and small browsers such as steenbok and impala, were attracted to burnt (open) areas then it is possible that tree population density should decrease in these areas. However, this was not the case, and browsers vacated burnt areas and moved into adjoining unburnt areas, possibly in an attempt to find cover from predators (personal observations). This may well have been as a result of the size of the area burnt, as the burning treatments were relatively small in size, compared to the size of natural fires. Unfortunately no quantitative data were collected regarding animal densities in the burning treatments pre- and post-burning, and these are no more than speculation. This highlights the importance of the patch dynamics of fire, and supports a more *laissez faire* point ignition approach to management burning, which results in areas of residual grass cover, and protection from predators, within the larger burnt area. With high grazer/browser densities, and the simultaneous implementation of burning large blocks, animals may be forced into burnt areas, with the result that seedlings (<50 cm) may be eradicated, leading to a situation where no recruitment takes place. For invasive species such as *Acacia borleae* and *Dichrostachys cinerea* this may be advantageous, but for other more sensitive, or threatened, species this may be disastrous, especially if this takes place over many years and the recruitment of successive cohorts is removed.

The only burning treatments that led to significant changes in tree height were the early head fires, and both types of late dry season burns, all of which led to decreases in tree height of 3.6 cm, 7.3 cm and 13.6 cm respectively (Table 7.11). This is as a result of the removal of leaf material through topkill, and these trends are the same as those found for the effect of topkill. Belsky (1984) showed that tree height was maintained, or reduced, by browsing and that fire had little additional effect, whereas Macdonald (1980) found that fire reduced the size of three *Acacia* species. With the exclusion of browsing and fire tree height increased significantly.

As with other woodland species, and found in other studies (Dublin 1995), mopane coppices profusely in response to burning. Fire in all seasons, and using both types of burning, led to an increase in the number of stems (Table 7.12). Mid dry season burns led to the greatest increase in number of stems. This is interesting as it suggests that low intensity fires (below 1 000 $kJ.s^{-1}.m^{-1}$) led to a significant increase in the number of stems, while early and late dry season burns (fire intensities greater than 1 000 $kJ.s^{-1}.m^{-1}$), led to significantly smaller changes in the number of stems. Also, for the treatments experiencing high fire intensities (early and late dry season) the head fires led to significantly more coppice stems than back fires. If this profuse coppicing, induced by burning, can be subjected to high levels of browsing pressure, then fire can be effective in bush control (Trollope 1974), and the shrub structure may be modified. Like the major portion of southern African savannas (Trollope 1980), this semi-arid area is characterised by rainfall which is too low and unreliable to enable adequate grass material to accumulate and support frequent fires, that can burn the coppice growth and control seedlings. It is also likely that repeated, intense, fires of over 1 000 $kJ.s^{-1}.m^{-1}$will result in less profuse coppicing, and the development of a more single-stemmed woodland population. The difficulty in this is that the potential for repeated, intense, fires is limited in these areas because of the environmental and soil characteristics that have led to the establishment of mopane, and therefore the occurrence of mopane shrubveld is inevitable, and cannot be altered by fire.

All burning treatments led to significant decreases in canopy diameter, whereas the control treatments all had increased canopy diameters (Table 7.13). This shows that burning, of any type and within any season, leads to a reduction in canopy diameter *i.e* a change in structure. As with changes in tree height, this response is also a reflection of the topkill experienced by trees during fires. Tainton et al. (1991) found the same results in the Kruger National Park, as well as van Wyk (1972) and West (1958) in Rhodesia. Mid dry season burns led to the largest decrease, followed in magnitude by the early and late head fires (Figure 7.15). Even though the mid dry season burns had the lowest fire intensity, the decrease in maximum canopy diameter is the greatest. This suggests that there is another, unrecorded, variable that is leading to this change. The inverse relationship between the increase in the number of stems and the decrease in canopy diameter of trees in the low intensity mid dry season burns can be explained in two ways:

1) Mid dry season burns result in the largest increase in number of stems, and it is this investment in additional stem growth that may lead to the canopy diameter decreasing at the expense of this investment in stems *i.e* the canopy diameter of the plant producing the most new coppice stems will decrease the most.
2) Alternatively, the photosynthetic requirements of the plant that coppices profusely are now partially met by the new coppice stems, and therefore canopy diameter can decrease as the total photosynthetic requirements are still being met. These constraints and tradeoffs have been identified in many terrestrial plants, and it is these allocation-based tradeoffs (Tilman 1990) that led to reductions in canopy diameter and canopy volume in mopane individuals. Fire and herbivory are major environmental constraints that impact the plant, and the tradeoffs that plants face in dealing with these constraints are directly attributable to differences in biomass and nutrient allocation patterns (Tilman 1990).

All seasons and types of fire led to significant decreases in leaf dry mass, whereas the control treatments increased in leaf dry mass (Table 7.14). The mean change in leaf dry mass per tree for all treatments was -0.122 kg. Although the number of stems increases in response to burning, the leaf biomass declines. This suggests that the attempt by the plant to invest in additional stem growth, in marginalising the damage incurred by fire, is not adequate, and that although there are more stems, the leaf dry mass decreases. This is an expense to the plant, and one that may impact the plants longevity over time. Guy (1981) found that biomass in mopane woodland decreased by 6%. This was also under conditions of elephant and fire damage, but at greater elephant densities. For back fires, there was no significant difference between seasons, but for head fires the late dry season burns led to a significantly greater decrease in leaf dry mass than the other two seasons (Figure 7.19). This lends quantitative support to the field observations made by Trollope *et al.* (1996) that head fires cause higher topkill of stems and branches as compared to back fires. In contrast to the effect of treatments on the change in number of stems and MCD, the change in leaf dry mass would appear to be most pronounced after high intensity fires, such as those of the late dry season head fires ($>1\ 500\ kJ.s^{-1}.m^{-1}$). This suggests that, as found by Glitzenstein (1995) and Trollope *et al.* (1996), variation in fire behaviour (intensity or temperature) may be much more important than season of burning, in predicting population dynamics. The nature, behaviour and intensity of a fire is not determined by the season in which it occurs, but rather by the specific fuel load, fire regime and environmental conditions under which the fire takes place. Owing to this specificity of fire behaviour and fire intensity, and the resultant impacts on tree structure and physiology, the effects of season of burning are not predictable, nor valid in determining the effects of such fires. Rather the specific fuel load, fire intensity and fire behaviour data will be more valid in determining the effect of fire on mopane woodlands.

Chapter 8

General discussion and conclusions

As with the majority of other savanna tree species, mopane shows tremendous resilience and persistence throughout its range. This is borne out by the fact that over its range, mopane remains the dominant species and in some cases competitively excludes other trees and/or grasses. Under pressure from fire and herbivory this species shows continued resilience, through prolific basal and aerial coppicing, and emergence of new growth from underground rootstocks. In this the initial focus was on the standing crop dynamics of the grass sward in mopane vegetation, and thereafter the influence of burning during different seasons, and with different types of fires. After testing the hypotheses stated at the end of the literature review, the following was determined:

Answers to questions posed

Standing crop dynamics

One standard disc pasture meter calibration equation cannot suffice for estimating standing crop for the whole year, because of the large spatial and temporal variation in the grass sward. The standard procedure described by Bransby and Tainton (1977) is not applicable to savanna grass swards, but the revised procedure (Trollope and Potgieter 1986), with which disc height accounts for more than 90% of the variation in standing crop, is recommended. However, in order to account for the spatial variation in grass sward structure, specific calibration equations must be developed for homogenous vegetation units *eg*. mopane woodland.

Standing crop for a particular month is highly dependent on the effective rainfall from the previous month, and standing crop tracks effective rainfall closely. Peak standing crop is positively related to annual rainfall, and the potential peak standing crop can be predicted. After peak standing crop has been achieved standing crop declines through the dry season as effective rainfall decreases, and this decline in standing crop can be estimated using a decrease function.

Mopane leaf quantification

Two distinct equations were developed: one for coppicing individuals, and one for non-coppicing individuals. At certain canopy volumes these equations are different to the equations developed for mopane areas north of the Soutpansberg in South Africa, and the equations derived in this study are therefore recommended for estimating leaf dry mass in the south-eastern lowveld of Zimbabwe.

Season of burning

The effect of season of burning was not consistent over all the parameters investigated. There was no significant difference between the fire intensities of the fires implemented in the three seasons. There was also no seasonal burning effect on the change in tree density. However, the percentage topkill between different seasons was highly significant, with late dry season burns resulting in higher levels of topkill. Tree height was reduced significantly by early and late dry season burns, whereas mid dry season burns did not significantly reduce tree height. Mid dry season burns led to the greatest increase in the number of stems per individual through coppicing, whereas mid dry season burns led to the greatest decrease in maximum canopy diameter. The seasonal effect of burning on change in leaf dry mass was not evident, except where late dry season head fires led to a greater decrease in leaf dry mass than the other two seasons.

Type of fire

Head fires were more intense than back fires, over all seasons. This fire intensity effect is evident in the other parameters investigated. Head fires led to significantly more topkill of mopane trees. Within seasons there was no significant difference in the density of trees between types of fire applied. There was no significant effect of type of fire on the change in tree height, nor on change in maximum canopy diameter. For the change in the number of stems per tree early and late dry season head fires led to greater increases in the number of stems than did back fires, and for change in leaf dry mass late head fires led to a significantly greater reduction in leaf dry mass than did back fires.

Fire intensity

It was found that fire intensities did not differ between seasons, but that head fires are more intense than back fires. Owing to this, head fires led to more topkill of mopane individuals, and because of the high fire intensities (environmental conditions being conducive), the late dry season fires led to the highest topkill. Burning had no effect on the recruitment or loss of individuals, irrespective of season or type of fire. Even with low fire intensities tree height was reduced. More intense fires led to a smaller increase in the number of coppice stems. Maximum canopy diameter and leaf dry mass are reduced by fire, whereas maximum canopy diameter and leaf dry mass increases when fire is excluded.

Conclusions

The spatial and temporal variation in standing crop is highly dependent on rainfall. Owing to the low basal cover of the mopane woodland areas, and structural heterogeneity between grass species and times of year, the use of the standard disc pasture meter, as described by Bransby and Tainton (1977), is unacceptable for estimating standing crop. To account for the spatial and specific variation in standing crop the revised procedure (Trollope and Potgieter 1986) is recommended. However the use of a single predictive equation, developed for the Kruger National Park in South Africa, is questionable. The assumption cannot be made that the grass structure and basal cover of Malilangwe Estate can be accurately estimated using a single equation developed for an area 50 times larger in size, and containing vastly different vegetation types and climates. Instead it is highly recommended to management that the revised procedure be carried out for each homogenous vegetation type within which standing crop needs to be estimated. To account for the temporal variation in standing crop (between seasons) it might be necessary to calibrate the disc pasture meter, using the revised procedure, for specific sampling events. Owing to financial and other constraints this may not be possible. The study of the effect of season on the accuracy of the revised procedure, is needed.

From this study it cannot be shown conclusively that there is a clear effect of season of burning across all the parameters studied. West's (1965) postulation that plant phenophase is critical in determining their susceptibility to fire, applies only to percentage topkill. Late dry season burns did lead to a significantly higher level of topkill, than did mid or early dry season burns. It is therefore concluded that the effect of season of burning on the damage to tree stems and branches (topkill) is influenced by season of burning because there was no significant difference between the fire intensities experienced in the three seasons, but there were significant differences in percentage topkill. Plants burnt at the end of the dry season (when the plant is preparing for new growth in response to increased day temperature and photoperiod) are more susceptible to topkill than plants burnt in the early or mid dry season. This phenophase effect was not evident for the other parameters investigated.

The effect of type of fire was highly significant for a number of parameters. Over all seasons, head fires were more intense, and it is this higher intensity that led to significant differences in response to head and back fires. However there was no significant difference in the density of trees burned as head or back fires. This provides further evidence that mopane is highly resistant to fire alone, and that population density is unaffected by fire. In contrast to this is the finding that fire changes the structure of the tree significantly. This supports evidence for other savanna areas, as well as other tree species (Wlaker 1985, Trollope *et al.* 1995, Trollope *et al.* 1996). The major influence of fire is to change the above-ground physiognomy of the tree component, whereby the distribution of individuals within each height class changes. The total number of individuals does not change, but there is an increase in the number of short individuals (< 150 cm) and tall individuals (> 351 cm). This is at the expense of individuals of intermediate height (151-350 cm).

From this study it has been ascertained that the effect of season of burning was not significant, except for percentage topkill. Maximal damage to individual mopane trees, through topkill of aerial extremities, takes place after late dry season fires. Fire damage is also greater after head fires, and therefore the maximum damage will be evident after late dry season head fires.

Possible long-term effects of burning in different seasons

Other than the quantitative effects determined in this study, there is an observational aspect of great importance, and this phenomenon may well impact mopane woodland dynamics with more frequent burning. Van Wyk (1971) claimed that frequency of burning appears not to have any significant effect on the density of woody plants, but that frequent burning reduces woody phytomass. This was also found by Kennan (1971), Tainton *et al.* (1991), Trollope (1983) and Trollope *et al.* (1996). Conversely Dublin (1996) showed that seedling mortality increased greatly with increasing fire intensity and burn number. The observations made on Malilangwe Estate are as follows:

Early dry season burns

These burns took place in June 1997, and mopane trees were in full leaf carriage. The immediate response to burning was a loss of leaves (July 1997), while unburnt trees remained in full leaf carriage. This disturbance early in the dry season led to the trees photosynthetic ability being reduced, as they lose leaves when they should be carrying full leaf carriage, and also until much later in the dry season (November/December 1997). The impact on the trees was further exaggerated at the end of the dry season (December 1997), when trees in the burnt areas flushed earlier than those in unburnt areas. This is the hottest time of the year, with daily maxima over 40°C. Trees in the burnt areas were therefore flushing and carrying leaves when the climatic conditions were most unconducive to photosynthetic processes (high temperatures and low water availability during November and early December, before the onset of the rains). Physiological stress leads the plant to senesce at this time of the dry season, but fire results in the plant bearing leaves when it is most unsuitable. The implications of continued early dry season treatments such as this may be severe.

Lewis (1987), Bell and Jachmann (1984) and Jachmann *et al.* (1987) did not observe this phenomenon, but it is unlikely that this is a localised incident. They found that early dry season burning moderated habitat use by elephants in riverine mopane woodlands by deferring elephant impact away from burnt areas, and simultaneously reduced the risk of intense late dry season burns. The disadvantages of early dry season burns (*i.e* more severe damage to the basal growth of grasses) are outweighed by the greater risk of seedling mortality through a slower moving fire, and by creating a mosaic of burnt/unburnt patches that reduce the frequency and spread of late dry season burns.

Late dry season burns

Late dry season burns were undertaken in November 1997. By January 1998 trees in the unburnt areas were in full leaf. However, trees burnt two months earlier remained leafless, although climatic and soil moisture conditions were conducive to leaf carriage. The leafless plants lost out on approximately 4 weeks of photosynthetic production, in comparison with trees in the unburnt areas that were able to utilise this period. Also, grass production was advantaged by this situation as the trees shed no shade and were not photosynthesising during this period. The grass sward therefore had a competitive advantage.

These observations prompt the following questions:

1) What is the physiological expense of losing leaves at a time when leaf carriage is vitally important?
2) What is the physiological expense of carrying leaves at the hottest time of the year, when protein denaturation may occur?
3) Assuming that the effect after one fire event may not be significant, what are the consequences of repeated burning and repeated leaf loss and leaf carriage 'out of sync' with the physiological constraints of the plant?
4) What are the consequences and tradeoffs of being leafless when physiologically it is the optimal period for photosynthesis (warm and wet as the rains have just started)?
5) What are the costs of being leafless when the grass sward is actively growing?

The short duration of this study did not allow for these questions to be addressed, but the posing thereof may well lead to investigation into the effects of frequency of different seasons and types of fire on mopane woodland. Sweet (1982) found that in *Acacia nigrescens/Combretum apiculatum* savannas the density of bush increased with increasing burning interval, as well as altering the community structure. I believe that frequent burning will not only impact the physiognomy of the trees, but when interacting with drought events and high elephant densities, will begin to impact the stand density of mopane woodlands.

Management recommendations

Management burning should be carried out with the intention of achieving one of the following objectives (Tainton 1999):

1) Removing moribund grass material that has accumulated and is now unacceptable to grazing ungulates,
2) control the encroachment of undesirable pants (especially woody species),
3) maintain or develop grass cover,
4) contribute to fire control by reducing fuel loads, or
5) stimulating out-of-season grass growth to provide green feed when it does not occur naturally.

Points three to five do not apply to Malilangwe Estate in general, but the first two points are scenarios that management do encounter. The specific objective will determine the season, type and frequency of fire to be applied. From the findings of this study it is advised that the following be used as a guide-line for determining when and how to burn mopane woodlands, in an attempt to achieve objective (1) or (2):

1) Removing moribund grass material

Malilangwe Estate is a sweetveld area, and the vegetation can support grazing ungulates for the full 12 months of the year. However after periods of high grass production and simultaneous low utilisation, the grass sward can become moribund and unacceptable for grazing ungulates. It is under these conditions, when the removal thereof is required, that surface fires that burn close to the ground are required, in the form of back fires. However there is the danger that these slow-moving back fires can damage the meristematic regions of the grass plant. Alternatively cool, low intensity, fires of less than 1 000 $kJ.s^{-1}.m^{-1}$ should be applied. This level of fire intensity can be attained when the management burning takes place when the air temperature is cool (approximately 20°c) and relative humidity is greater than 45%. It is advised that these burns be carried out at the end of the dry season/start of the wet season when the grass plants are dormant and the fire hazard low, but close enough to the onset of the rainy season as to minimise the length of time that the soil will be exposed. The frequency of controlled burning to remove moribund material will depend on the rate of accumulation of such material, as determined by rainfall and grazing utilisaton.

2) Control encroachment of undesirable plants

To maintain or reduce the level of encroachment by undesirable species (especially trees) high intensity fires are required ($>1\ 500\ kJ.s^{-1}.m^{-1}$). These fire intensities will be achieved if the fuel load is in excess of 2 500 $kg.ha^{-1}$, the air temperature is approximately 29°C and the relative humidity less than 30%. Under these conditions, and with wind speeds not greater than 6 $m.s^{-1}$, high fire intensities will result that will lead to significant topkill of trees and shrubs up to 250 cm in height. The frequency of these burning events is species-dependent. Multiple fires may be needed, or single intense burns. If possible, the size of the burnt area should be large so that the grazing utilisation will not be excessive. These types of fires are recommended for the areas where encroachment by woody species has occurred into previously grassland areas, or where a more open savanna woodland is desired.

In the mopane-dominated areas high intensity fires will lead to topkill, but also to coppicing. High levels of coppicing are undesirable, as it leads to a more dense and aesthetically unappealing woodland. However the more intense the fire the smaller the increase in the number of stems per individual. Therefore, by implementing high intensity fires the level of coppicing will be reduced. Tree density will not be changed by fire application, but the interaction between fire and post-fire browsing by elephants and black rhino may well lead to a significant decrease in stand density.

The conclusions from this investigation must be seen for their true value: one set of insights into the effects of different seasons and types of fire on mopane woodland, with inferences to the effect of frequency of burning. The large variability in rainfall and standing crop in the south-eastern lowveld of Zimbabwe result in large spatial and temporal variations in fuel load and fuel characteristics. Also the environmental conditions and fire behaviour, both of which are specific to individual fire events, will in turn lead to variation in the effects of individual fires, in different seasons, and using different types of burning. Apart from the effects of fire alone, the interaction of fire and large browsers such as elephants and black rhino must be recognised, as together, they have a highly significant impact on the species and structural diversity of mopane woodlands, making them central in determining the potential changes that take place in these woodlands.

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Appendix 1 Monthly rainfall figures for Malilangwe Estate (1951 to 1998) as supplied by the Meteorological Services Department in Harare

	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	ANNUAL
51/52	0	11.7	34	42.9	76.2	184.4	318.3	57.4	13.7	0	15.2	69.6	823.4
52/53	7.6	0	5.1	0	67.3	177	216.7	24.4	107.2	0	0	0	605.3
53/54	0	7.9	0	16	36.6	44.7	87.4	56.1	32.5	50.3	5.3	5.6	342.4
54/55	0	0	0	6.6	138.4	258.8	260.1	143.8	76.2	38.1	0	0	922
55/56	0	0	0.8	20.3	49	173.5	34.8	348.2	77.5	6.1	0	9.7	719.9
56/57	0	0	17.5	0	75.5	47.2	72.1	78.2	35.1	13.5	5.6	0	344.7
57/58	2.5	7.4	0.5	51.1	79.2	64.5	296.7	160.3	11.2	36.8	2.8	20.1	733.1
58/59	0.8	0	17.8	29.2	25.1	105.4	240.8	123.4	26.7	59.9	7.9	13.5	650.5
59/60	22.1	8.9	14.5	2	145.3	263.9	15.2	104.4	31.2	64	0	18	689.5
60/61	6.1	0	6.6	32	88.4	99.6	60.7	130.6	50.5	59.7	0	32	566.2
61/62	6.1	4.3	0	33.8	70.4	21.1	279.1	29	107.2	16.3	2.5	0	569.8
62/63	0	0	0	2	118.4	102.6	94.5	248.4	6.4	40.4	0	8.9	621.6
63/64	0	0	0	70.1	0	83.6	28.2	210.6	22.9	3.3	6.4	0	425.1
64/65	0	0	0	0	49.3	115.3	27.9	19.8	0	1.3	2.5	5.1	221.2
65/66	0	2.5	27.2	3.8	105.2	11.4	117.6	111.3	38.9	4.3	3.8	5.1	431.1
66/67	0	0	63.5	38.9	51.1	89.4	127.8	113	48.3	18.8	7.1	2	559.9
67/68	9.1	11.4	4.3	28.2	37.8	39.4	16.3	145.3	11.9	28.2	30.7	7.4	370
68/69	0	0	0	5.1	88.6	118.9	54.1	67.6	126.5	47.2	0	0	508
69/70	9.4	0	5.8	42.2	108	137.9	51.8	85.1	5.1	3	0	33	481.3
70/71	3	0	0	10.9	31	127.5	166.9	70.9	4.6	5.6	16.5	1.8	438.7
71/72	0	0	2.5	23.6	88.8	47.3	274.7	116.9	45.8	21.4	5.9	0	626.9
72/73	1.2	0	0	13	8.5	20	92	22	31.5	19.5	0	5.5	213.2
73/74	1	30	37.5	32	46	206.2	33.5	190.5	71	69	5	0	721.7
74/75	19	0	31	4.5	192.5	121.5	83	164	48.5	75.5	46.5	3	789
75/76	0	35.5	0	0	25.5	116.5	126	49.5	157.5	22	69	0	601.5
76/77	0	0	16	0	127	89	69	325.5	66.5	25.3	0.5	0	718.8
77/78	0	19	53	9	22	154	229	142	56.8	60.2	6.4	0	751.4
78/79	5.5	0	0	35	96	131	47	100.5	129.5	4.5	23	2.5	574.5

79/80	9.5	10.5	0.6	84	88.5	96	144.5	104.5	120.5	10.5	0	0	669.1
80/81	1.5	15	81	16.5	86	61	95	178	6.5	34	68	0.5	643
81/82	4.5	0.5	41	43.5	109	17.5	76	145	26	24.5	25	0	512.5
82/83	0.4	0	0.3	32.5	25	48	47	6	25	19	8.5	5	216.7
83/84	22	20	0	42	26	173.5	70	60	49	25	0	0	487.5
84/85	3.5	0	10	84.5	58.5	124.5	217.3	94.5	0	0	37.5	17	647.3
85/86	40	0	73.5	59	58.9	76.1	112.3	25.5	20	139.8	5.5	0	610.6
86/87	0	0	0	27.5	27.5	128.5	31	91.5	8	0	0	0	314
87/88	0	5.5	20.5	24	18.5	373.5	91	61	87	1	21.5	31.5	735
88/89	0	6.5	2.5	53	36.5	30.5	25.5	131.5	24	55	0	22.5	387.5
89/90	0	4	0	56.5	49	92.5	148.7	23.5	19	30.5	0	0	423.7
90/91	0	0	11	0	33	61	51	116	69.5	0	9	6.5	357
91/92	0	0	0.5	1.5	4.5	21.5	29	0	10.5	3.5	0	1	72
92/93	10	0	0.5	5	42.5	154	79	268.5	8.5	26.5	0	6	600.5
93/94	34	5	0	51	140.5	118.5	44	10.2	11.5	0	0.5	1	416.2
94/95	0	4	2	15.5	3.9	193	39	268.5	42	25	14	0	606.9
95/96	42.5	0	0	0	32	82	300	205	33	33	13.5	5	746
96/97	33.5	6	4	2.5	64.5	66.5	167.5	119.5	72.5	36	20	0	592.5
97/98	8.5	0	9.5	17	40.2	70.4	184.3	63	17.9	3.8	0	0	414.6
MIN	0	0	0	0	0	11.4	15.2	0	0	0	0	0	72
MAX	42.5	35.5	81.0	84.5	192.5	373.5	318.3	348.2	157.5	139.8	69.0	69.6	922.0
MEAN	6.5	4.6	12.6	24.8	63.7	109.4	116.5	115.1	44.5	26.8	10.3	7.2	542.0
SD	11.1	8.0	20.4	23.1	42.9	72.2	88.7	82.4	38.9	27.4	16.4	12.9	180.4
CV%	173	174	162	93	67	66	76	72	88	102	158	180	33
%Cont	1.2	0.8	2.3	4.6	11.7	20.2	21.5	21.2	8.2	5	2	1.3	

Appendix 2: Treatments, transect numbers, GPS coordinates and magnetic compass bearings for mopane woodland transects on Malilangwe Estate

GARMIN GPS 45 (SERIAL # 34514047)
SILVA COMPASS (Type 16)

EB1

131) 21° 04' 44.0" S	31° 56' 41.9" E	160
132) 21° 04' 42.5" S	31° 56' 42.0" E	138
133) 21° 04' 43.0" S	31° 56' 41.6" E	146
134) 21° 04' 43.0" S	31° 56' 42.1" E	136
135) 21° 04' 41.8" S	31° 56' 44.0" E	160
136) 21° 04' 41.2" S	31° 56' 44.8" E	142
137) 21° 04' 41.3" S	31° 56' 45.7" E	146
138) 21° 04' 40.6" S	31° 56' 46.9" E	150
139) 21° 04' 39.9" S	31° 56' 47.5" E	164
140) 21° 04' 39.8" S	31° 56' 48.8" E	162

EB2

21) 21° 05' 12.7" S	31° 56' 31.6" E	50
22) 21° 05' 14.9" S	31° 56' 33.4" E	80
23) 21° 05' 16.1" S	31° 56' 34.2" E	64
24) 21° 05' 14.8" S	31° 56' 33.1" E	94
25) 21° 05' 16.7" S	31° 56' 35.3" E	83
26) 21° 05' 18.8" S	31° 56' 37.0" E	76
27) 21° 05' 17.5" S	31° 56' 35.0" E	68
28) 21° 05' 20.7" S	31° 56' 36.1" E	62
29) 21° 05' 19.4" S	31° 56' 36.3" E	70
30) 21° 05' 18.9" S	31° 56' 37.3" E	80

EB3

31) 21° 05' 39.1" S	31° 56' 53.2" E	64
32) 21° 05' 39.8" S	31° 56' 54.7" E	64
33) 21° 05' 39.0" S	31° 56' 55.4" E	42
34) 21° 05' 40.4" S	31° 56' 53.7" E	62
35) 21° 05' 41.1" S	31° 56' 56.3" E	60
36) 21° 05' 42.0" S	31° 56' 57.1" E	62
37) 21° 05' 42.0" S	31° 56' 55.2" E	64
38) 21° 05' 43.9" S	31° 56' 59.9" E	36
39) 21° 05' 44.0" S	31° 57' 00.9" E	60
40) 21° 05' 47.4" S	31° 57' 02.0" E	70

EH1

111)	21° 03' 40.4" S	31° 56' 08.4" E	84
112)	21° 03' 44.0" S	31° 56' 07.4" E	94
113)	21° 03' 44.0" S	31° 56' 09.6" E	80
114)	21° 03' 42.9" S	31° 56' 12.4" E	82
115)	21° 03' 41.2" S	31° 56' 11.3" E	72
116)	21° 03' 44.5" S	31° 56' 12.9" E	60
117)	21° 03' 44.8" S	31° 56' 15.0" E	76
118)	21° 03' 44.8" S	31° 56' 15.7" E	78
119)	21° 03' 46.8" S	31° 56' 12.3" E	76
120)	21° 03' 50.9" S	31° 56' 14.6" E	10

EH2

121)	21° 04' 26.2" S	31° 56' 20.4" E	92
122)	21° 04' 26.3" S	31° 56' 20.3" E	11
123)	21° 04' 26.9" S	31° 56' 21.3" E	11
124)	21° 04' 25.8" S	31° 56' 21.5" E	11
125)	21° 04' 28.5" S	31° 56' 21.1" E	118
126)	21° 04' 28.8" S	31° 56' 21.0" E	140
127)	21° 04' 27.4" S	31° 56' 20.3" E	120
128)	21° 04' 28.5" S	31° 56' 21.1" E	130
129)	21° 04' 27.3" S	31° 56' 22.5" E	109
130)	21° 04' 29.3" S	31° 56' 21.2" E	130

EH3

91)	21° 04' 43.8" S	31° 56' 44.6" E	348
92)	21° 04' 41.6" S	31° 56' 41.0" E	334
93)	21° 04' 42.3" S	31° 56' 40.4" E	360
94)	21° 04' 42.4" S	31° 56' 43.9" E	008
95)	21° 04' 41.2" S	31° 56' 42.9" E	342
96)	21° 04' 43.2" S	31° 56' 42.1" E	350
97)	21° 04' 40.0" S	31° 56' 44.7" E	350
98)	21° 04' 41.2" S	31° 56' 44.1" E	316
99)	21° 04' 41.5" S	31° 56' 44.1" E	324
100)	21° 04' 40.2" S	31° 56' 45.0" E	358

MB1

101)	21° 02' 55.4" S	31° 57' 31.3" E	164
102)	21° 02' 55.7" S	31° 57' 31.9" E	150
103)	21° 02' 55.2" S	31° 57' 30.7" E	192
104)	21° 02' 55.4" S	31° 57' 30.3" E	180
105)	21° 02' 56.4" S	31° 57' 28.3" E	170
106)	21° 02' 57.2" S	31° 57' 27.2" E	176
107)	21° 02' 58.4" S	31° 57' 27.5" E	70
108)	21° 02' 57.9" S	31° 57' 29.6" E	78
109)	21° 02' 59.2" S	31° 57' 29.0" E	70
110)	21° 02' 58.0" S	31° 57' 29.0" E	110

MB2

81)	21° 04' 11.4" S	31° 57' 43.7" E	164
82)	21° 04' 11.4" S	31° 57' 42.1" E	190
83)	21° 04' 12.4" S	31° 57' 42.9" E	180
84)	21° 04' 14.1" S	31° 57' 42.7" E	156
85)	21° 04' 13.2" S	31° 57' 41.5" E	176
86)	21° 04' 13.6" S	31° 57' 42.2" E	158
87)	21° 04' 14.0" S	31° 57' 40.5" E	158
88)	21° 04' 15.2" S	31° 57' 41.0" E	154
89)	21° 04' 15.7" S	31° 57' 39.2" E	122
90)	21° 04' 16.2" S	31° 57' 39.1" E	174

MB3

1) 21° 04' 04.1" S	31° 58' 14.9" E	276
2) 21° 04' 06.6" S	31° 58' 13.3" E	283
3) 21° 04' 06.7" S	31° 58' 12.9" E	283
4) 21° 04' 07.4" S	31° 58' 10.1" E	286
5) 21° 04' 10.0" S	31° 58' 08.7" E	316
6) 21° 04' 13.6" S	31° 58' 08.1" E	322
7) 21° 04' 12.7" S	31° 58' 12.2" E	310
8) 21° 04' 16.1" S	31° 58' 09.0" E	294
9) 21° 04' 14.7" S	31° 58' 09.6" E	294
10)21° 04' 14.2" S	31° 58' 07.2" E	328

MH1

71) 21° 04' 11.6" S	31° 57' 45.6" E	16
72) 21° 04' 11.7" S	31° 57' 42.0" E	334
73) 21° 04' 13.3" S	31° 57' 41.3" E	340
74) 21° 04' 11.1" S	31° 57' 41.2" E	316
75) 21° 04' 13.4" S	31° 57' 40.9" E	354
76) 21° 04' 12.0" S	31° 57' 39.1" E	344
77) 21° 04' 13.5" S	31° 57' 38.3" E	340
78) 21° 04' 14.1" S	31° 57' 38.4" E	346
79) 21° 04' 13.5" S	31° 57' 36.5" E	350
80) 21° 04' 14.0" S	31° 57' 36.1" E	312

MH2

11) 21° 05' 33.5" S	31° 57' 36.3" E	308
12) 21° 05' 35.5" S	31° 57' 39.0" E	323
13) 21° 05' 39.1" S	31° 57' 38.7" E	326
14) 21° 05' 38.6" S	31° 57' 37.2" E	302
15) 21° 05' 38.1" S	31° 57' 35.4" E	316
16) 21° 05' 40.1" S	31° 57' 34.4" E	312
17) 21° 05' 40.8" S	31° 57' 34.1" E	310
18) 21° 05' 42.8" S	31° 57' 35.0" E	322
19) 21° 05' 43.2" S	31° 57' 32.6" E	302
20) 21° 05' 45.6" S	31° 57' 33.3" E	276

MH3

141) 21° 05' 52.2" S	31° 57' 06.2" E	80
142) 21° 05' 52.0" S	31° 57' 05.4" E	100
143) 21° 05' 51.9" S	31° 57' 06.3" E	110
144) 21° 05' 53.4" S	31° 57' 06.8" E	66
145) 21° 05' 53.7" S	31° 57' 06.8" E	74
146) 21° 05' 54.8" S	31° 57' 06.9" E	92
147) 21° 05' 54.6" S	31° 57' 05.9" E	70
148) 21° 05' 55.1" S	31° 57' 07.8" E	92
149) 21° 05' 53.5" S	31° 57' 09.1" E	74
150) 21° 05' 55.5" S	31° 56' 06.9" E	58

LB1

151) 21° 03' 31.7" S	31° 56' 06.4" E	24
152) 21° 03' 32.4" S	31° 56' 07.7" E	20
153) 21° 03' 32.3" S	31° 56' 08.6" E	09
154) 21° 03' 32.7" S	31° 56' 09.0" E	22
155) 21° 03' 31.5" S	31° 56' 10.4" E	16
156) 21° 03' 29.2" S	31° 56' 11.7" E	30
157) 21° 03' 28.7" S	31° 56' 11.9" E	30
158) 21° 03' 28.1" S	31° 56' 13.8" E	17
159) 21° 03' 28.0" S	31° 56' 14.7" E	354

LB2

191)	21° 03' 02.1" S	31° 58' 34.1" E	291
192)	21° 03' 01.0" S	31° 58' 34.3" E	302
193)	21° 03' 00.1" S	31° 58' 34.1" E	294
194)	21° 02' 59.2" S	31° 58' 34.5" E	292
195)	21° 02' 58.9" S	31° 58' 35.2" E	328
196)	21° 02' 58.0" S	31° 58' 34.3" E	292
197)	21° 02' 56.7" S	31° 58' 34.3" E	278
198)	21° 02' 55.8" S	31° 58' 34.0" E	290
199)	21° 02' 53.1" S	31° 58' 35.1" E	276
200)	21° 02' 51.8" S	31° 58' 36.4" E	298

LB3

201)	21° 02' 45.7" S	31° 58' 26.9" E	180
202)	21° 02' 45.9" S	31° 58' 25.9" E	160
203)	21° 02' 46.4" S	31° 58' 25.1" E	152
204)	21° 02' 45.9" S	31° 58' 24.6" E	176
205)	21° 02' 45.9" S	31° 58' 23.8" E	179
206)	21° 02' 45.5" S	31° 58' 23.4" E	189
207)	21° 02' 45.8" S	31° 58' 21.8" E	166
208)	21° 02' 46.5" S	31° 58' 21.4" E	172
209)	21° 02' 47.1" S	31° 58' 20.3" E	176
210)	21° 02' 48.0" S	31° 58' 19.0" E	178

LH1

161)	21° 03' 22.7" S	31° 56' 23.5" E	16
162)	21° 03' 22.3" S	31° 56' 24.4" E	355
163)	21° 03' 21.4" S	31° 56' 25.2" E	358
164)	21° 03' 20.5" S	31° 56' 25.6" E	357
165)	21° 03' 18.8" S	31° 56' 26.0" E	329
166)	21° 03' 18.5" S	31° 56' 26.8" E	309
167)	21° 03' 18.6" S	31° 56' 27.9" E	41
168)	21° 03' 17.9" S	31° 56' 29.1" E	339
169)	21° 03' 16.2" S	31° 56' 32.2" E	344
170)	21° 03' 16.7" S	31° 56' 35.7" E	326

LH2

171)	21° 03' 06.2" S	31° 56' 42.0" E	288
172)	21° 03' 05.1" S	31° 56' 42.3" E	276
173)	21° 03' 04.6" S	31° 56' 42.6" E	288
174)	21° 03' 01.9" S	31° 56' 42.0" E	265
175)	21° 03' 01.4" S	31° 56' 42.0" E	257
176)	21° 03' 01.0" S	31° 56' 41.7" E	280
177)	21° 02' 59.6" S	31° 56' 41.0" E	266
178)	21° 02' 58.9" S	31° 56' 40.8" E	249
179)	21° 02' 58.1" S	31° 56' 39.4" E	242
180)	21° 02' 58.1" S	31° 56' 39.1" E	225

LH3

181)	21° 03' 53.7" S	31° 58' 19.7" E	293
182)	21° 03' 53.0" S	31° 58' 20.8" E	300
183)	21° 03' 52.1" S	31° 58' 21.3" E	298
184)	21° 03' 51.5" S	31° 58' 21.3" E	318
185)	21° 03' 51.0" S	31° 58' 21.9" E	271
186)	21° 03' 50.5" S	31° 58' 21.8" E	291
187)	21° 03' 49.1" S	31° 58' 23.1" E	284
188)	21° 03' 47.6" S	31° 58' 23.9" E	290
189)	21° 03' 47.0" S	31° 58' 23.8" E	294
190)	21° 03' 46.2" S	31° 58' 23.4" E	[illegible]

C1			
51)	21° 02' 52.8" S	31° 57' 31.6" E	360
52)	21° 02' 52.6" S	31° 57' 32.3" E	348
53)	21° 02' 51.9" S	31° 57' 30.6" E	352
54)	21° 02' 51.3" S	31° 57' 28.6" E	336
55)	21° 02' 53.1" S	31° 57' 26.3" E	344
C2			
61)	21° 03' 47.5" S	31° 55' 54.7" E	256
62)	21° 03' 39.1" S	31° 56' 07.1" E	273
63)	21° 03' 41.1" S	31° 56' 07.5" E	256
64)	21° 03' 42.6" S	31° 56' 10.0" E	254
65)	21° 03' 42.6" S	31° 56' 08.6" E	262
C3			
66)	21° 04' 25.6" S	31° 56' 19.5" E	268
67)	21° 04' 27.4" S	31° 56' 19.0" E	266
68)	21° 04' 29.3" S	31° 56' 18.2" E	270
69)	21° 04' 28.8" S	31° 56' 20.1" E	273
70)	21° 04' 30.2" S	31° 56' 21.5" E	282
C4			
56)	21° 04' 39.1" S	31° 56' 20.7" E	280
57)	21° 04' 38.8" S	31° 56' 18.3" E	258
58)	21° 04' 39.6" S	31° 56' 17.7" E	270
59)	21° 04' 39.1" S	31° 56' 21.0" E	248
60)	21° 04' 42.3" S	31° 56' 23.9" E	250
C5			
41)	21° 05' 47.6" S	31° 57' 02.2" E	236
42)	21° 05' 17.4" S	31° 56' 32.3" E	238
43)	21° 05' 17.7" S	31° 56' 30.4" E	234
44)	21° 05' 17.7" S	31° 56' 31.7" E	268
45)	21° 05' 16.7" S	31° 56' 32.2" E	232
C6			
46)	21° 05' 55.7" S	31° 57' 05.1" E	230
47)	21° 05' 56.0" S	31° 57' 06.5" E	242
48)	21° 05' 54.5" S	31° 57' 10.0" E	214
49)	21° 05' 55.8" S	31° 57' 08.1" E	236
50)	21° 05' 55.8" S	31° 57' 07.6" E	208

E = Early dry season (autumn)

M = Mid dry season (winter)

L = Late dry season (spring)

C = Control (no burn)

B = Backburn

H = Headburn