SEED AND SEEDLING DYNAMICS OF CERTAIN *ACACIA* SPECIES AS AFFECTED BY HERBIVORY, GRASS COMPETITION, FIRE, AND GRAZING SYSTEM

by

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DECLARATION

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution

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ABSTRACT

The influence of herbivory, grass competition and grazing system on emergence, growth and survival of *Acacia* seedlings in burnt and unburnt areas was investigated in their first growing season, from September 1997 to May 1998. The study was aimed at determining possible reasons for the increase in woody plant density in semi-arid savannas, specifically the effect of excluding small-mouthed herbivores from domestic and livestock systems, and switching from continuous grazing to rotational grazing systems. The effect of fire intensity and maximum fire temperature on seed viability, germination and mortality, specifically with regard to back *versus* head fires and seed size, were investigated.

Variability among species in the number of seedlings emerging generally resembled differences in viability. Emergence of *Acacia karroo* and *Acacia tortilis* was poorer than that of *Acacia nilotica* under grass competition. Emergence was lower in burnt and open areas, the latter depending on *Acacia* species. Herbivory did not affect seedling emergence, in both domestic and wildlife systems.

Seedling survival and growth was adversely affected by small-mouthed herbivores in both domestic and livestock systems, whilst large-mouthed herbivores exerted no direct effects on woody seedlings, except to a small degree by trampling. Seedlings showed better growth and survival under low grass competition, which also resulted in greater leaf-to-height ratios, indicating that grass interference with irradiance affects woody seedlings. This effect appeared to be greater for cattle and rotational grazing, and for burning, in domestic and wildlife systems respectively. Woody seedling establishment was also better in burnt areas. Whilst seedling growth was better under rotational than continuous grazing, survival was not significantly different. Grass competition influenced seedling establishment to a greater extent than herbivory, whilst burning made a greater impact than grass competition.

Seed mortality in response to maximum fire temperature was inversely related to seed size, and trends in seed germination and mortality, although very variable, appeared to be influenced by threshold fire intensities and maximum temperatures. Back fires had hotter maximum temperatures and fire intensities at ground level than head fires, which result in greater seed mortality following fire.

Based on the current study it is likely that the removal of grass competition, burning, and a change from continuous to rotational grazing systems, and small-mouthed to large-mouthed herbivores, will result in an increase in woody seedling establishment.

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CHAPTER 1

INTRODUCTION

Savannas make up 35% of South Africa's land area, and are the basis of two major industries, namely cattle ranching and wildlife-related tourism (Scholes & Walker 1993). A change in character or reduction in productivity of these rangelands therefore potentially represents a huge economic loss. The distinguishing feature of savannas is the co-dominance of trees and grasses. An understanding of the mechanisms controlling the structure and function of this plant formation is therefore of great importance. Fixed determinants (rainfall regime and soil), variable determinants (fire and herbivores) and the effects of chance (episodic) events govern the structure and function of savannas (Walker 1985). Man impacts on savannas through management of fire and herbivory, which maintain and shape the character of savannas. Savannas are changing, and the process of woody plant encroachment into grassland has been recorded in various parts of Africa (Hoffman & O'Connor 1999; Roques *et al.* 2001), Australia (Hodgkinson & Harrington 1985) and America (Launchbaugh 1955; Madany & West 1983; Archer 1989). The process of bush encroachment is the increase in density of the woody component in a savanna. Various reasons for bush encroachment have been suggested, including the impact of overgrazing (Noy-Meir 1982; Scholes & Walker 1993), reduction of fire frequency (Bille 1985 in: Tothill & Mott 1985; Hoffman & O'Connor 1999; Roques *et al.* 2001) and change in the composition and management of herbivores (Du Toit 1972 a; Scholes & Walker 1993; Hoffmann & O'Connor 1999). Whilst the dynamics of established woody plants have received some attention (Tchie & Gakahu 1984; Teague 1989 a, Moreno & Oechel 1991), relatively few studies of woody plant increases have focused on the seedling establishment phase, although this is probably the critical life history stage for population persistence and expansion (Harper 1977; Goldberg 1990).

Fire can influence the success of woody seed viability and germination (Pieterse & Cairns 1987; Bradstock & Auld 1995; Babalwa *et al.* 1997), the growth and survival of seedlings (Story 1952; Trollope 1980), and the success of established woody individuals (Rutherford 1981; Trollope 1983; Walker 1985; Ben-Shahar 1996). Mature woody plants are seldom killed by fire, but seedlings can experience high mortality from fire (Trollope 1984 a). The impact of a fire is determined by the type of fire and fuel load (Rutherford 1981; Trollope 1983). A poorly investigated aspect of fire is the change in competition after a burn between the herbaceous layer and woody seedlings. This merits attention as factors which decrease grass competition may enhance woody plant growth (Knoop & Walker 1985) and should also promote woody seedling establishment. Fire may not be the sole agent determining woody

plant dynamics in a savanna, but it is instrumental in controlling woody biomass and density in interaction with other factors, such as herbivory.

An animal's size has a fundamental influence on its metabolism and hence its food and energy needs (Owen-Smith 1999), and therefore its impact on the vegetation. To meet its high relative requirement for food, a small animal selects concentrated foods. This selective behaviour is possible by virtue of their low absolute energy requirement, and because small ruminants have small mouths and are therefore able to select small items of concentrated foods. Large herbivores have a high absolute energy requirement and large mouthparts, and therefore feed less selectively. During early stages of growth, when woody seedlings are especially vulnerable to defoliation (Teague & Walker 1988), the pressure of large herbivores on tree seedlings is low (Ben-Shahar 1996). However, herbivory by small mammals can prevent the recruitment of woody seedlings (Belsky 1984; Auld 1995), and the elimination of small-mouthed browsers can promote woody seedling recruitment (Prins & Van der Jeugd 1993). It is further suspected that the change from sheep or mixed cattle and sheep to cattle only has resulted in encroachment of *A. karroo* in the eastern Cape (Du Toit 1972 a) as cattle reduce grass competition (Brown & Booysen 1967; Bush & Van Auken 1995) and woody seedlings are not utilized by cattle.

A variety of direct and indirect effects of herbivory may therefore interact to promote woody plant seedling establishment in grass communities. The phenomenon of 'bush encroachment' in semi-arid savannas has been attributed to competitive release when grass cover is reduced through heavy grazing (Skarpe 1990), although this is a point of contention (Chirara *et al.* 1998; Brown & Archer 1999). Cattle and sheep can engender and maintain distinct patterns of height variation within grass swards through selective grazing (Edwards *et al.* 1996), with short patches interspersed within areas of relatively tall herbage (Hardy 1995), that may influence variation of woody seedling success within a grass sward. The reduction of grass fuel loads by heavy grazing has in extreme situations rendered fire ineffective as a tool for suppressing the growth of woody plants (Chirara *et al.* 1998; Roques *et al.* 2001). In the absence of fire, woody seedlings are provided with an opportunity to escape from the grass layer and become established. This renders a plant more tolerant of defoliation (Cooper & Owen-Smith 1986; Sweet & Mphinyane 1986). Grazing systems may also afford seedlings an opportunity of escaping defoliation. Rotational grazing systems may afford seedlings an opportunity to establish if the rotation is in synchrony with its emergence, which decreases the probability of encounter of an animal with a woody seedling. Furthermore, low stocking rates increase the probability of a seedling being missed by an animal. This applies primarily to sheep as they feed selectively (O'Reagain & Stuart-Hill 1991) and probably exploit nutritious woody seedlings.

A number of changes have occurred in the pattern of land use in southern African savannas that may affect their character. The removal of small-mouthed herbivores, such as sheep, goats and impala, the switch from continuous to rotational grazing systems, and the limited use of fire in savannas is now commonplace. The literature (chapter 2, 'Literature Review') suggests that these changes may be key influences on change in the structure of semi-arid savannas through their effect on woody seedling establishment. This issue formed the central focus of this study.

An experiment was set up in 1996 and 1997 to investigate the effect of fire and herbivory on the establishment, growth and survival of seedlings of four *Acacia* species, namely, *A. karroo*, *A. nilotica*, *A. sieberiana* and *A. tortilis*, in order to address a dearth of knowledge on seedling dynamics in relation to bush encroachment. Wildlife and livestock systems were investigated. For wildlife systems, the importance of herbivory by small-mouthed selective animals was investigated by comparing wildlife reserves with and without impala (*Aepyceros melampus*), a species known to affect seedling recruitment of *Acacia*. The study design allowed this difference to be examined in the context of grass competition and fire. The latter refers to the influence of burning before seedling emergence on woody seedling establishment. For livestock systems, the effect of herbivory by livestock of different body size (cattle *versus* sheep), grazing system (continuous *versus* rotational grazing) and stocking rate was investigated using a field experiment.

These experiments were set up in order to address the following objectives:

a) To assess whether fire and herbivory function as important filters for the establishment of seedlings of *A. karroo, A. nilotica, A. tortilis* or *A. sieberana*.

b) In terms of herbivory, to assess the importance of body size, hence size of mouthparts, of a herbivore for its impact on seedling populations of woody individuals.

c) To assess whether fire results in substantial mortality of *Acacia* seeds and, if so, whether this depends on fire characteristics.

d) To assess the role of grass competition in seedling recruitment, including the interaction of grass competition, fire and defoliation.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

An increase in density of woody plants in savannas and grasslands has been widely reported, a phenomenon commonly termed as bush encroachment. These increases have largely been attributed to overgrazing and to the protection against fire, the result of human management. Another management-induced response which has largely been overlooked is the removal of small-mouthed herbivores from agricultural and wildlife systems, and a change from continuous to rotational grazing systems. Small-mouthed herbivores have been excluded from domestic and wildlife systems as a consequence of the belief that these animals are in part responsible for veld degradation.

The current state of understanding of bush encroachment will be reviewed, with special emphasis on how this is influenced by browsing, and its interaction with grass competition, fire and rainfall.

2.2 Structure of savannas

The unifying feature of savannas is the dual significance of herbaceous and woody plants (Walker 1985), a system characterized as being unstable (Walker & Noy-Meir 1982). The question of the existence of a tree-grass equlibrium in undisturbed savannas is widely discussed in the literature (Walker & Noy-Meir 1982; Walker *et al.* 1981; Belsky 1994). Walter (1971) hypothesized that water is the limiting factor in semi-arid savannas, and that grasses are superior competitors for water in the surface horizons of the soil, while trees have exclusive access to water in the deeper horizons. However, a number of studies suggest that tree and grass roots exploit overlapping areas (Knoop & Walker 1985; Scholes & Walker 1993; Belsky 1994), and provide evidence that grass and woody root components under certain conditions occupy the same space and compete for moisture in the same horizons. Rainfall has an overriding effect on savanna dynamics, and more arid savannas exhibit a much less predictable growth pattern, tending to respond closely to rainfall events (Walker 1985). An increase in the density of woody individuals is related to a decrease in aridity, water availability being a dominant determinant of savanna structure and function at the dry end of the savanna spectrum (Scholes & Walker 1993). Seedlings are susceptible to dessication (Du Toit 1967) and exhibit poor survival during dry years (O'Connor 1995).

Most semi-arid savannas are characterized by at least some portion of the year, or relatively frequent series of years, when soil moisture is sufficient for shrub seedling emergence and establishment.

The inherent structure and functioning of savannas is determined primarily by soil water and nutrients, whilst fire and herbivory, classified as secondary determinants, modify the inherent structure imposed by the primary determinants (Walker 1985). Changes to secondary determinants, whether by human intervention or natural processes, may result in an increase in the woody individuals if these changes encourage successful dispersal, germination and seedling establishment (O'Connor 1996). It is the relative increase in density of the woody component in savannas that is termed bush encroachment.

2.3 Reasons for bush encroachment

An increase in the woody component in African savannas has been widely documented (Van Vegten 1983; Smith & Goodman 1987; Hoffman & O'Connor 1999; Roques *et al.* 2001). Woody seedling establishment has been described as the critical life history stage in woody plant recruitment (Harper 1977; Goldberg 1990), whilst the escape of established seedlings from the herbaceous layer, and consequently the fire trap, has also been recognised as a critical life history stage for woody individuals (Higgins *et al.* 2000). Numerous influences bear upon seedling establishment.

Grass competition may adversely affect woody seedlings (Schultz *et al.* 1955; Brown & Booysen 1967; Cooper 1982; Knoop & Walker 1985; Cohn *et al.* 1989; Bush & Van Auken 1990; Madany & West 1993; Bush & Van Auken 1995; Brown *et al.* 1998), although grass competition has not had an effect under some circumstances (Brown & Archer 1989, 1999; O'Connor 1995; Chirara *et al.* 1998). The rapid growth of gasses may afford them a competitive advantage over woody species, although the degree to which tree-grass competition is able to control woody density is still uncertain (Menaut *et al.* 1990). Rainfall has a primary effect on variation in herbaceous biomass in semi-arid regions (Dye & Spear 1982; Donaldson 1979), and an increase in moisture availability has been shown to increase survivorship of woody seedlings (Wellington & Noble 1985; O'Connor 1995). Therefore, the rapid development of an adequate root system, as in *Prosopis glandulosa* var. *glandulosa* (Brown & Archer 1990), *Acacia karroo* (Du Toit 1967), and other legume species, is important in enabling seedlings to access soil moisture and nutrients beyond the zone effectively utilized by grasses.

A widely prevalent assumption is that the historical range expansion and encroachment of many woody species has been facilitated by the introduction of domestic

livestock and subsequent 'overgrazing' (Walker *et al.* 1981; Madany & West 1983, Roques *et al.* 2001), and the associated reduction in grass competition on woody plants (Skarpe 1990; Jeltsch *et al.* 1996). The relative significance of grazing to trends in yield or basal cover increases as the aridity of the environment increases, but stocking rate rather than the system of grazing has the greatest influence (Du Toit 1972 a; Donaldson 1979).

In mesic savannas it is possible to maintain savanna structure with fire alone because rainfall is sufficient for enabling grass material to accumulate under grazing conditions to support frequent enough fires to burn down the coppice growth and control woody seedlings (Trollope 1983). The direction of change in woody plant density can be determined by fire frequency (Roques *et al.* 2001). Fire *per se* favours the development and maintenance of predominantly grassland vegetation by destroying juvenile trees and shrubs and preventing the development of more mature plants to a taller fire resistant stage (an 'out-of-fire stage). Fire acts as a grass-dependent recruitment control for woody plants (Higgins *et al.* 2000; Roques *et al.* 2001), since the frequency and intensity of fires depends on the fuel load provided by the herbaceous layer, and woody plant parts are usually only susceptible to fire if they occur within the flame zone of the fire (Trollope 1984 b). Consequently, as a result of grazing, relatively more woody plants survive burning, and are less impacted in terms of height, canopy volume and biomass (Trollope 1980). However, under favourable conditions fire has been advocated to control bush encroachment (Trollope 1974; Trollope 1984 b; Sweet & Tacheba 1985). Fire serves the purpose of maintaining woody vegetation at an available height and in an acceptable state for browsers (Trollope 1983; Walker 1985), whilst browsers perform an important function in maintaining woody plants at a height accessible to fire (Trollope 1984 b; Owen-Smith 1988).

Relatively few studies on woody plant increase consider herbivore composition. Whilst bush encroachment has been associated with an absence of browsers (Roques *et al.* 2001), an absence of small-bodied herbivores can be important in woody plant establishment (Prins & Van der Jeugd 1993). Relaxation of herbivore pressure by impala owing to disease outbreaks was concluded to be the determining factor of three episodes of seedling recruitment of *A. tortilis* over the course of a century at Lake Manyara in East Africa, (Prins & Van der Jeugd 1993). Punctuated disturbances by epidemics among these ungulates create narrow windows for seedling establishment, which may explain the occurrence of even-aged stands. This is linked to current land management strategies which advocate the removal of small-mouthed herbivores, especially mixed feeders such as impala and goats. Bush encroachment of animal production systems has been attributed to the absence of browsers (Du Toit 1972 a). Pastoral use by domestic livestock has concentrated heavily on the grass

component, resulting in an increase in the woody plant component, at the expense of the former.

Acacia karroo, A. nilotica and A. tortilis have been identified as important encroaching species in southern Africa, which show remarkable tolerance to a wide range of environmental conditions (Du Toit 1972 a; Van Vegten 1983; O'Connor 1995; Hoffman & O'Connor 1999).

Whilst the influence of fire and overgrazing on bush encroachment has been relatively well investigated, the impact of herbivore composition has received little attention. The latter must be seen as an important area of study, especially in the light of current changes in land management.

2.4 Influence of fire and herbivory on woody seedlings
2.4.1 Fire

Fire can be an important management tool for controlling bush encroachment due to the potentially destructive effect of fire on existing savanna vegetation (Trollope 1983; Tchie & Gakahu 1985; Walker 1985). However, fire may also benefit seedling recruitment by breaking dormancy of hard seeded *Acacia* species (Sabiiti & Wein 1987; Auld & O'Connell 1991). It is necessary to differentiate between the influence of fire on the existing community as well as the potential recruitment following fire (Jordaan 1995).

Germination of woody seeds at or near the soil surface might be enhanced by the passage of fire (Pieterse & Cairns 1987; Sabiiti & Wein 1987; Hodgkinson 1991), to the extent that gains in shrub reduction by fire-induced mortality may be nullified by shrub recruitment through fire-enhanced germination. In leguminous species fire can break hard-seededness by mechanical alteration of the seed coat, which results in increased water intake and gas exchange, thereby allowing subsequent imbibition and germination (Pieterse & Cairns 1986; Bradstock & Auld 1995). Seed mortality can outweigh the beneficial effect of inducing seed germination of *Acacia gerrardii* and *A. sieberiana* under conditions of high temperature (Mucunguzi & Oryem-Origa 1996). The tolerance of *A. karroo* to high temperatures experienced during and after the passage of fire, and the stimulation of germination by fire, may be a factor that contributes to its ability to encroach in disturbed areas (Mbalo & Witkowski 1997). The passage of fire has also been reported to increase the germination of other *Acacia* species (Sabiiti & Wein 1987; Hodgkinson & Oxley 1990; Auld & O'Connell 1991; Mucunguzi & Oryem-Origa 1996). Furthermore, the germination of *Acacia* species is influenced by the thickness of the testa (Lamprey *et al.* 1974).

The effect of heat treatment on seed germination may depend on heat intensity and duration of exposure (Pieterse & Cairns 1987; Mucunguzi & Oryem-Origa 1996). Short exposure of seeds can stimulate germination whilst prolonged exposure can be detrimental to the seeds. Whilst seed mortality depends on duration of exposure, temperatures greater than 60 °C can be sufficient to break seed dormancy of legume species (Hodgkinson & Oxley 1990; Bradstock & Auld 1995). Dormancy-breaking temperatures for hard-seeded legumes range from 45 °C to 90 °C, whilst heat exposure for 4 minutes in the range of 90 °C to 110 °C appears to be lethal to all seed tested (Martin *et al.* 1975). The lethal temperature threshold may be between 70 and 80 °C (Hodgkinson & Oxley 1990).

Fire may indirectly affect seed germination in the post-fire phase (Auld & Bradstock 1996). Soil temperatures at a site burnt in winter and an unburnt site in summer were not sufficiently high to have a significant effect on dormant legume seeds in the seedbank. In contrast, post-fire soil temperatures at a site burnt in summer were sufficient to cause the breaking of dormancy of some seeds in the soil seedbank, independent of the actual soil temperatures reached during the passage of fire. The ambient temperature significantly influenced soil temperatures up to 60 mm, and increased levels of solar radiation on the soil surface post-fire were considered responsible for favourable soil temperatures for germination. Burning can reduce soil moisture (Anderson 1965), which has been attributed to relatively higher soil temperatures and increased evaporation from the warmer, blacker surface (Savage 1980). Significant increases in soil heat and net radiation, and decreases in surface reflection, occur within a few days after burning, and soil temperature and soil heat are greater four weeks post-fire in burnt sites relative to unburnt sites (Savage & Vermeulen 1983). As a result, the soil can be heated to the extent that conditions are favourable for breaking seed dormancy, and consequently for germination. However, post-fire conditions can become less favourable for germination as higher soil temperatures during the interim between fire and establishment of a new cover may result in a temporarily drier soil surface after burning than before (Heady & Child 1994).

The effect of a fire on woody plant mortality is strongly dependent on the relationship between the temperature profile and plant height. Topkill usually occurs only when the flame height exceeds the canopy height (Trollope 1984 b). A consistent finding for woody savanna species is that individuals smaller than flame height (about 2 m tall) suffer the loss of their aerial portions with fire, but usually respond by extensive coppicing, with the post-fire stem

number usually exceeding that of the pre-fire number (Trollope 1980; Tchie & Gakahu 1984; Sweet & Tacheba 1985). One of the reasons for the success of *A. karroo* is that it has the ability to coppice strongly following the death or removal of aerial parts by fire or other means (Teague & Walker 1988). As a consequence *A. karroo* plants are capable of withstanding both intense and frequent defoliations (Teague 1989 b). Mortality of mature trees due to fire alone is seldom found (Rutherford 1981; Trollope 1983; Sweet & Tacheba 1985; Sweet & Mphinyane 1986).

Acacia karroo seedlings can show resistance to fire within a year of germination (Story 1952). All seedlings less than two months old may be killed by fire, whilst one-year old seedlings tend to survive. Surviving seedlings also produce relatively more coppice growth than unburnt seedlings. Seedlings are therefore difficult to control with the use of fire alone once they have reached a critical size. Furthermore, in the absence of regular fires the bush can progress to the stage where fires cannot reach the main stems of the trees in thickets, only the edges are burnt and the centres are left unburnt (Walker 1985). Once woody plants have become dominant and suppress the grass, fire is no longer effective as there is not enough grass fuel to support a sufficiently intense fire (Trollope 1983).

Fire intensity is variable and depends on the amount and structure of fuel, its moisture content, and the prevailing atmospheric humidity and windspeed (Trollope 1983). Resprouting of woody individuals in post-fire conditions can be delayed by an increase in fire intensity, whilst post-resprouting mortality can also increase (Moreno & Oechel 1991). However, the type of fire implemented (surface head burn or back burn) can also influence fire intensity. The dynamics of back fires have not been thoroughly investigated, with the result that the potential of back fires for savanna management has not been evaluated. Back fires have their maximum heat concentrated near the ground, whilst head fires have their maximum heat well above the ground (Trollope 1983). A higher mortality of small woody individuals occurred in a back than in a head fire (Rutherford 1981), even though fire intensity was greater in the head fire. No literature was found examining the effect of temperature and duration of fire on seed mortality of *Acacia* species.

Grass competition adversely affects woody seedling survival and growth (Brown & Booysen 1967; Stuart-Hill & Tainton 1989; Bush & Van Auken 1990). As fire can significantly decrease herbaceous biomass accumulation and growth (Grossman *et al.* 1981), post-fire conditions may be favourable for seedling germination and establishment due to the removal of the grass layer, and consequently a reduction of competition for resources including light (Schultz *et al.* 1955). Seedlings of certain *Acacia* species growing in the shade can be more etiolated than seedlings grown in full sunlight (Milton 1982). Whilst increases in bush density (Jordaan 1995) and seedling establishment (Ben-Shahar 1996) have

been attributed to the temporary removal of the grass layer by fire, no quantitative data were found in the literature that focussed directly on changes to the competitive ability of woody seedlings in the post-fire period.

2.4.2 Herbivory
2.4.2.1 Animal type

Body size determines the feeding behaviour of browsers. It affects the maximum height at which they can feed (Bergstrom 1992), and the type of material they select. An animal's size has a fundamental influence on its metabolism and hence its food and energy needs (Owen-Smith 1985 a). Time-energy constraints in different ruminant species are unique for a particular body size (Demment 1983). The utility of a food is a function of nutrient content and depends on the handling and processing costs associated with consuming that food (Stephens & Krebs 1986). Owen-Smith (1985 b) based an optimisation model on these considerations, predicting that smaller browsers required progressively more protein in their diet. As a result of the allometric relationship between body mass and diet quality, small-bodied herbivores must feed more selectively than large-bodied herbivores to meet daily energy requirements (Gordon & Illius 1996) and therefore utilize more nutritious food items, such as woody seedlings. By virtue of their low absolute energy requirement, small-bodied animals have more time available for selective grazing (O'Reagain & Stuart-Hill 1991). When considering domestic animals, cattle have a higher absolute energy demand than sheep due to their size, but sheep have a higher relative energy demand (Mentis 1981). Hence sheep require a relatively higher energy diet and consequently graze more selectively. This requirement is assisted by their smaller mouthparts which can (a) select smaller mouthfuls of higher quality forage, and (b) graze much closer to the ground, thereby selecting newly sprouting grass (Mentis 1981), and woody seedlings. Thus the smallest browsers are forced to pick out only the highest quality plant parts, whilst large browsers can afford to be less selective. The relative importance of the various components of plant structure is not constant, and should vary between animal species of different body size.

2.4.2.2 Implications for savannas

The natural savanna vegetation of Africa evolved in the presence of a multi-species herbivore population with a wide range of diet preferences. The absence of small-bodied herbivores therefore represents a departure from natural conditions. These animals utilize both woody and herbaceous vegetation, and, together with periodic fires, can maintain grassland or open

woodland (Frost & Robertson 1985). In multi-species systems, consisting of a combination of browsing ungulates that favour different height levels, there would be greater utilization of the vegetation. This could potentially increase animal production by one third over cattle alone in typical savanna vegetation (Owen-Smith 1985 a). In south-eastern Zimbabwe the mean utilization of available browse was about 8% in an area with cattle and about 17% in a game area (Taylor & Walker 1978). Exclusion of the suite of browsers that feed on lower height levels can therefore reduce productivity, whilst allowing woody individuals to escape herbivory. Consequently, an increase in the density of woody plants is predicted.

2.4.2.3 Feeding ecology of relevant animal species

Impala and goats are mixed feeders, utilizing varying proportions of grass and browse (Aucamp 1976; Cooper 1982; Trollope 1984 c; Owen-Smith 1985 a), and therefore impact on the vegetation over a much greater vertical plane than is the case with sheep or cattle. Bite size and hence grass intake rate of sheep is strongly correlated with plant height, reaching a maximum at a plant height of about 15 cm and declining thereafter (O'Reagain et al. 1996). Although sheep and cattle are preferential grazers, sheep also utilize limited quantities of browse (Story 1952), as do cattle (Rees 1974; Donaldson 1979; Pitt et al. 1998). Goats have broader muzzles than impala, tend to take larger bites, and as a result can cause more damage to the plants by biting off whole shoots (Cooper 1982). Goats can reach plants 1.2 m to 1.5 m in height (Teague & Walker 1988; Aucamp 1976), whilst males can reach up to 2.0 m (Teague 1989 a). However, the average feeding level of small-bodied herbivores is close to the ground, and the likelihood of them encountering and consuming woody seedlings is far greater than for larger herbivores. Small-bodied hebivores furthermore retard the growth of woody plants within the grass layer, preventing them growing to an 'out-of-fire' stage, where they are less susceptible to fire. Importantly, their small size and mouthparts allow them to utilize nutritious woody material close to ground level, such as woody seedlings.

Although black rhino have been observed feeding on vegetation about 30 cm off the ground in the Masai Mara Game Reserve (Owen-Smith 1988), black rhino browse by biting off mainly larger twigs and are not very selective. Black rhino restrict most of their feeding to vegetation less than 1.5 m in height, and do not browse higher than 2.5 m (Owen-Smith 1988; Kotze & Zaccharias 1993; Breebaart 2001). In addition, available browse should not be hindered by long grass (Emslie & Adcock 1993). The likelihood of rhino encountering and feeding on emerging woody seedlings is highly unlikely. Although giraffe make reasonable use of vegetation below 2.5 m (Breebaart 2001), they generally feed on trees and shrubs too tall (5 m) to be reached by smaller browsers (Owen-Smith 1993), and thus avoid

competing with them. Whilst kudu have been found to browse vegetation below 2 m (Leuthold 1978; Owen-Smith 1985 a), it is unlikely that they significantly impact on woody plants within the grass layer. Branch breaking by kudu can have a significant impact on woody plant parts at higher levels, whilst little attention is devoted by kudu to seedlings or regeneration below 20 cm in height. Eland of both sexes can break down branches with their horns to reach foliage above 2.4 m (Owen-Smith 1985 a). However, eland consume a high proportion of grass, which can comprise up to 60% of their feeding time, and their impact on woody plants whilst utilizing the grass sward merits further attention.

Studies have consistently found that wildlife browser species, with the exception of giraffe but including kudu, eland and black rhino, concentrate their foraging at less than 2 m above ground (Goodman 1975; Owen-Smith 1985 a; Breebaart 2001). However, there is no insight about their utilization of emerging seedlings.

2.5 Plant-herbivore interaction
2.5.1 Browsing

Browsing ungulates can have important influences on ecosystem dynamics by damaging regenerating woody plants (Owen-Smith & Robbins 1993). However, adult woody plants are very resistant to herbivory (Teague & Walker 1988; Gowda 1997), and browsers cause very little mortality of woody plants, even when browsing is sufficient to markedly alter plant size and structure (Walker 1985).

Woody plant defence increases with increased herbivory and age of the plant (Cumming 1982; Milewski *et al.* 1991; Brooks & Owen-Smith 1994). The sensitivity of *Acacia* species to defoliation depends on the frequency and intensity of defoliation, phenophase of the plant, location of browsing within the plant, and type of defoliation agent (O'Connor 1996). *Acacia karroo* was found to be most susceptible to defoliation and young shoot removal during the spring flush when carbohydrate levels were at their lowest (Teague & Walker 1988). Importantly, woody seedlings are more prone to defoliation (Teague 1988; Seif El Din & Obeid 1971; Brown & Archer 1989), and older plants less inclined to sustain heavy losses due to herbivory (Sweet & Mphinyane 1986; Cooper & Owen-Smith 1986). Seedling survival and shoot growth of *Acacia senegal* in response to simulated browsing is age dependent (Seif El Din & Obeid 1971), with young seedlings (less than 38 days old) being the most vulnerable. The absence of defoliation may therefore provide seedlings a window of opportunity to attain a critical size, after which it is less vulnerable.

For *A. karroo*, seedling mortality is only caused by simulated defoliation when it is conducted at ground level (Story 1952). The same result might be expected of herbivores.

More mature individuals can coppice if the plant is cut off above the junction of the stem and root (Scott 1949). Small browsing antelope maintained trees at less than 31 cm for 3 years in an African study (Belsky 1984). Browsers therefore appear to maintain woody plants at a height accessible to fire.

Herbivory by rabbits, more so than kangaroos, had the most significant effect on the survival of *Acacia* species, more significant than seedling clustering, topography, the presence of a eucalypt canopy, and distance from the edge of fires (Cohn & Bradstock 2000). During dry periods, when other forage becomes scarce, vertebrate grazing on *Acacia* species seedlings will be higher (Auld 1995). However, mortality of seedlings is directly related to rainfall, irrespective of whether or not seedlings are protected from herbivory (Cohn & Bradstock 2000). Sufficient spring rainfall appears to be more important than summer rainfall, possibly as this facilitates the establishment of an adequate root system which can carry the seedling through subsequent periods of below-average rainfall.

Compensatory growth can occur in *A. karroo* (Teague & Walker 1988; Teague 1989 a), *Acacia nigrescens* (Du Toit *et al.* 1990) and *A. tortilis* (Du Toit *et al.* 1990). Defoliation of *A. karroo* by goats stimulated leaf and shoot growth relative to non-defoliated plants (Teague & Walker 1988), with these effects integrated across the entire plant (Teague 1989 a). Successive defoliations are additive, with more frequent defoliations resulting in a greater decrease in carbohydrate reserves (Teague 1989 b).

Physical deterrents on browsing, such as thorns and spines, can be induced by herbivory (Young 1987; Milewski *et al.* 1991). Also spinescence of *Acacia tortilis* and *A. nilotica* depends on tree age (Brooks & Owen-Smith 1994), as juvenile trees possess longer thorns than adult trees, which may be more effective for defence against browsers (Milewski *et al.* 1991). Furthermore, juvenile trees have smaller closely-spaced leaves between thorns, which restrict leaf losses (Cooper & Owen-Smith 1986). Thus leaf size and thorniness might act together in defence of trees against browsing ruminants (Brooks & Owen-Smith 1994). Although younger plants are more spinescent than older plants (Cumming 1982), seedlings are soft and fleshy in the early phenophases, and they lack lignified thorns.

The abovementioned morphological features do not prevent animals from feeding but reduce bite size and biting rate (Cooper & Owen-Smith 1986), and the rate of intake of browse (Teague 1989 c). The utility of food to an animal depends on nutrient content and handling and processing costs associated with consuming that food (Stephens & Krebs 1986). Thorns increase the herbivore's handling time of the food, thus reducing its acceptability (Cooper & Owen-Smith 1986). This suggests that once leaf density has been reduced below some critical level, the herbivore will move to another tree, thus preventing the tree from being irrevocably damaged (Coe & Coe 1987).

2.5.2 Grass competition and grazing

Woody seedlings establishing in a perennial grassland are likely to face competition from grass plants. Generally, when water and nutrients are plentiful, above-ground competition, primarily for light, is most important. When resources are poor, below-ground competition is most important (Wilson 1988). Sustained heavy grazing of grasses may promote the establishment of woody seedlings (Walker *et al.* 1981; Skarpe 1990) by reducing above- and below-ground grass competition, and resource use (Knoop & Walker 1985; Holland & Detling 1990). This increases irradiance at ground level (Van Auken & Bush 1991) and increases availability of below-ground resources (McNaughton *et al.* 1983; Caldwell *et al.* 1987). Heavy grazing by livestock, and associated reduction of the herbaceous layer, can promote the establishment and growth of woody plants (Madany & West 1983). Competition depresses seedling growth of some *Acacia* species that can be offset by levels of irradiance (Van Auken & Bush 1991) or heightened by increased nutrient availability (Cohn *et al.* 1989).

As opinions on the the effect of grass competition on woody seedlings differ, it is questionable if a reduction in competition by herbs via livestock grazing improves woody seedling success in all instances. Seedlings of *Acacia karroo* (O'Connor 1995) and *Prosopis glandulosa* (Brown & Archer 1999) fare as well or better under grass competition . Rates and patterns of seed dispersal may be the primary determinants of *P. glandulosa* encroachment on present-day landscapes in semi-arid regions (Brown & Archer 1999).

The change from heavy, continuous, non-selective utilization of the veld to lighter, rotational management may have resulted in bush encroachment (Trollope 1983) . Rotational and resting programmes allow seedlings and cropped bushes to become woody and thorny and therefore more resistant to utilization by livestock (Milewski *et al.* 1991). Stocking rate makes a greater impact than does either the season of grazing, or the grazing system adopted (Heady & Child 1994). Increasing the stocking rate does not change selection patterns of grazing animals, but merely accelerates them (Stoltsz & Danckwerts 1990). Where cattle and sheep graze together, increasing the overall stocking rate significantly increases the extent of patch grazing, as does increasing the stocking rate of cattle (Hardy 1995). However, increasing the stocking rate of sheep only does not significantly increase the extent of patch grazing, but increases their intensity. These selective habits lead to non-uniform grazing of grassland, resulting in undergrazed and overgrazed patches (Hatch & Tainton 1990; Hatch 1991; Edwards *et al.* 1996), with short patches interspersed within areas of relatively tall herbage (Hardy 1995). Livestock graze selectively regardless of the grazing method or

stocking density (Danckwerts *et al.* 1983; Kreuter & Tainton 1988). A number of vegetational and soil changes occur as a result of patch grazing, which modifies conditions for seedling recruitment.

Whilst there may be no significant difference in soil moisture among patches of varying grass biomass in some instances (Hatch & Tainton 1990), significant reductions in soil moisture have been reported (Fuls 1992). Soil compaction is significantly greater on patches as compared to non-patches (Hatch & Tainton 1990; Fuls 1992). An increase in cattle grazing pressure can also significantly increase the effect of trampling on regenerating tree seedlings (Pitt *et al.* 1998). High fertility of dung and urine, with that produced by ruminants being especially high in nitrogen content (McDonald *et al.* 1992), play a vital role in nutrient cycling. Urination may be an important factor in the initiation and the development of patches, probably due to a higher nutritional value of the affected sward (Lutge *et al.* 1995). Enhanced survival and growth of 1st-year *Acacia* seedlings were attributed to animal-induced improvements in soil conditions (Reid & Ellis 1995).

An increase in height in response to a reduction in light levels is a strategy adopted by plants in an effort to obtain a height where more light is available for photosynthesis, shown to result in an increase in the leaf-to-height ratio (Milton 1982; O'Connor 1995). Smith and Shackleton (1988) showed that growth in height of *A. tortilis* seedlings was stimulated by reduced light levels resulting in an inverse relationship between the ratio of plant height-to-shoot weight and light availability.

2.5.3 Interaction of fire and herbivory

Fire increases the palatability of the grass sward to grazers (Walker 1985) and maintains woody vegetation at an available height and in an acceptable state for browsers (Trollope 1983; Walker 1985). Conversely, browsers perform an important function in maintaining woody plants at a height accessible to fire (Trollope 1984 b; Owen-Smith 1988).

Large reductions in bush density have been shown by using browsers in conjunction with fire (Trollope 1974; Trollope 1983; Sweet & Mphinyane 1986; Moreno & Oechel 1991). The introduction of a browsing animal can control coppice growth of the bush following fire by continuous browsing on regrowth, causing mortality amongst different bush species. Plants out of synchrony were eaten more frequently by herbivores, and new growth on these defoliated plants was repeatedly browsed until the plant died, probably because carbohydrate reserves were exhausted (Moreno & Oechel 1991).

Grasses suppress woody recruitment by fuelling fires which kill or stunt woody seedlings so that they are unable to grow above the grass layer and escape fires (Bond & Van

Wilgen 1996). This results in the formation of typically multi-stemmed shrubs, which dominate communities as adults but struggle to emerge from the herbaceous layer as juveniles (Bond & Van Wilgen 1996). Such stunted plants may persist in the grass layer for decades (Menaut *et al.* 1990) until they die through progressive weakening as a result of repeated fires, or until a break in the fire regime affords these plants a window of opportunity to escape the danger zone and grow into adults. Grazing reduces fuel for fires and decreases the frequency and intensity of fire, which can favour woody plant encroachment (Brown & Archer 1990; Roques *et al.* 2001).

Rhino browsing can increase as a result of fire, and individuals of normally unpalatable species are eaten after burning (Emslie & Adcock 1993). Fire also eliminates tall grass which can detract from the acceptibility of browse to rhino (Kotze & Zaccharias 1993). Browsing by elephants caused a decline in mature *A. tortilis* woodlands whilst tree regeneration was suppressed by giraffe browsing and periodic burning, leading to an overall decline in the extent of *A. tortilis* woodlands (Pellew 1983 a, b).

2.6 Addressing gaps in the literature

Very little emphasis has been placed on woody seedling dynamics in savanna ecosystems, especially the establishment of seedlings in their first year after emergence. Furthermore, no experimental studies could be found which directly examined the impact of animal type on woody seedling dynamics at this stage. The influence of grass competition on woody plants has received some attention, although little of this work has focussed on emerging seedlings. No studies were found that considered the effect of burning, in terms of the reduction in herbaceous biomass, on woody seedling germination. The effect of grazing system, and its interaction with animal type, on woody seedling establishment has also not been investigated. Importantly, the interaction of grass competition, herbivory, and fire in determining woody seedling dynamics at the emerging stage has not been examined. Lastly, the impact of fire type on seed germination has not been studied.

This study was designed to address the gaps in the literature, particularly the interactions outlined above involving animal type.

CHAPTER 3

STUDY AREAS

3.1 Selection of study areas

Abu Madi Game Ranch and Weenen Nature Reserve were selected by virtue of their animal species composition, as the former contained large populations of small-mouthed herbivores and the latter did not. This allowed for comparison between two systems, similar in structure and functioning, that were distinctly different in terms of animal species composition. Ukulinga Research Farm was chosen to examine the impact of domestic livestock, namely cattle and sheep, on woody seedlings in a domestic system. Although the study areas were separated geographically by large distances (Figure 3.1), all three were considered savanna systems.
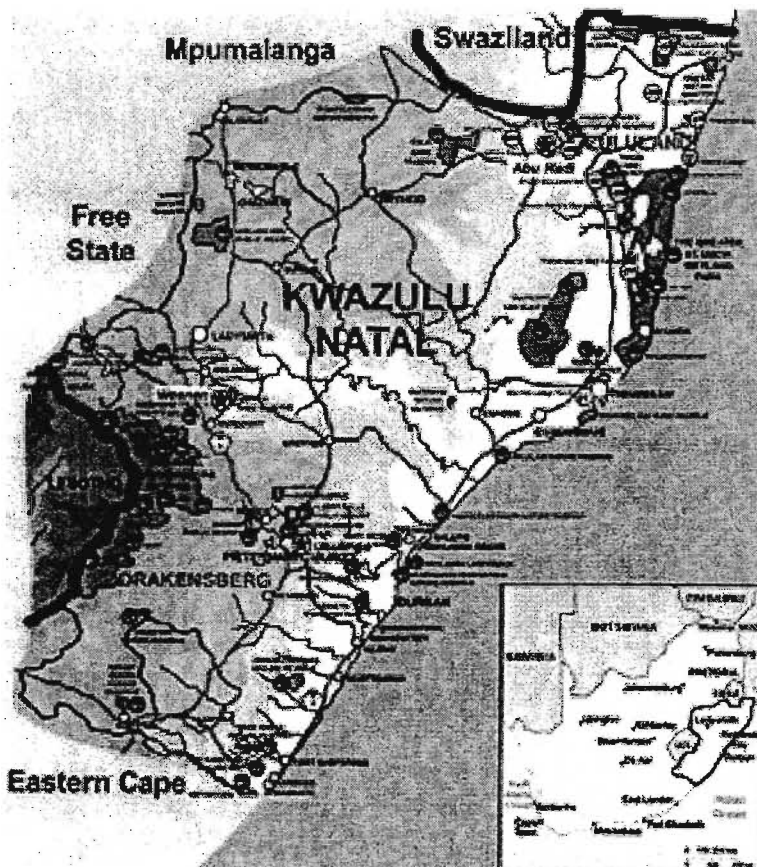

Figure 3.1 Location of study areas within KwaZulu-Natal (maps: Wildnetafrica & graphicmaps).

3.2 Ukulinga Research Farm

One trial was conducted at Ukulinga Research Farm, University of Natal, 6 km south-east of Pietermaritzburg (29°24'E, 30°24'S; 700 m a.s.l.). The 30-year mean annual rainfall at Ukulinga is 733 mm with a standard deviation of $^{\pm}126$ mm. The mean monthly rainfall over the experimental period was generally above-average (Figure 3.2). Average annual maximum and minimum daily temperatures are 25.7°C and 8.9°C respectively. Light to moderate frosts are encountered during the winter months.

The trial was situated on the east-facing slope of a small plateau, dominated by Willowbrook, Bonheim, Rensburg and Westleigh soils (Figure 3.3). Other less abundant soils on the trial are Bainsvlei, Avalon, Clovelly and Mispah soils. The study area can be described as Southern Tall Grassveld (Acocks 1953), although it tends to be mixed veld. A small drainage line crossed part of the study area, which was avoided in the experiment. A large amount of *Chloris gayana* occurs in this grassland, ostensibly because a *C. gayana* pasture is found adjacent to the study site. *Acacia karroo, A. nilotica* subsp. *kraussiana* and *A. sieberiana* var. *woodii* were characteristic of this veld type. Common grasses were *Hyparrhenia hirta, Sporobolus africanus, Aristida congesta* subsp. *barbicollis* and *Eragrostis plana*. The veld tends to be sour, declining in forage quality in the drier winter months. Elements of Valley Bushveld (Acocks 1953) were also evident in the form of *A. nilotica* subsp. *kraussiana* and *Ziziphus mucronata*, as well as *Eragrostis curvula* and *Aristida congesta*. Species nomenclature follows Arnold & De Wet (1993).
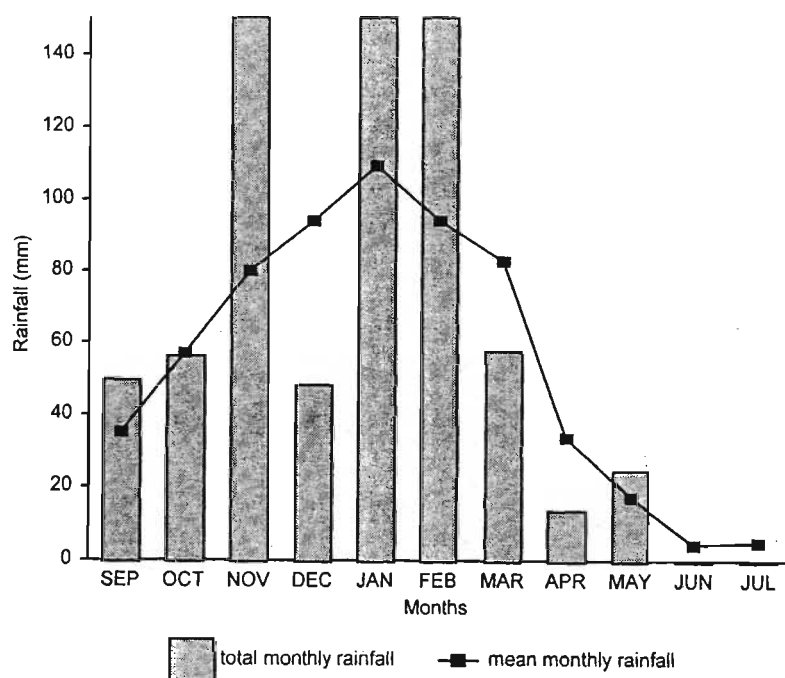

Figure 3.2 Mean monthly rainfall (solid line) of Ukulinga Research Farm (WCR Report No 109/1/89, Dent *et al* 1987), and its monthly rainfall from September 1997 to July 1998 (bars).
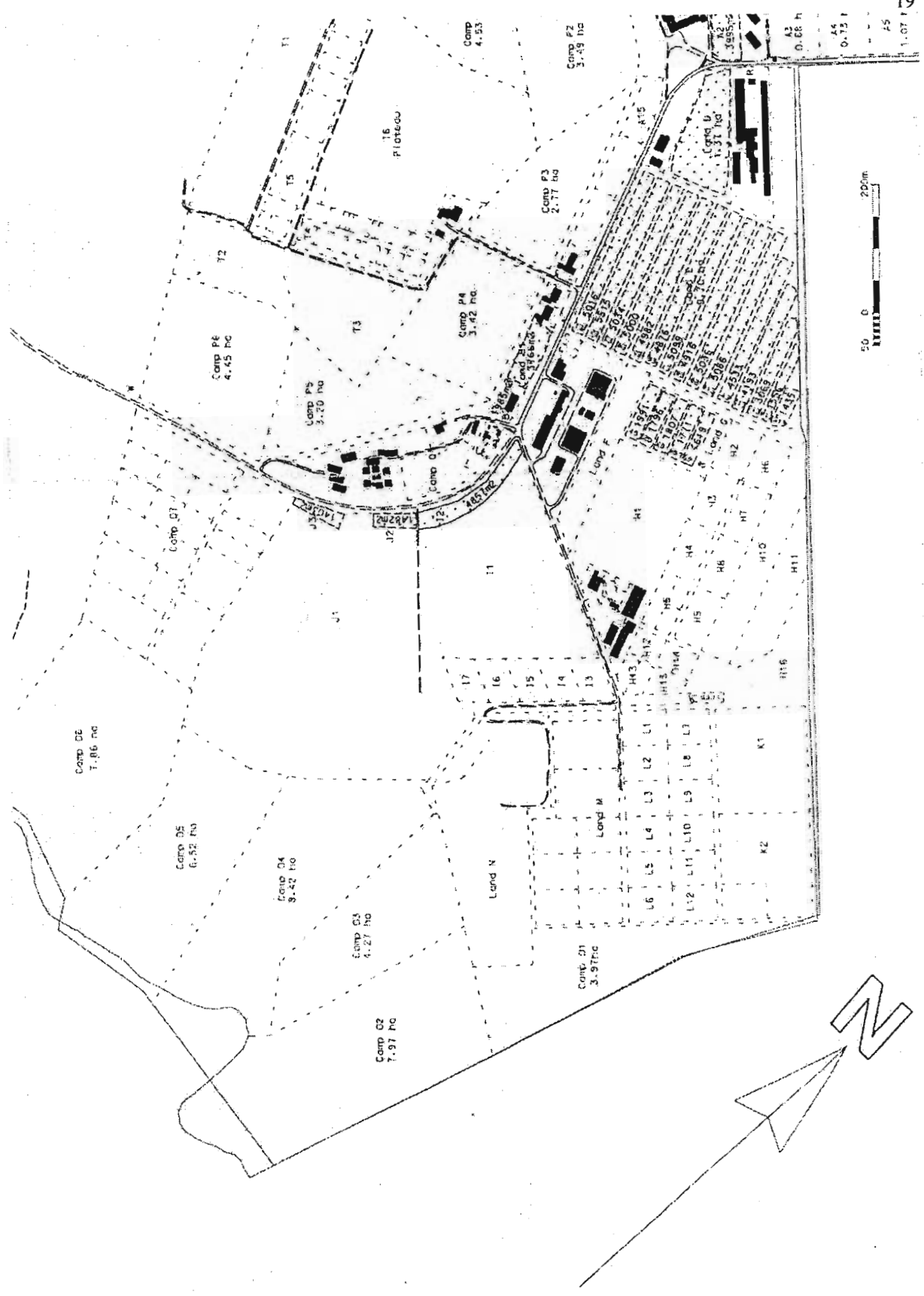
Figure 3.3 Locality of the study area within Ukulinga Research Farm (camp 07).

3.3 Abu Madi Game Ranch

Abu Madi is situated about 15 km from Mkuze in Zululand, KwaZulu-Natal (31°58'E, 27°37'S; 200 m a.s.l.) Annual precipitation varied between 1014 mm and 417 mm (1993 to 1998) with a mean of 658 mm and a standard deviation of 313.2 mm. The mean monthly rainfall over the experimental period was generally above and similar to the average, with the exception of December (Figure 3.4). Temperatures vary between 9°C in winter and 40°C in summer.

Abu Madi (468 ha) is located on the on the well-developed foreplain interior of the Lebombo Mountains in the Lowveld (Acocks veld type 10, Acocks 1953). The basalt-derived soils are heavy and shallow (mean depth - 195 mm). The vegetation is characteristic of the open *Acacia nigrescens - Sclerocarya - Themeda* Savanna of the Lowveld. Common bush species include *A. nilotica, A. tortilis, Ziziphus mucronata, Schotia brachypetala* and *Ozoroa engleri,* whilst common grass species include *Panicum maximum, Aristida bipartita* and *Urochloa mosambicensis.*

The experimental area was an open woodland with a moribund grass sward in which distinct bare patches occur (Figure 3.5). The bare patches were characterized by sparsely scattered heavily-utilized woody plants growing in stunted form (< 0.5 m in height), and a complete absence of grass cover. Whilst patches varied in shape and size, larger (>80 m^2) patches were selected for the experiment. The patch character was attributed to heavy utilization by nyala (*Tragelaphus angasii*) and impala populations, which maintain the character of these areas by returning to browse on the regrowth in these areas. Emerging woody seedlings were subject to competition from annual grasses and forbs, which germinated after rainfall, but only occupied large areas of the patches towards the end of the growing season. This vegetation structure is probably the result of the animal species mix at Abu Madi, (Table 3.1) which includes a large component of mixed feeders.

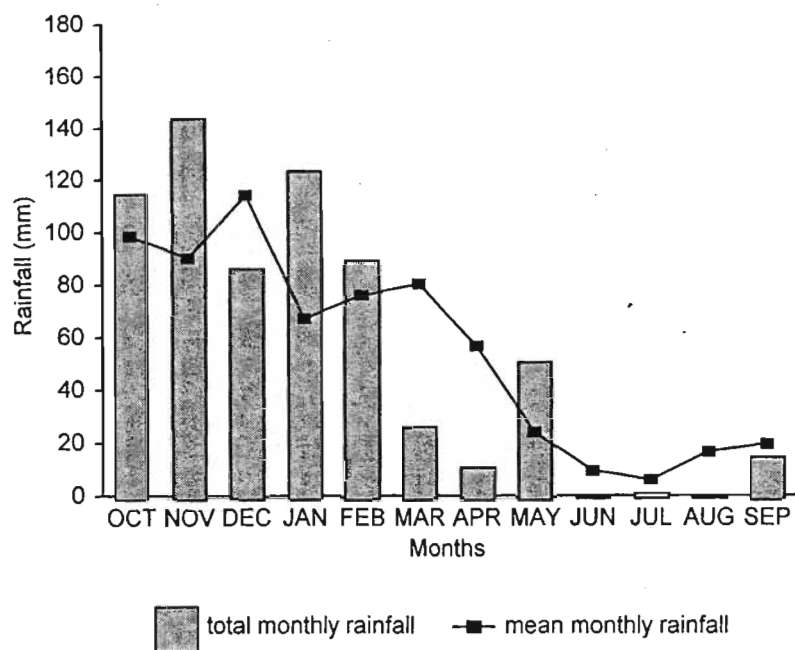Nomenclature of animal species follows Skinner & Smithers (1990).

Figure 3.4 Mean monthly rainfall (solid line) of Abu Madi Game Ranch (1993 - 1998), and its monthly rainfall from October 1997 to September 1998 (bars).

Table 3.1 Estimated stock numbers at Abu Madi Game Ranch for the period 1997/1998

| Name	Estimated stock number
Blesbuck (*Damaliscus dorcas phillipsi*)	12
Bushpig (*Potamochoerus porcus*)	12
Giraffe (*Giraffa camelopardalis*)	3
Grey Duiker (*Philantomba monticola*)	6
Impala (*Aepyceros melampus*)	180
Kudu (*Tragelaphus strepsiceros*)	23
Mountain Reedbuck (*Redunca fulvorufula*)	9
Nyala (*Tragelaphus angasii*)	80
Red Duiker (*Cephalophus natalensis*)	6
Reedbuck (*Redunca arundinum*)	2
Warthog (*Phacochoerus aethiopicus*)	250
Wildebeest (*Connochaetes taurinus*)	58
Zebra (*Equus burchelli*)	39
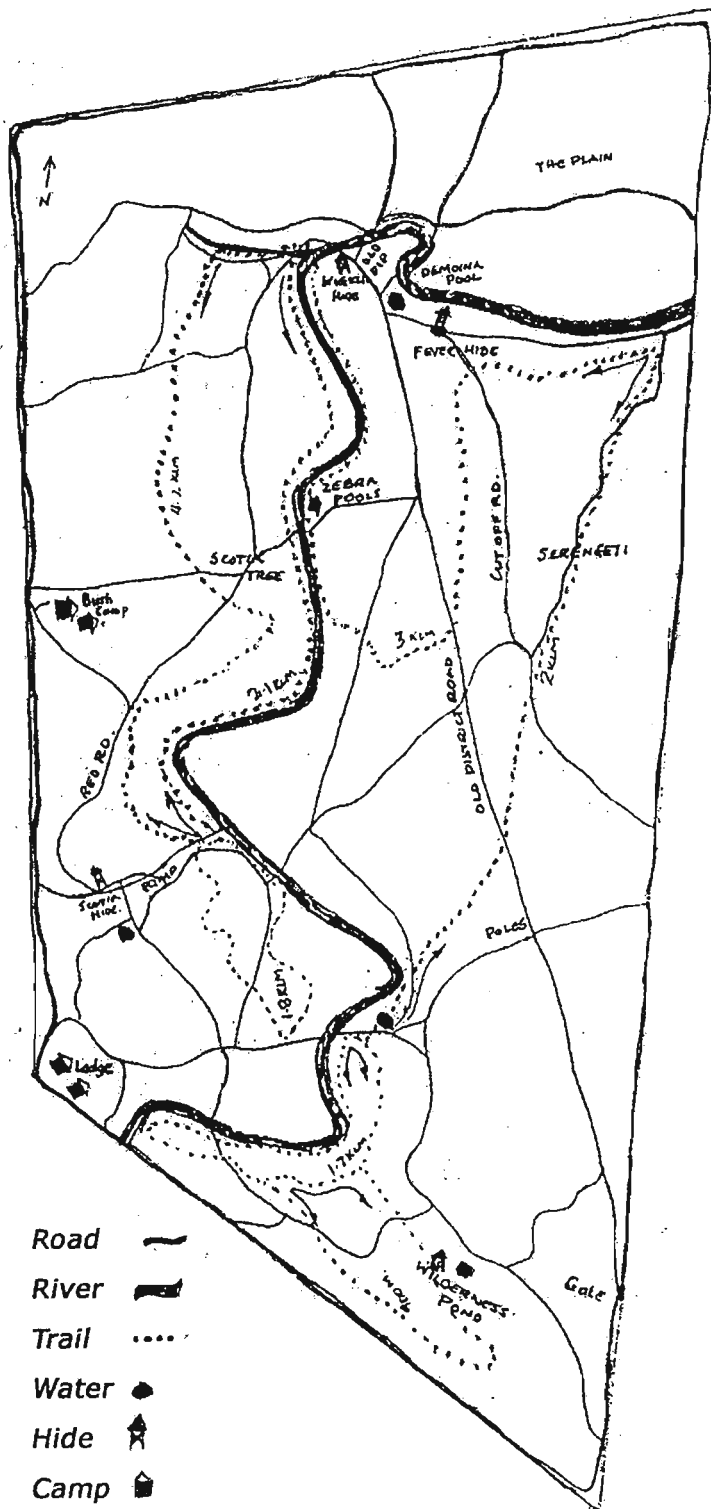
Figure 3.5 Locality of the experimental sites within Abu Madi Game Ranch.

3.4 Weenen Nature Reserve

Weenen Nature Reserve (4923 ha) is situated about 28 km north-east of Estcourt and 10 km west of the small town of Weenen (28°50'S, 30°02'E; 900 m - > 1300 m a.s.l.). Annual precipitation has varied from 1039 mm to 489 mm (1981 to 1997) with a mean of 732 mm and standard deviation of 229 mm. The mean monthly rainfall over the experimental period was generally above and similar to the average, with the exception of December (Figure 3.7). Minimum and maximum temperatures vary between 1°C in winter and 37°C in summer. Moderately severe to severe frosts also occur commonly in winter in the valley bottoms (Edwards 1967).

Weenen Nature Reserve is situated on the Draycott plain. Altitude varies from approximately 940 m in the north to 1220 m in the Umthunzini hills, dropping to 900 m along the Bushmans River in the south (Figure 3.7). The topography in the northern and central regions is undulating while the southern and eastern regions are steep rocky slopes. The Bushmans, Nyandu and uNothongo rivers drain the reserve and flow into the Tugela River. The reserve is underlain by shales, mudstones and sandstone of the Beaufort series (Estcourt and Adelaide Formations), but many dolerite outcrops occur throughout the reserve (Hughes 1989). The major soil forms are Mispah, Shortlands and Valsrivier derived from dolerite. Katspruit, Rensburg and Oakleaf soil forms occur in the valleys, derived from Ecca shales and sandstones. The soils have undergone extreme soil erosion as a result of previous mismanagement. The majority of the area is characterized by soils less than 300 mm in depth.

Whilst valleys are of Natal Valley Bushveld (veld type 23, Acocks 1953), the predominant vegetation types in the reserve were sparse open woodland and medium open woodland (Breebaart et al. 2001). There are no distinct patches in the herbaceous layer as at Abu Madi Game Ranch. Sparse open woodland comprises areas of true grassland, dominated by *Themeda triandra* and *Tristachya leucothrix* and old lands that now function as grasslands and consist mainly of *Hyparrhenia hirta*. The common woody species are *A. sieberiana, A. karroo, A. nilotica, Acacia caffra* and *Rhus dentata*. The medium open woodlands include the aforementioned species as well as numerous others, such as *A. tortilis, Acacia robusta, Ozoroa paniculosa* and *Euclea crispa*. The study took place in sparse open woodland.

The reserve has large numbers of large herbivores, and very small populations of mixed feeders such as the grey duicker and bushbuck (Table 3.2). Impala and nyala are absent from the reserve.
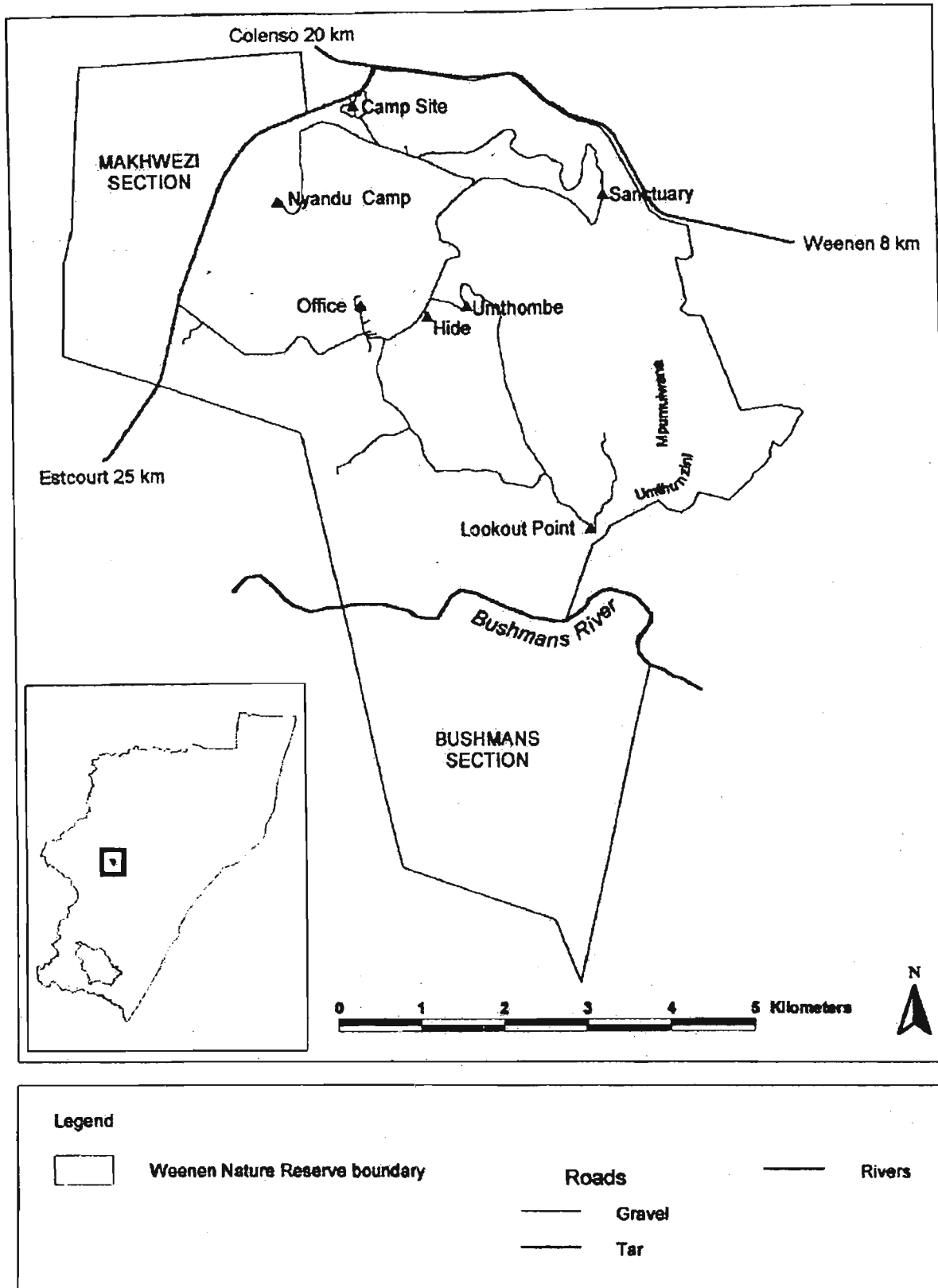
Figure 3.6 Locality of Weenen Nature Reserve within KwaZulu-Natal, South Africa, and the study area (excluding Bushmans and Makhwezi sections) within the reserve (Breebaart 2001).
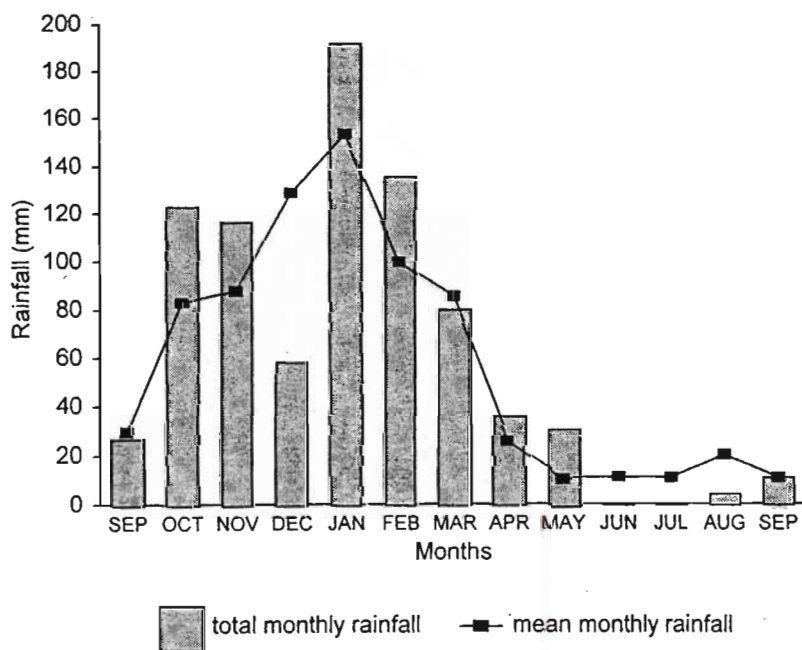
Figure 3.7 Mean monthly rainfall (solid line) taken at Weenen Nature Reserve (1981- 1998), and monthly rainfall from September 1997 to September 1998 (bars).

Table 3.2 Estimated stock numbers at Weenen Nature Reserve for the period 1997/1998

Name	Estimated stock number
Black Rhinoceros (*Diceros bicornis*)	9
White Rhinoceros (*Ceratotherium simum*)	38
Eland (*Taurotragus oryx*)	60
Giraffe (*Giraffa camelopardalis*)	40
Kudu (*Tragelaphus strepsiceros*)	240
Red Hartebeest (*Alcelaphus buselaphus*)	130
Zebra (*Equus burchelli*)	150
Bush Buck (*Tragelaphus scriptus*)	uncommon
Water Buck (*Kobus ellipsiprymnus*)	uncommon
Red Duiker (*Cephalophus natalensis*)	uncommon
Grey Duiker (*Philantomba monticola*)	uncommon
Klipspringer (*Oreotragus oreotragus*)	uncommon

CHAPTER 4

THE INFLUENCE OF ANIMAL TYPE, GRASS COMPETITION AND FIRE ON SEEDLING ESTABLISHMENT OF *ACACIA KARROO*, *ACACIA NILOTICA* AND *ACACIA TORTILIS*

4.1 Introduction

Bush encroachment has in part been attributed to a change in the composition and management of herbivores, particularly the removal of browsers from savanna systems (Du Toit 1972 a, b; Scholes & Walker 1993). Browsing by small-bodied mammals has been shown to retard recruitment of woody plants at the seedling stage (Belsky 1984; Prins & Van der Jeugd 1993; Auld 1995), whilst herbivory by large-bodied mammals has not been shown to affect woody seedlings. As the relationship between energy intake and body weight is a function of bite dimensions and the nutrient density of the food source (Illius & Gordon 1987), small-bodied herbivores must feed more selectively, and are therefore likely to utilize nutritionally rich food such as woody seedlings. Furthermore, there is a partial separation between animals of different size in their use of different height layers of browse (Owen-Smith 1985 b). Impala and nyala (small-mouthed ungulates occurring at Abu Madi Game Ranch) feed much closer to the ground than giraffe, kudu or eland (large-mouthed ungulates found at Weenen Nature Reserve). As the woody seedling stage has been described as the critical life history stage in woody plant recruitment (Harper 1977; Goldberg 1990; Brown & Archer 1989), small-bodied herbivores may assist in preventing bush encroachment.

The impact of browsers also interacts strongly with fire. Fire keeps the browse palatable and within the reach of browsers, while browsers keep woody plants within the flame zone (Trollope 1983; Scholes & Walker 1993). Hence, small-bodied mammals perform an essential role in retarding woody plant recruitment by maintaining woody seedlings at a level at which they are susceptible to fire. Herbivory influences savanna structure directly, but also indirectly by reducing the grass biomass.

As seedling establishment in semi-arid savannas can be affected by water (Auld 1987; O'Connor 1995; Brown *et al.* 1998; Brown & Archer 1999) and nutrient availability (Brown *et al.* 1998), it was expected that competition for resources between grasses and woody seedlings would be important. Whilst many studies predict that in an area of reduced grass competition an emerging woody seedling should have a greater chance of establishing than a seedling emerging in a vigorous sward (Schultz *et al.* 1955; Brown & Booysen 1967; Knoop & Walker 1985; Bush & VanAuken 1990; Bush & Van Auken 1991; Bush & Van Auken 1995), other studies challenge such findings (O'Connor 1995; Brown & Archer 1999).

Some *Acacia* species such as *A. tortilis* (Smith & Goodman 1986; Smith & Shackleton 1988; Belsky 1994) and *A. nilotica* (Smith & Goodman 1986) are very heliophytic, and respond negatively to decreases in light availability, whereas *A. karroo* has been shown to be tolerant of low irradiance (O'Connor 1995). It was therefore expected that *A. tortilis* and *A. nilotica*, more so than *A. karroo*, should benefit by a reduction in shading from the herbaceous layer.

Increases in plant production following a fire have been attributed to improved microclimatic conditions, removal of nutrient-immobilizing plant debris, release of readily available nitrogen, phosphorous, and cations, and enhanced nitrogen fixation (Hulbert 1969; Rice & Parenti 1978; Savage & Vermeulen 1983; Knapp & Seastedt 1986). Whilst woody seedling establishment may benefit from fire because of an increase in nutrient availability (Brown *et al.* 1998) and a temporary decrease in above-ground herbaceous biomass, an increase in nutrient availability has also been shown to improve the competitive ability of grasses over less nutrient-restricted *Acacia* seedlings (Cohn *et al.* 1989; VanAuken & Bush 1991). To investigate whether burning before woody seedling emergence impacts on seedling recruitment, the establishment of seedlings emerging on burnt and unburnt areas at Weenen Nature Reserve was compared.

It was hypothesized that herbivore composition influenced the success of seedling recruitment, specifically that areas devoid of small-bodied herbivores were more prone to seedling establishment than areas stocking large herbivores. This hypothesis was tested by looking at two study sites, namely Weenen Nature Reserve and Abu Madi Game Ranch. The former was lacking in large populations of small-mouthed browsers but had high populations of large-mouthed browsers, whilst the latter had large populations of small-mouthed browsers. It was further hypothesized that woody seedlings emerging in 'bare' patches in the veld at Weenen Nature Reserve and Abu Madi Game Ranch would have better chances of survival than seedlings emerging within a grass sward because of reduced competition, and that in conditions of reduced irradiance *A. karroo* seedling establishment would be superior to that of *A. nilotica* and *A. tortilis*. A potential side effect of reduced grass competition is an increase in visibility and accessibility of the seedling to herbivores. Large 'bare' patches existed naturally at Abu Madi Game Ranch, whilst at Weenen Nature Reserve these were artificially created.

The following questions were addressed in this chapter.

1) Do small-bodied herbivores have a greater impact on *Acacia* seedling establishment than large-bodied herbivores. Specifically, it was expected that mammalian herbivory would affect seedling establishment on Abu Madi (small-bodied herbivores abundant) but not at Weenen Nature Reserve (small-bodied herbivores absent)

2) Does grass competition have a negative or no effect on *Acacia* seedling establishment, or does the effect depend on species. Specifically, do *A. karroo, A. tortilis* and *A. nilotica* differ in response to grass competition?

3) Does burning before seedling emergence have a positive effect on *Acacia* seedling establishment. Specifically, does burning before seedling emergence, which reduces aboveground competition from the grass sward, have a positive effect on *Acacia* seedling establishment? Does the effect depend on species?

4.2 Materials and Method

4.2.1 Seed preparation

Species relatively common to each area were selected: *A. nilotica* and *A. tortilis* at Abu Madi; *A. karroo* and *A. nilotica* at Weenen. Seeds were collected from mature trees in the study area and examined for bruchid beetle parasitism. Seeds were washed in distilled water, and any seeds that floated or that had bruchid holes in the seed testa were discarded.

To scarify the seed testa, *A. nilotica* seeds were soaked in 1 M sulphuric acid for 45 minutes, whilst *A. tortilis* and *A. karroo* seeds were soaked for 30 minutes rendering them water-permeable. The seeds were then washed in distilled water and allowed to dry at room temperature before germination and viability trials were conducted to test for the effectiveness of scarification of seeds. Firstly, to test for viability, 100 mechanically scarified seeds were placed in a 1 % solution of tetrazolium chloride in petri dishes on filter paper for 12 hours, then cut in half, and inspected for staining of the physiologically active tissue, the embryo. To test for germinability 100 scarified seeds were placed in petri dishes on filter paper and observed for 21 days. The number of seeds germinating over that period was noted, germination being defined as the emergence of a radicle. Seeds that had not germinated and were not rotten were tested for viability.

4.2.2 Treatments

Planting commenced at Abu Madi on the 7 October 1997 and at Weenen Nature Reserve on the 10 October 1997, immediately after substantial rainfall (22 mm and 17 mm, respectively). Factorial experimental designs were set up in each study area to investigate the effects of herbivory and grass competition on seedlings of the selected woody species. *Acacia nilotica* and *A. tortilis* were planted at Abu Madi, and *A. karroo* and *A. nilotica* seeds were planted at Weenen. Four treatment combinations per species were set up randomly involving all combinations of exposed to or protected from herbivory, and unaltered or reduced competition from the herbaceous sward. To account for spatial variation across sites at each study area, seeds were planted at four locations at Abu Madi and at eight locations at Weenen. The experimental design at Weenen incorporated the effect of the abovementioned factors in response to veld burning prior to seedling germination. Four of the eight sites at Weenen were placed in different areas that had received a winter burn and four sites in areas that had not been burnt, that is, a split-plot design. At Abu Madi, 25 seeds were planted

individually for each treatment combination in every plot, whereas at Weenen, 50 seeds were planted individually for each treatment combination (including the burn factor) in every plot.

At Abu Madi a natural patch structure had formed due to continuous revisiting and heavy utilization of plant regrowth in certain patches of veld by herbivores, and avoidance of the adjacent under-utilized moribund areas. This vegetational structure lent itself to an experimental design considering the influence of grass competition on woody seedlings as the heavily-utilized patches were devoid of grass and the under-utilized patches had abundant grass. As a natural patch structure did not exist at Weenen, patches were created by clearing all herbaceous material in a 0.5 m radius ('open areas') before planting seeds, causing as little disturbance of the soil as possible. The grass plants were removed at ground level using a short-handle spade, taking care to disturb the soil as little possible. Areas not cleared of grass plants were considered to experience normal grass competition ('grass areas'). In order to exclude herbivory by mammals, except rodents, small cylindrical cages (30 cm high, 21 cm diameter, mesh size 25 mm × 25 mm) were placed over half of the seeds planted within 'grass areas' and over half of the seeds planted in 'open areas'. Insect herbivory was potentially present in all treatments. At both sites the seeds were planted 5 mm below the soil surface to ensure good contact between the seed testa and the soil. Seeds were planted at least 1 m away from each other to avoid interactions among seedlings.

4.2.3 Monitoring of seedlings

The survival and growth of seedlings from emergence (first recorded 13 days and 19 days after planting at Abu Madi and Weenen, respectively) until the end of the growing season was checked at intervals. At Abu Madi plants were monitored from the 20 October to the 31 May (13, 45, 82, 126, 169 and 213 days) whilst at Weenen Nature Reserve plants were monitored from 29 October to 20 April (19, 45, 83, 122 and 170 days). The appearance of cotyledons above the ground was defined as emergence of a seedling. All *Acacia* seedlings which emerged could be safely assumed to have been derived from the seed planted in this experiment because the seeds were planted at specific positions which could be relocated with the use of a tape measure. Non-destructive measures of growth taken on each occasion were seedling height and leaf number. For seedlings that did not survive, it was assumed most either withered *in situ* when soil moisture was critically low or disappeared between sampling periods due to unknown causes.

4.2.4 Analysis

The effect of treatment on the proportion of individuals emerging was tested separately for Abu Madi and Weenen using an analysis of variance (Genstat 5 Committee 1987), and differences in means were illustrated graphically using least significant differences (p<0.05). At Abu Madi the effects of species, herbivory and competition were tested by general analysis of variance, whilst a split-plot analysis of variance was needed at Weenen to account for fire in addition to the abovementioned explanatory variables. The significance of all higher order interactions were tested. The assumption that seedlings were independent of each other seemed reasonable as each seedling was spaced no less than 1 m apart from another, and they had been randomly allocated to treatment..

At both locations the relationship between treatments in terms of survival over the growing season was investigated with the use of a generalized linear model (GLM). A logistic model (Genstat 5 Committee 1987) was used to describe the binomial data, which recorded the presence (1) or absence (0) of seedlings at each recording interval. Differences in the predicted number of seedlings surviving per treatment combination were illustrated graphically. Seedling survival at each recording stage was examined in terms of the proportion of seedlings that survived relative to the total number of seedlings that germinated, and survival and mortality of seedlings relative to the number surviving at each previous recording interval. The predicted number of seedlings surviving were appropriate for interpretation as summaries of the data rather than as forecasts of new observations and were viewed as such. Only the first cohort of seedlings that germinated were examined as subsequent seedling germination was too low for statistical analysis.

To account for random and fixed effects at Abu Madi and Weenen, a residual maximum likelihood (REML) analysis was undertaken to test for significant differences in the growth of seedlings over the growing season in terms of mean leaf number, seedling height and leaf-to-height ratios per treatment combination (Genstat 5 Committee 1987). Differences in the means of seedling growth in response to treatment over the growing season were illustrated by plotting their means and 95 % confidence limits, but only for treatment combinations that had large enough sample sizes.

4.3 Results

4.3.1 Seed viability

The percentage viability of seedlings differed very little from the percentage germination, and apart from *A. tortilis,* percentages were consistently above 80 % (Table 4.1). The best results for viability and germination were obtained for *A. karroo*, followed by *A. nilotica*, and *A. tortilis.* Seedling emergence in the field followed a similar pattern, albeit at much lower percentages (Figure 4.1).

Table 4.1 Percentage germination and viability of (a) *A. karroo* and *A. nilotica* seeds taken from Weenen Nature Reserve, and (b) *A. nilotica* and *A. tortilis* seeds taken from Abu Madi Game Ranch in 1997

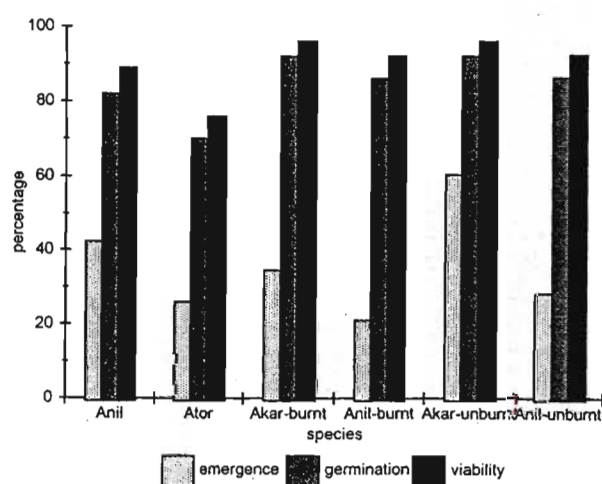| Species	Germination (%)	Viability (%)
(a)		
A. karroo	92	96
A. nilotica	86	92
(b)		
A. nilotica	82	89
A. tortilis	70	76

Figure 4.1 Laboratory germination and viability *versus* emergence in the field, for Abu Madi (first two sets of bars) and Weenen (last four sets of bars).

4.3.2 Abu Madi Game Ranch

4.3.2.1 Seedling emergence

Most (94.8 %) of the seedlings that emerged during the experimental period had emerged by the 13th day after planting, whilst a few had emerged by day 45, and none thereafter. Testing for differences among treatments was based on the total number of seedlings that emerged over the entire season (Table 4.2).

Both species and grass competition had a strong main effect on emergence, but the effect of one depended on the other (Table 4.3). Although emergence of *A. nilotica* and *A. tortilis* species was determined by their interaction with grass competition, in general fewer seedlings emerged when planted in the grass sward, highlighting the importance of grass competition as a main effect. *A. tortilis* seedlings showed significantly poorer emergence than *A. nilotica* seedlings when exposed to grass competition but not when in 'open areas'. The difference in emergence of species was reflected in the laboratory work, where *A. nilotica* seedlings were found to have better germination and viability than *A. tortilis* seedlings (Figure 4.1). Herbivory did not affect seedling emergence.

Table 4.2 The percentage, number, mean (number of seeds per treatment), and least significant differences (5% level) of means of *A. nilotica* and *A. tortilis* seedling emergence for all treatment combinations at Abu Madi Game Ranch

Treatment	A. nilotica				A. tortilis			
	%	number	mean	LSD	%	number	mean	LSD
open areas	49.5	99	12.4	3.535	40.0	80	10.0	3.535
grass areas	35.0	70	8.8	3.535	12.0	24	3.0	3.535
caged	48.5	97	12.1	3.535	26.0	52	6.5	3.535
uncaged	36.0	72	9.0	3.535	26.0	52	6.5	3.535
caged × open areas	55.0	55	13.8	4.999	42.0	42	10.5	4.999
caged × grass areas	42.0	42	10.5	4.999	10.0	10	2.5	4.999
uncaged × open areas	44.0	44	11.0	4.999	38.0	38	9.5	4.999
uncaged × grass areas	28.0	28	7.0	4.999	14.0	14	3.5	4.999

Table 4.3 ANOVA table of the number of *A. nilotica* and *A. tortilis* seedlings that emerged at Abu Madi Game Ranch

Source	Degrees of freedom	Pr>F
Species	1	<0.001
Herbivory	1	0.337
Competition	1	<0.001
Species × Herbivory	1	0.182
Species × Competition	1	0.012
Herbivory × Competition	1	0.900
Species × Herbivory × Competition	1	0.544
Residual	21	

4.3.2.2 Seedling survival

Considering the logistic model for seedling survival relative to the total number of seedlings that germinated, the addition of time, competition, herbivory, and species to the model significantly reduced the deviance of the model, accounting for 29.2 % of the deviance. The standard errors of the predictions were used to illustrate differences in the means of treatment combinations (Figure 4.2).

The estimated coefficients of the logistic regression model indicated that time was the overriding factor determining survival of seedlings, and treatment had a relatively small effect (Table 4.4). Furthermore, as shown by trends in survival (Figure 4.2), although seedling survival decreased with grass competition, *A. tortilis* seedlings, and herbivory (Table 4.4), their effect was strongest at the start of the experimental period (Figure 4.2). Time must be considered inadequate as an explanatory variate, as it may encompass many factors, such as rainfall. However, rainfall was unlikely to have played a role in seedling survival as it only became limiting towards the end of the season (Figure 3.3). Further investigation of factors resulting in seedling mortality is needed.

The logistic regression for age-specific mortality and survival produced a better regression, accounting for 87 % of the deviance in the model. The addition of time, competition, herbivory and species significantly reduced the deviance of the logistic model. Standard errors of the predictions were used to illustrate differences in the means of treatment combinations (Figure 4.3). The highest mortality/lowest survival occurred between day 13 and day 45, at the early stages of seedling development. Thereafter, seedling survival improved but seedling number continued to decline at a steady constant rate. The estimated coefficients of the logistic regression model for age-specific survival (Table 4.5) reflected

those for survival relative to the total number of seedlings that germinated. Treatment differences were maintained throughout the experimental period (Figure 4.3).

Although herbivory and a reduction of grass competition had no effect on seedling emergence, the exclusion of herbivores and grass competition significantly improved seedling survival, the greatest effect taking place within the first monitoring period after emergence (Figure 4.2, 4.3). Furthermore, grass competition exerted a greater effect on seedling mortality than herbivory. Although both species illustrated the same trend, *A. nilotica* exhibited better survival than *A. tortilis* across all treatments.

Acacia nilotica   *Acacia tortilis*
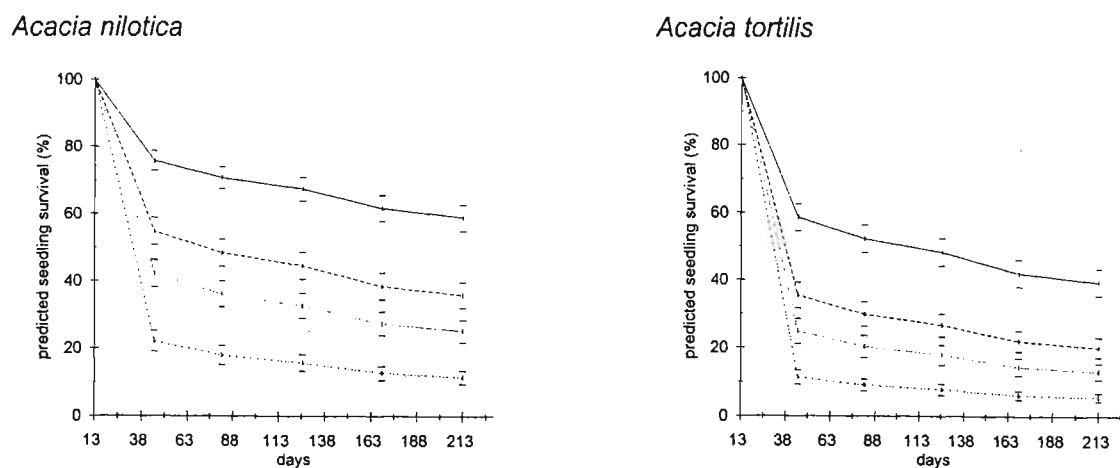
Figure 4.2 Differences in predicted survival of *A. nilotica* and *A. tortilis* seedlings at Abu Madi Game Ranch, in 'open areas' protected from herbivory (solid line) and not protected from herbivory (——), and in 'grass areas' protected from herbivory (···) and not protected from herbivory (—·—·), illustrating differences in treatment combinations (bars are standard errors)
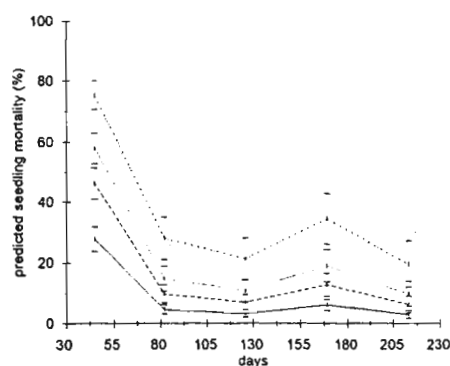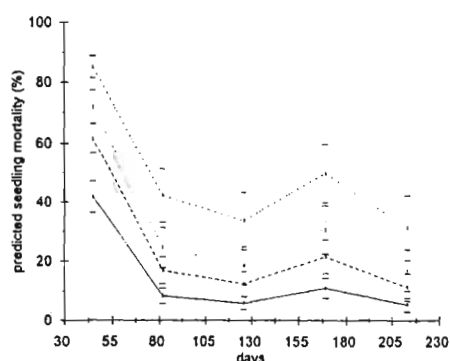
Table 4.4 Estimates of the parameters of the logistic regression model of seedling survival at Abu Madi Game Ranch

Treatment	estimate	se	t(*)	P
Constant	9.810	3.530	2.78	0.005
time 2	-9.610	3.530	-2.72	0.006
time 3	-9.870	3.530	-2.80	0.005
time 4	-10.030	3.530	-2.84	0.004
time 5	-10.280	3.530	-2.91	0.004
time 6	-10.400	3.530	-2.95	0.003
Grass competition (grass areas)	-1.453	0.140	-10.36	<0.001
No herbivory (caged seedlings)	0.945	0.123	7.66	<0.001
A. tortilis	-0.791	0.129	-6.13	<0.001

(a) *Acacia nilotica*
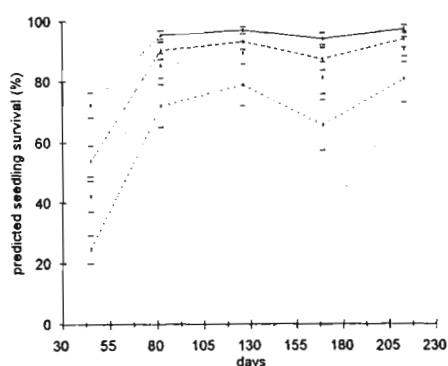
(b) *Acacia nilotica*

Acacia tortilis
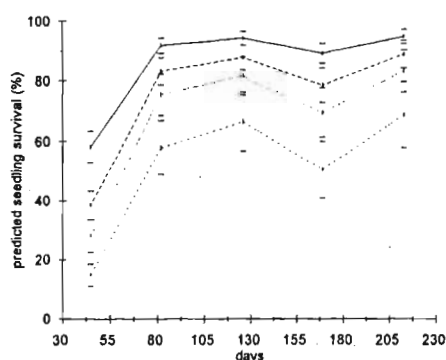
Acacia tortilis

Figure 4.3 Differences in predicted age-specific (a) survival and (b) mortality of *A. nilotica* and *A. tortilis* seedlings at Abu Madi Game Ranch, in 'open areas' protected from herbivory (solid line) and not protected from herbivory (———), and in 'grass areas' protected from herbivory (···) and not protected from herbivory (—·—·), illustrating differences in treatment combinations (bars are standard errors)

Table 4.5 Estimates of the parameters of the logistic regression model of age-specific seedling survival at Abu Madi Game Ranch

Treatment	estimate	se	t(*)	P
Constant	0.154	0.209	0.74	0.461
time 2	2.064	0.310	6.65	<0.001
time 3	2.430	0.376	6.47	<0.001
time 4	1.763	0.320	5.51	<0.001
time 5	2.532	0.447	5.67	<0.001
Grass competition (grass areas)	-1.275	0.228	-5.60	<0.001
No herbivory (caged seedlings)	0.804	0.207	3.89	<0.001
A. tortilis	-0.626	0.216	-2.90	0.004

4.3.2.3 Seedling growth

To examine differences in seedling growth, the mean response of seedlings to treatment combinations (only those that had large enough sample sizes; n>10) were plotted (Figure 4.4). As a result means of *A. tortilis* seedlings in grass areas could not be plotted.

Growth occurred only during the rainy season. Leaf number and seedling height increased to a maximum around 126 and 169 days after planting (Figure 4.4). Thereafter growth ceased abruptly, and a drastic decrease in leaf number and slight decrease in seedling height was witnessed.

Seedlings protected from herbivory had significantly more leaves and were taller throughout the experimental period in open areas (Table 4.6, Figure 4.4 a, b, f, g), but only after 82 days in grass areas (Figure 4.4 c, h).

Competition was clearly a factor that influenced the growth of seedlings negatively (Table 4.6), as seedlings in the open fared better than seedlings growing within a grass sward, in terms of leaf number (Figure 4.4 d, e), height (Figure 4.4 f, h) and leaf-to-height ratio (Figure 4.4 i, j). However, the interaction of herbivory and competition proved to be significant at the beginning of the growing season, as herbivory only had an effect on seedling growth in open areas (Figure 4.4 a, b, f, g, k) and not in grass areas (Figure 4.4 c, h, l) at these times. Herbivory significantly decreased both leaf number and height per seedling towards the later stages of the growing season in all areas.

A. nilotica had greater leaf numbers and seedling heights than *A. tortilis* over the experimental period (Figure 4.4 a to g), whilst the leaf-to-height ratio did not differ (Table 4.6). Seedlings of *A. nilotica* growing in open areas had significantly higher leaf-to-height ratios than seedlings growing in the grass sward (Figure 4.4 i & j). Although species were

shown to be significantly different in leaf number and seedling height, there were generally no differences between species in terms of leaf-to-height ratios. Both species were therefore considered together (Figure 4.4 k, l). Herbivory made a significant impact on the leaf-to-height ratio in the middle of the growing season. Seedlings exposed to herbivory had higher leaf-to-height ratios than those protected from herbivory, but only in the open areas (Figure 4.4 k) and not in the grass layer (Figure 4.4 l).

Table 4.6 REML analysis for the response of *A. nilotica* and *A. tortilis* seedlings at Abu Madi Game Ranch to herbivory and competition, in terms of (a) leaf number, (b) seedling height (cm) and (c) leaf-to-height ratio. Key to treatments: S = species, H = herbivory, C = competition

(a)

Time (days)	13		45		82		126		169		213	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
S	0.0	NS	19.4	<.001	12.3	<.001	7.2	<.01	15.6	<.001	4.5	<.05
H	0.4	NS	4.0	<.05	9.1	<.005	19.6	<.001	28.7	<.001	0.9	NS
C	13.2	<.001	0.2	NS	1.4	NS	0.9	NS	12.2	<.001	0.0	NS
H × C	0.0	NS	8.4	<.005	4.8	<.05	1.6	NS	0.6	NS	0.2	NS

(b)

Time (days)	13		45		82		126		169		213	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
S	15.0	<.001	2.3	NS	13.2	<.001	23.0	<.001	15.6	<.001	11.9	<.001
H	1.0	NS	1.6	NS	1.5	NS	10.1	<.01	28.7	<.001	5.8	<.025
C	4.6	<.05	16.9	<.001	23.9	<.001	33.9	<.001	12.2	<.001	5.4	<.025
H × C	0.6	NS	10.5	<.005	2.2	NS	1.4	NS	0.3	NS	0.1	NS

(c)

Time (days)	13		45		82		126		169		213	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
S	1.7	NS	6.5	<.025	0.7	NS	3.4	NS	1.3	NS	2.4	NS
H	0.0	NS	3.9	<.05	7.9	<.005	4.1	<.05	0.1	NS	0.7	NS
C	33.7	<.001	1.7	NS	13.9	<.001	18.9	<.001	8.8	<.005	4.3	<.05

Figure 4.4 Differences of means (± 95 % confidence limits) in: leaf number per plant between **a)** caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'open areas', **b)** caged (solid line) and uncaged (broken line) *A. tortilis* seedlings growing in 'open areas', **c)** caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'grass areas' **d)** caged *A. nilotica* seedlings growing in 'open areas (solid line) and caged *A. nilotica* seedlings growing in 'grass areas' (broken line), **e)** uncaged *A. nilotica* seedlings growing in 'open areas' (solid line) and uncaged *A. nilotica* seedlings growing in 'grass areas' (broken line); height per plant between **f)** caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'open areas', **g)** caged (solid line) and uncaged (broken line) *A. tortilis* seedlings growing in 'open areas', **h)** caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'grass areas'; leaf/height per plant between **i)** caged *A. nilotica* seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line), **j)** uncaged *A. nilotica* seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line), **k)** caged (solid line) and uncaged (broken line) *Acacia* spp. seedlings grouped in 'open areas', and **l)** caged (solid line) and uncaged (broken line) *Acacia* spp. seedlings grouped in 'grass areas'.

(a) Acacia nilotica in open areas
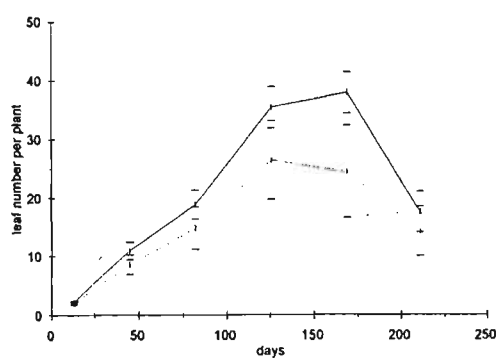
(b) Acacia tortilis in open areas
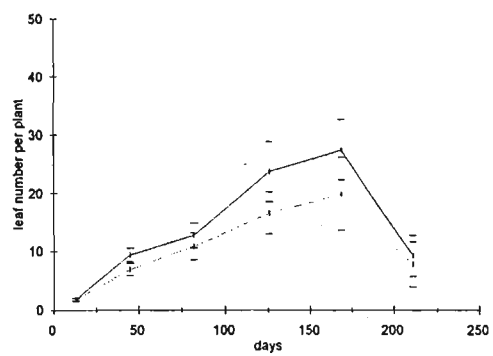
(c) Acacia nilotica in grass areas
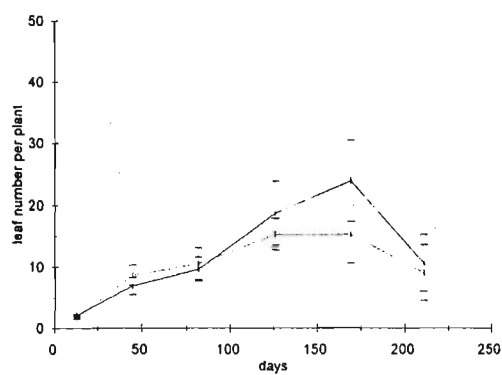
(d) Acacia nilotica in caged areas
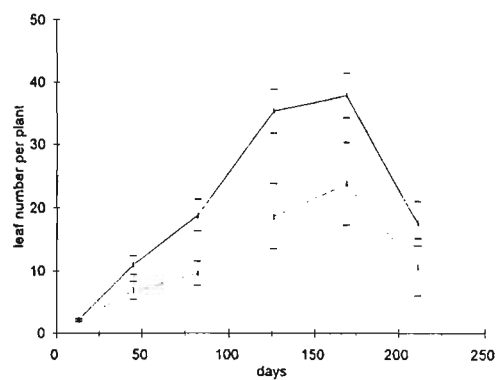
(e) Acacia nilotica in uncaged areas
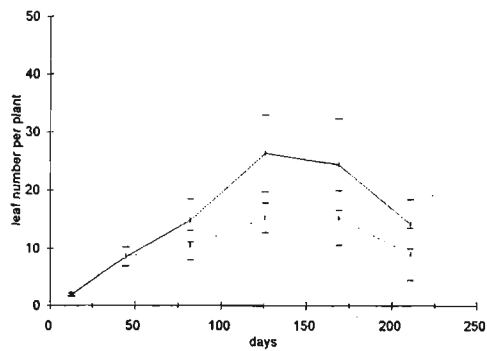
(f) Acacia nilotica in open areas
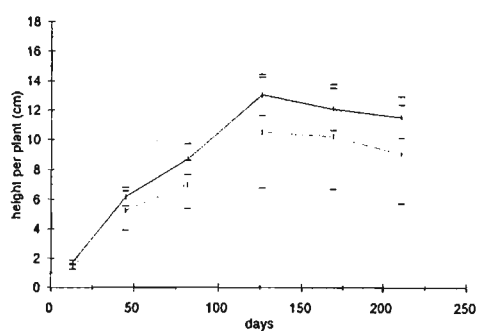
(g) Acacia tortilis in open areas
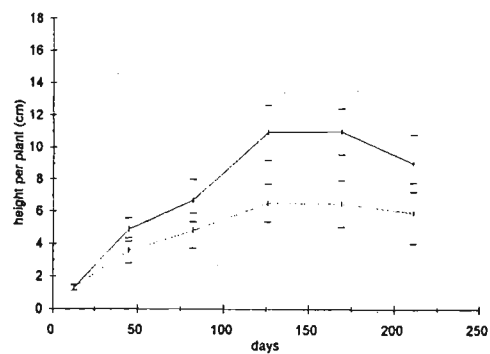
(h) Acacia nilotica in grass areas
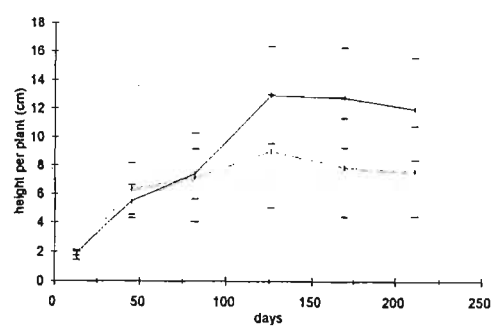
(i) Acacia nilotica in caged areas
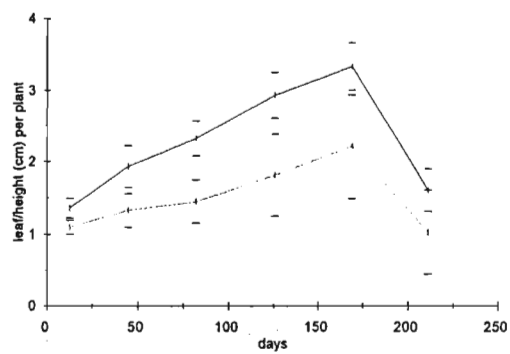
(j) Acacia nilotica in uncaged areas
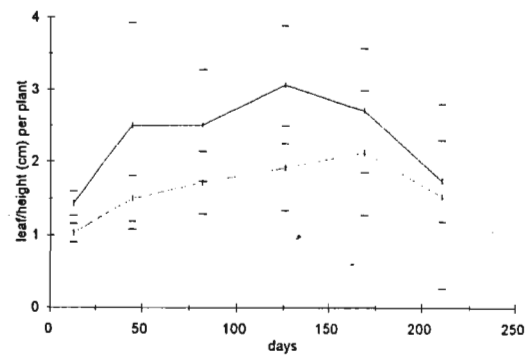
(k) Acacia spp. in open areas
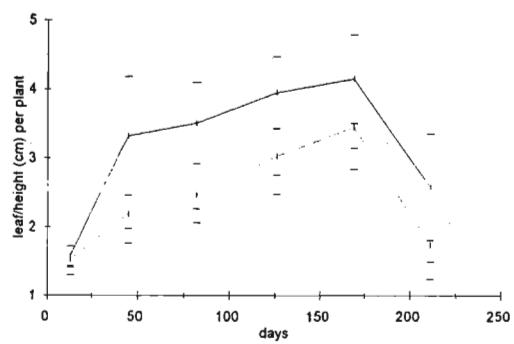
(l) Acacia spp. in grass areas
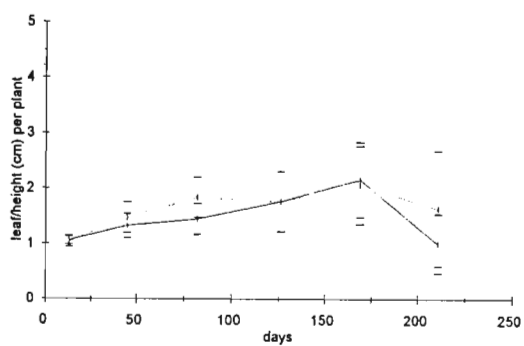
4.3.3 Weenen Nature Reserve

4.3.3.1 Seedling emergence

Most of the seedlings (95.6 %) that emerged during the experimental period had emerged by the 19th day after planting, whilst a few emerged by day 45, and even fewer thereafter. Testing for differences among treatments was based on the total number of seedlings that emerged over the entire season (Table 4.7).

Although species, grass competition and fire had strong main effects on emergence, their interaction was significant (Table 4.8). Whilst seedling emergence was greater in unburnt areas than in burnt areas, emergence within unburnt areas was greater in open areas than grass areas, whilst no significant difference was found between open and grass areas that were burnt. It appears that burning ameliorated the effect of the grass sward on emergence, resulting in similar emergence in open and grass areas that were burnt. The interaction of fire and species arises from fire having had a far more detrimental effect on *A. karroo* than on *A. nilotica*, although fire had a detrimental effect on both species. For both species, but especially for *A. karroo*, the direction of competition depended on whether it was burnt or unburnt. For both species in unburnt conditions, grass had an obvious negative effect, but the scale of this negative effect appeared to be greater for *A. karroo*. For burnt areas, seedling emergence did not differ significantly between open and grass areas for *A.* karroo and *A. nilotica.* These result suggest that competition had a stronger effect on *A. karroo.*

Emergence was greater for seeds not protected from herbivory, albeit at the 10 % level (P = 0.078). This finding is counter intuitive as cages were assumed to benefit seedling emergence, assuming similar environmental conditions in corresponding sites, as emerging seedlings would be afforded protection from herbivores if browsing impacted seedlings at this stage. What can be deduced is that herbivory did not negatively impact on seedling emergence.

Table 4.7 The percentage, number, mean number of seeds per treatment and least significant differences (5% level) of means of *A. karroo* and *A. nilotica* seedling emergence for all treatment combinations that emerged in (a) burnt and (b) unburnt areas at Weenen Nature Reserve

(a) burnt

Treatment	A. karroo				A. nilotica			
	%	number	mean	LSD	%	number	mean	LSD
species	34.5	138	8.63	2.085	21.0	84	5.25	2.085
open areas	28.5	57	7.12	2.752	23.0	46	5.32	2.752
grass areas	40.5	81	10.13	2.752	20.5	41	5.12	2.752
caged	31.0	62	7.75	2.752	20.0	40	5.00	2.752
uncaged	38.0	76	9.50	2.752	22.0	44	5.50	2.752
caged × open areas	27.0	27	6.75	3.855	23.0	23	5.75	3.855
caged × grass areas	35.0	35	8.75	3.855	17.0	17	4.25	3.855
uncaged × open areas	30.0	30	7.50	3.855	20.0	20	5.00	3.855
uncaged × grass areas	46.0	46	11.50	3.855	24.0	24	6.00	3.855

(a) unburnt

Treatment	A. karroo				A. nilotica			
	%	number	mean	LSD	%	number	mean	LSD
species	60.3	241	15.06	2.085	28.0	112	7.00	2.085
open areas	72.0	144	18.00	2.752	34.5	69	8.63	2.752
grass areas	48.5	97	12.13	2.752	21.5	43	5.37	2.752
caged	58.5	117	14.63	2.752	24.5	49	6.12	2.752
uncaged	62.2	124	15.50	2.752	31.5	63	7.87	2.752
caged × open areas	66.0	66	16.50	3.855	32.0	32	8.00	3.855
caged × grass areas	51.0	51	12.75	3.855	17.0	17	4.25	3.855
uncaged × open areas	78.0	78	19.50	3.855	37.0	37	9.25	3.855
uncaged × grass areas	46.0	46	11.50	3.855	26.0	26	6.50	3.855

Table 4.8 ANOVA table of the number of *A. karroo* and *A. nilotica* seedlings that emerged at Weenen Nature Reserve

Source	Degrees of freedom	Pr>F
Wholeplot - Fire	1	0.009
Species	1	<0.001
Herbivory	1	0.078
Competition	1	0.023
Species × Herbivory	1	0.890
Species × Competition	1	0.818
Herbivory × Competition	1	0.818
Fire × Species	1	0.001
Fire × Herbivory	1	0.890
Fire × Competition	1	<0.001
Fire × Species × Herbivory	1	0.435
Fire × Herbivory × Competition	1	0.158
Fire × Competition × Species	1	0.035
Competition × Herbivory × Species	1	0.299

4.3.3.2 Seedling survival

Considering the logistic model for seedling survival relative to the total number of seedlings that germinated, the addition of time, competition, herbivory, species and fire to the model significantly reduced the deviance of the model, but only accounted for 15.3 % of the deviance. The standard errors of the predictions were used to illustrate differences in the means of treatment combinations (Figure 4.5).

Seedling mortality was highest at the beginning of the growing season, within a few days following seedling emergence (Figure 4.5), and thereafter seedling survival stabilized and seedling numbers continued to decline at a constant rate in all treatments. Age-specific survival and mortality also illustrated this trend clearly (Figure 4.6).

The estimated coefficients of the logistic regression model indicated that time had the greatest effect on seedling survival, and treatment had a comparatively small effect (Table 4.9). Seedling survival was significantly higher in areas of reduced grass competition. The significantly lower seedling survival due to 'no burn' was expected, as a decrease in grass biomass due to burning was envisioned to benefit seedling survival. Herbivory did not affect seedling survival negatively, as unprotected seedlings survived better than protected seedlings. Whilst *A. nilotica* seedlings showed poorer seedling survival than *A. karroo*, both species demonstrated similar patterns in survival and mortality after day 45. *Acacia karroo* seedlings showed superior seedling survival to *A. nilotica* seedlings across all treatments.

Rainfall in December 1997 was well below average (Figure 3.5), but was only likely to have impacted seedling mortality after day 45 (6 December) (Figure 4.5). The likelihood that rainfall had a significant effect on woody seedling survival was considered small, especially as October, November, January and February had above-average rainfall.

The logistic regression for age-specific mortality and survival produced a better regression. The addition of time, competition, burning and species significantly improved the model for age-specific survival and mortality, accounting for 43.6 % of the deviance. Importantly, the inclusion of herbivory as a factor did not significantly improve the model, and therefore made no significant impact on age-specific seedling survival. Standard errors of the predictions were used to illustrate differences in the means of treatment combinations (Figure 4.6). The estimated coefficients of the logistic regression model (Table 4.10) confirmed that seedlings fared better in burnt areas and under reduced grass competition.

The most obvious feature of seedling survival was the relatively higher seedling mortality up to day 83 (Figure 4.6). Furthermore, although survival and mortality became constant following day 83, a significant difference between treatments was maintained

throughout the season. Burning exerted a greater effect on seedling mortality than grass competition.
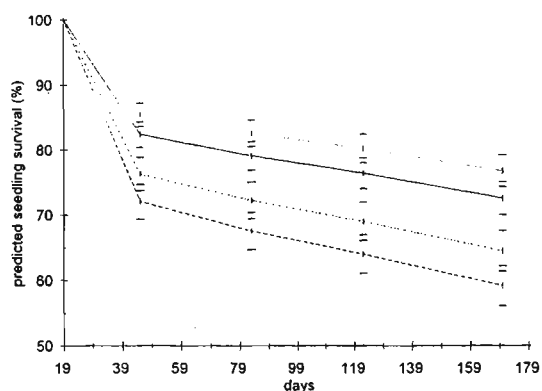
(a) *Acacia karroo burnt*
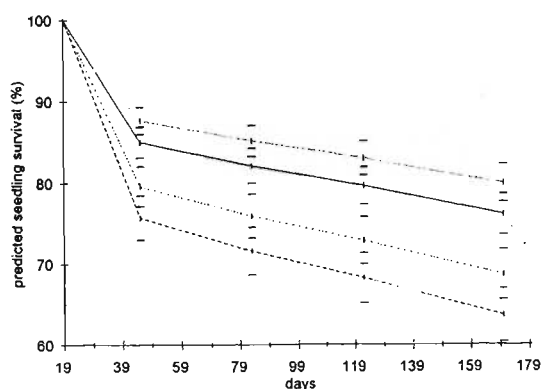
(a) *Acacia nilotica burnt*
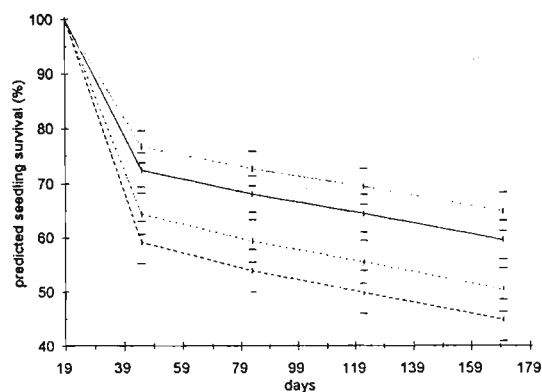
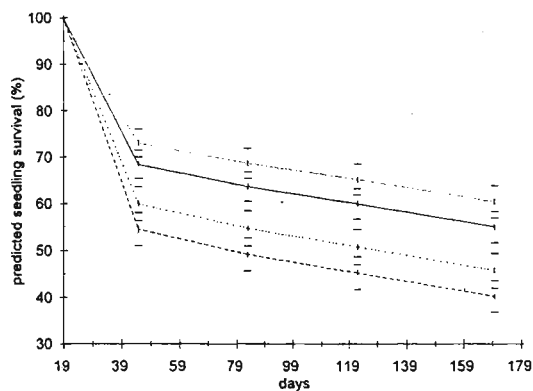(b) *Acacia karroo unburnt*

(b) *Acacia nilotica unburnt*

Figure 4.5 Differences in predicted survival of *A. karroo* and *A. nilotica* seedlings at Weenen Nature Reserve in (a) burnt and (b) unburnt areas, in 'grass areas' not protected from herbivory (solid line) and protected from herbivory (——), and in 'open areas' not protected from herbivory (···) and protected from herbivory (–·–·), illustrating differences in treatment combinations (bars are standard errors).
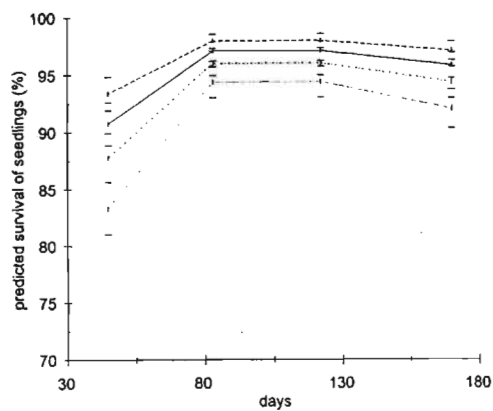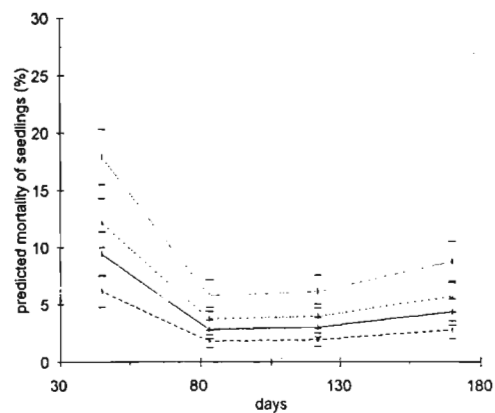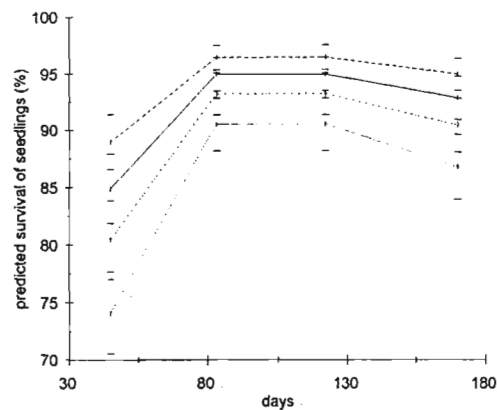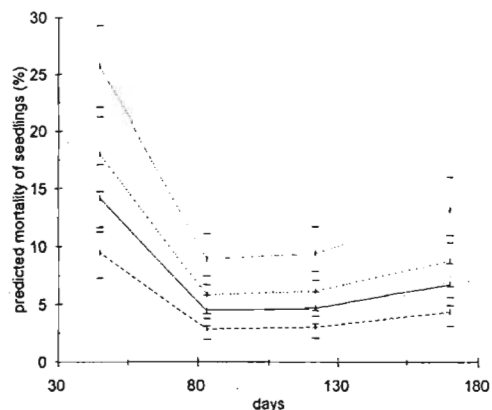
(a) *Acacia karroo*

(b) *Acacia karroo*

(a) *Acacia nilotica*

(b) *Acacia nilotica*

Figure 4.6 Differences in predicted age-specific (a) survival and (b) mortality of *A. karroo* and *A. nilotica* seedlings at Weenen Nature Reserve, in burnt areas of normal (solid line) and reduced (——) grass competition, and in unburnt areas of normal ($\cdots$) and reduced (—·—) grass competition, illustrating differences in treatment combinations (bars are standard errors).

Table 4.9 Estimates of the parameters of the logistic regression model of seedling survival at Weenen Nature Reserve

Treatment	estimate	se	t(*)	P
Constant	10.070	2.670	3.78	<0.001
time 2	-8.110	2.660	-3.04	0.002
time 3	-8.320	2.660	-3.12	0.002
time 4	-8.480	2.660	-3.18	0.001
time 5	-8.690	2.660	-3.26	0.001
unburnt	-0.190	0.106	-1.80	0.072
Normal grass competition	-0.223	0.102	-2.18	0.029
No herbivory (caged seedlings)	-0.597	0.100	-5.96	<0.001
A. nilotica	-0.770	0.104	-7.38	<0.001

Table 4.10 Estimates of the parameters of the logistic regression model of age-specific seedling survival at Weenen Nature Reserve

Treatment	estimate	se	t(*)	P
Constant	-1.522	0.164	-9.28	<0.001
time 3	-1.262	0.262	-4.81	<0.001
time 4	-1.206	0.262	-4.59	<0.001
time 5	-0.828	0.237	-3.49	<0.001
unburnt	-0.740	0.206	-3.59	<0.001
Normal grass competition	-0.456	0.190	-2.40	0.016
A. nilotica	0.460	0.185	2.49	0.013

4.3.3.3 Seedling growth

To examine differences in seedling growth, the mean response of seedlings to treatment combinations were plotted (Figure 4.7 & 4.8). The REML analysis (Table 4.11) showed that there were no significant differences between the growth of caged and uncaged seedlings throughout the experimental period in either burnt or unburnt areas (Figure 4.7). Herbivory did not therefore affect either seedling survival, or growth.

Growth only occurred during the rainy season, leaf number and seedling height increasing to a maximum around 122 days after planting. Thereafter a decrease in leaf number and seedling height was witnessed. Whilst *A. nilotica* grew taller and had more leaves than *A. karroo*, there was no difference in leaf-to-height ratio between the species (Table 4.11 c).

Whilst figure 4.7 could be examined to establish treatment differences, pooling of species allowed for clearer interpretation of treatment differences (Figure 4.8). Furthermore, the effect of treatment was not contingent upon species, and all three species responded

similarly to treatment. Seedling leaf number was promoted by a reduction in grass competition (Figure 4.8 a & b), whilst plant height was promoted by an increase in grass competition (Figure 4.8 c & d), and fire significantly increased seedling leaf number (Figure 4.8 g to j). Seedlings exhibited significantly greater leaf-to-height ratios per plant when growing in conditions of reduced grass competition (Figure 4.8 e & f), and in areas that were burnt before seedling emergence (Figure 4.8 k to n).

Table 4.11 REML analysis for the response of *A. nilotica* and *A. tortilis* seedlings at Weenen Nature Reserve to fire, herbivory and competition, in terms of (a) leaf number, (b) seedling height (cm) and (c) leaf-to-height ratio (leaf no/cm)

(a)

Time (days)	19		45		83		122		170	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
Fire	1.4	NS	2.8	NS	10.6	<.005	4.8	<.05	4.6	<.05
Species	23.8	<.001	24.3	<.001	89.1	<.001	94.7	<.001	24.7	<.001
Herbivory	0.0	NS	0.1	NS	1.4	NS	0.1	NS	0.4	NS
Competition	16.7	<.001	3.6	NS	16.2	<.001	16.3	<.001	2.5	NS

(b)

Time (days)	19		45		83		122		170	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
Fire	0.0	NS	17.0	<.001	0.0	NS	0.5	NS	0.4	NS
Species	19.2	<.001	27.5	<.001	68.1	<.001	154.9	<.001	99.4	<.001
Herbivory	0.0	NS	2.4	NS	4.9	<.05	0.9	NS	3.1	NS
Competition	59.0	<.001	32.0	<.001	7.0	<.01	17.8	<.001	6.6	<.025

(c)

Time (days)	19		45		83		122		170	
Term	Wald	P	Wald	P	Wald	P	Wald	P	Wald	P
Fire	9.9	<.01	0.1	NS	4.6	<.05	13.4	<.001	11.3	<.001
Species	1.7	NS	0.1	NS	2.9	NS	2.3	NS	1.2	NS
Herbivory	0.3	NS	2.8	NS	2.5	NS	3.7	NS	0.0	NS
Competition	20.8	<.001	5.0	<.05	43.0	<.001	87.4	<.001	38.4	<.001

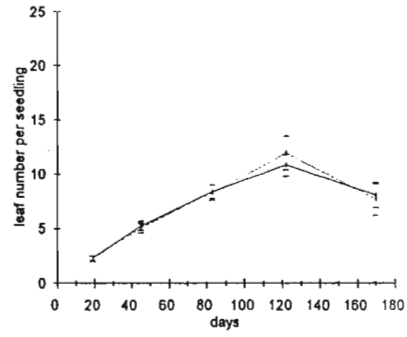**Figure 4.7** Differences of means (± 95 % confidence limits) at Weenen Nature Reserve in 1) burnt and 2) unburnt areas in: mean leaf number between a) caged (solid line) and uncaged (broken line) *A. karroo* seedlings growing in 'open areas', b) caged (solid line) and uncaged (broken line) *A. karroo* seedlings growing in 'grass areas', c) caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'open areas', d)caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'grass areas'; and mean height between e) caged (solid line) and uncaged (broken line) *A. karroo* seedlings growing in 'open areas', f) caged (solid line) and uncaged (broken line) *A. karroo* seedlings growing in 'grass areas', g) caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'open areas', h)caged (solid line) and uncaged (broken line) *A. nilotica* seedlings growing in 'grass areas'.

1(a) *Acacia karroo* in open areas
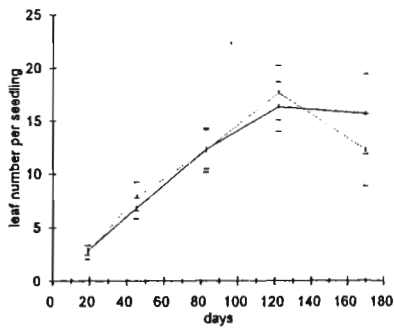
1(b) *Acacia karroo* in grass areas
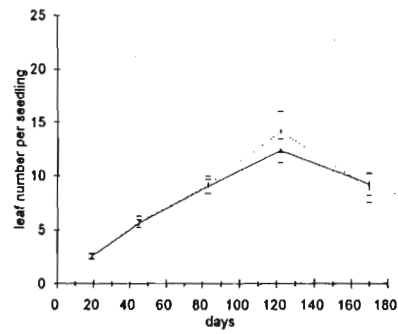
1(c) *Acacia nilotica* in open areas
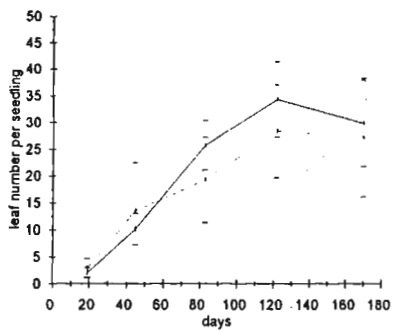
1(d) *Acacia nilotica* in grass areas
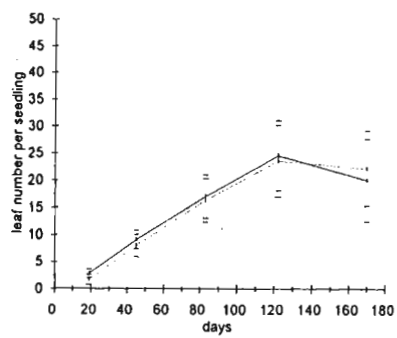
1(e) *Acacia karroo* in open areas
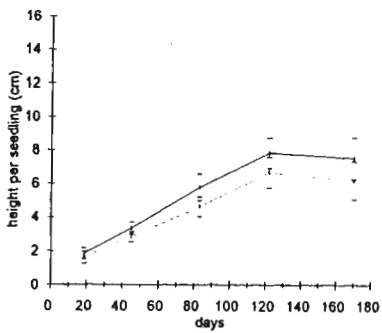
1(f) *Acacia karroo* in grass areas
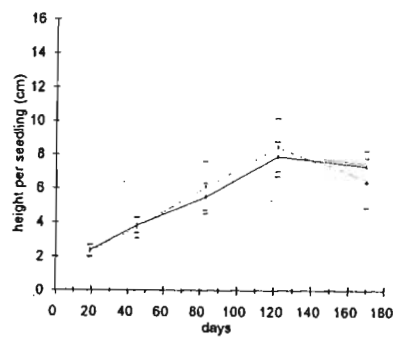
1(g) *Acacia nilotica* in open areas
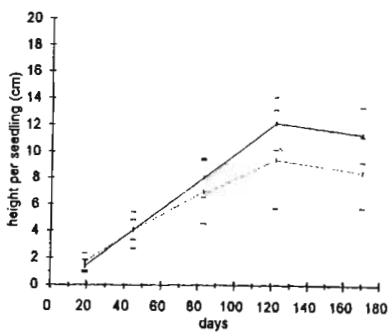
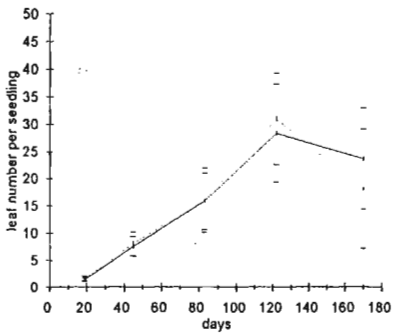1(h) *Acacia nilotica* in grass areas
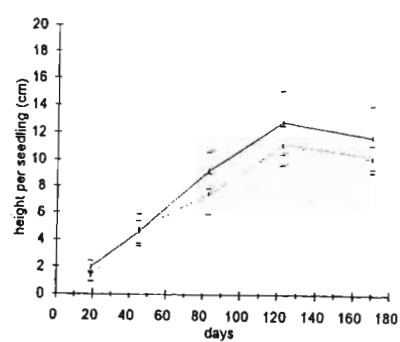
2(a)   *Acacia karroo*   in open areas
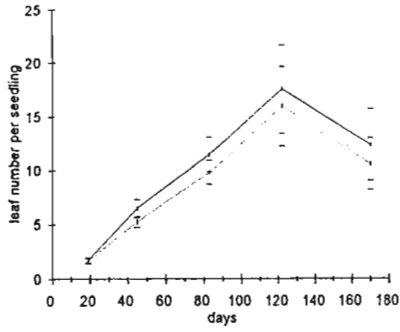
2(b)   *Acacia karroo*   in grass areas

2(c)   *Acacia nilotica*   in open areas

2(d)   *Acacia nilotica*   in grass areas

2(e)   *Acacia karroo*   in open areas

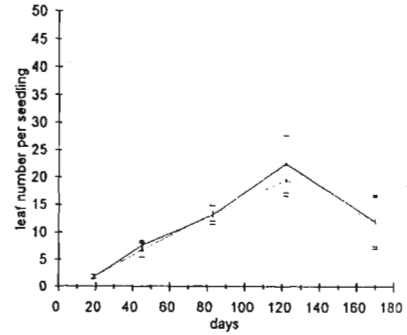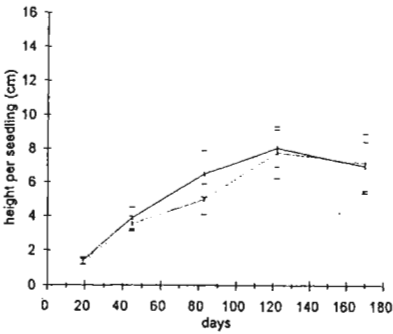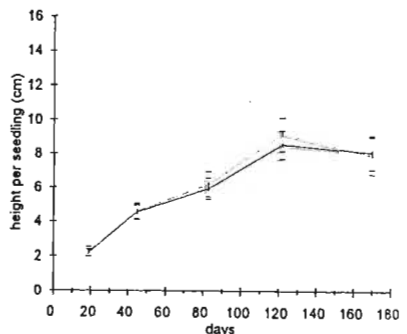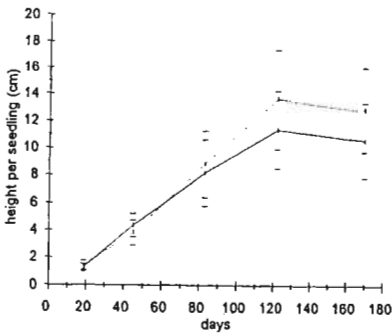2(f)   *Acacia karroo*   in grass areas

2(g)   *Acacia nilotica*   in open areas

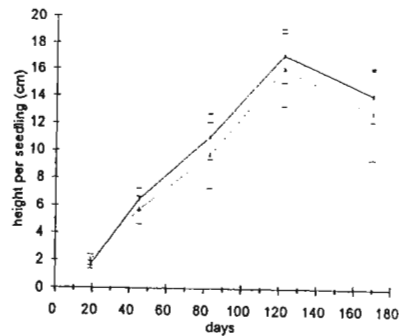2(h)   *Acacia nilotica*   in grass areas

Figure 4.8 Differences of means (± 95 % confidence limits) at Weenen Nature Reserve for all species pooled in: mean leaf number of a) caged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line), and b) uncaged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line); mean seedling height of c) caged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line), and d) uncaged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line); mean leaf-to-height ratios of e) caged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line), and f) uncaged seedlings growing in 'open areas' (solid line) and 'grass areas' (broken line); mean leaf number of g) caged seedlings in 'open areas' growing in burnt (solid line) and unburnt (broken line) areas, h) caged seedlings in 'grass areas' growing in burnt (solid line) and unburnt areas (broken line), i) uncaged seedlings in 'open areas' growing in burnt (solid line) and unburnt areas (broken line), j) uncaged seedlings in 'grass areas' growing in burnt (solid line) and unburnt areas (broken line); mean leaf-to-height ratios of k) caged seedlings in 'open areas' growing in burnt (solid line) and unburnt areas, l) caged seedlings in 'grass areas' growing in burnt (solid line) and unburnt areas (broken line), m) uncaged seedlings in 'open areas' growing in burnt (solid line) and unburnt areas (broken line), n) uncaged seedlings in 'grass areas' growing in burnt (solid line) and unburnt areas (broken line).

(a) caged seedlings
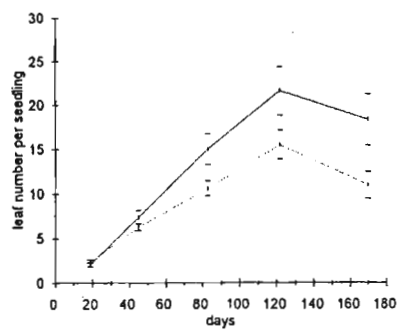
(b) uncaged seedlings
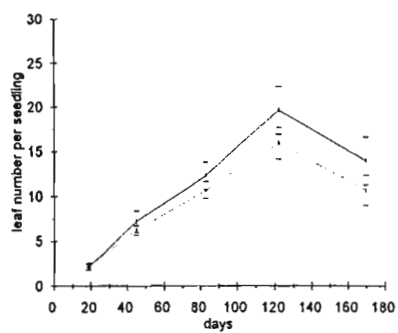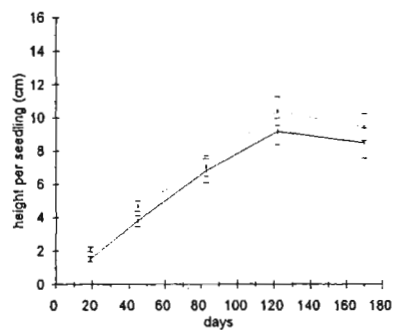
(c) caged seedlings
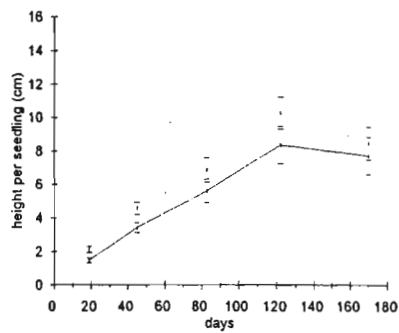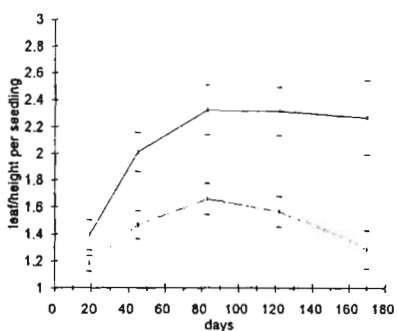
(d) uncaged seedlings

(e) caged seedlings
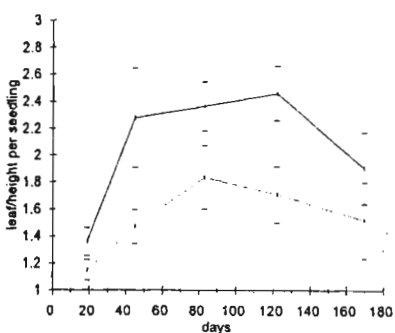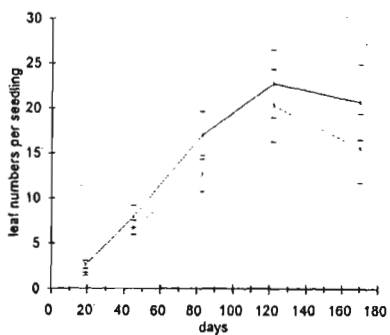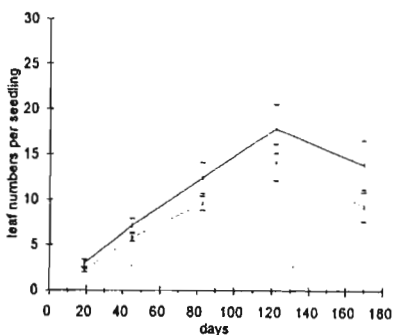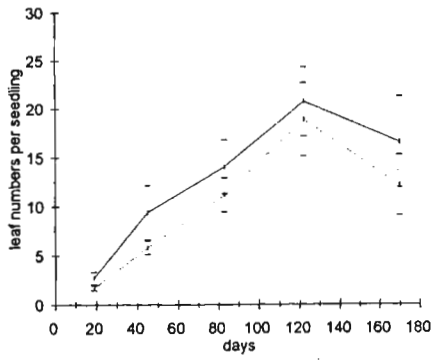
(f) uncaged seedlings
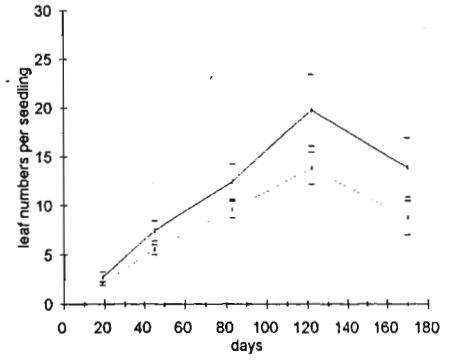
(g) caged seedlings in open areas

(h) caged seedlings in grass areas

(i) uncaged seedlings in open areas

(j) uncaged seedlings in grass areas

(k) caged seedlings in open areas
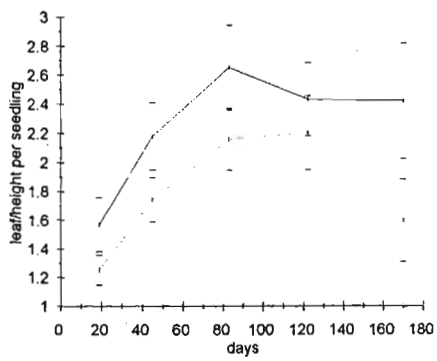
(l) caged seedlings in grass areas
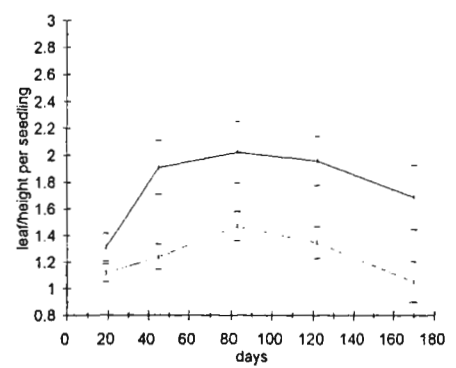
(m) uncaged seedlings in open areas
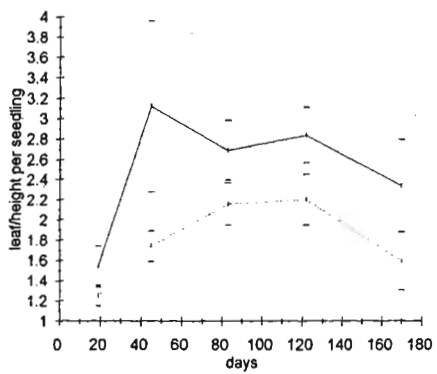
(n) uncaged seedlings in grass areas
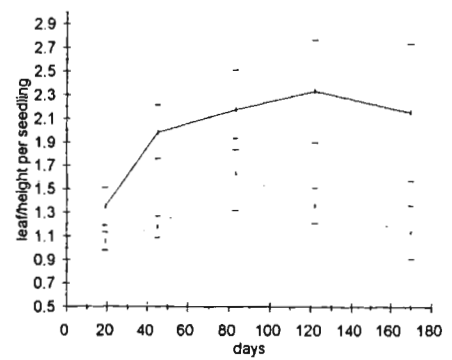
4.4 Discussion

4.4.1 General trends

Most of the seedlings that emerged over the entire season at Abu Madi and Weenen emerged soon after planting, within 13 and 19 days respectively. Most seeds therefore germinated immediately after imbibition in response to sufficient rainfall. Laboratory experiments showed that scarification by sulphuric acid was effective in releasing viable seeds from dormancy, and therefore differences in seedling emergence in the experiments could be viewed as consequences of prevailing conditions and treatments imposed. Species differences witnessed at seedling emergence conform to trends in seed viability and germination examined in the laboratory tests (Figure 4.1). *Acacia karroo* illustrated the greatest viability and germinability, followed by *A. nilotica* and lastly *A. tortilis*.

Generally, as seedling survival and growth are independent of seed viability, differences between species after emergence can be seen to relate to their success in the field. Seedling survival of *A. karroo* was greater than that of *A. nilotica* at Weenen, whilst the survival of *A. nilotica* was superior to that of *A. tortilis* at Abu Madi. These trends were reflected in the adult populations at Abu Madi (pers. observation) and at Weenen (Breebaart *et al.* 2001). The superior survival of *A. karroo* offers a reason for the documented success of this species as a woody encroacher in certain areas (Acocks 1953; Friedel 1987; O'Connor 1995).

A consistent finding with Weenen and Abu Madi was that highest seedling mortality occurred at the beginning of the season within 6 to 7 weeks of emergence, irrespective of treatment, becoming less thereafter and showing a slight increase at the end of the growing season. The initial decline in seedling numbers is not unexpected for natural populations where self-thinning is operating, but as these seedlings were planted at artificially low densities this was a surprising outcome. The level of recruitment of woody plants has been linked with rainfall patterns (Ernst 1988; Hodgkinson 1991; Cohn & Bradstock 2000), and sufficient water availability at the beginning of the growing season may be more important for seedling survival than water availability in later months (Cohn & Bradstock 2000). This was not considered the cause of mortality in these experiments as rainfall was above average at the beginning of the growing season. More intensive monitoring is necessary to discover which factors are responsible for initial mortality of seedlings. Seedling mortality at the end of the growing season was definitely related to water stress, as seedlings were wilting.

Acacia nilotica had greater leaf numbers, seedling heights and leaf-to-height ratios per seedling than *A. tortilis* and *A. karroo,* at Abu Madi and Weenen respectively. A consistent pattern of superior survival and growth was witnessed for species, and differences in survival could not be attributed to any specific treatment.

4.4.2 Effect of herbivory on seedling establishment

Whilst herbivory made no significant impact on seedling emergence at Abu Madi, herbivory appeared to decrease seedling emergence at Weenen, even though no signs of defoliation were found on seedlings during the entire experimental period. This may have been due to trampling, which can inflict mortality on perennial grass seedlings (Salihi & Norton 1987) and woody seedlings (Pitt *et al.* 1998). Furthermore, herds of large herbivores, such as those at Weenen, are expected to have a greater effect through trampling than small herbivores. Woody seedling emergence therefore does not appear to be affected by herbivory, at least not within 13 days since planting. Germinating seedlings had not risen much above the soil surface after this period, generally did not consist of more than the cotyledons and one or two leaves, and would therefore not have been easily visible to mammalian herbivores. The probability of seedlings being encountered by herbivores under these conditions was considered small.

If the critical period for survival after emergence is envisioned to extend past 13 days, the results may have been different considering that the effect of sheep grazing on woody seedlings was apparent by the 45th day since planting. In fact, the highest percentage mortality between recording intervals occurred within the first 45 days since planting. More intense monitoring is needed to establish at which stage herbivory makes an impact. As herbivory had no effect on seedling survival at Weenen, other factors are likely to have played a role in this mortality.

Seedling survival at Weenen did not follow expected trends as seedlings exposed to potential herbivory had lower mortalities than those protected from herbivory (Figure 4.5). Protection from herbivory should potentially be beneficial to survival, not detrimental, inferring that the cages protecting the seedlings were themselves exerting a negative effect on seedling survival. This was unlikely as the soil was not unduly disturbed whilst anchoring the cages over buried seeds. However, the abovementioned trends were for survival relative to the total number of seedlings that emerged, whilst herbivory did not significantly influence age-specific survival (Figure 4.6). The effect of herbivory on survival relative to the total number that germinated appears to have been a consequence of differences established during

emergence. The model on age-specific survival was considered a better model as it was independent of differences in emergence and it accounted for a far greater percentage of the variance. It was therefore concluded that herbivory did not negatively affect seedling survival at Weenen.

In contrast, seedling survival was adversely affected by herbivory at Abu Madi (Figure 4.2 & 4.3), to the greatest extent in the first few weeks following emergence, and to a lesser extent during the rest of the season. Seedlings were visibly affected by herbivory, as portions' of the seedlings, including stem material, were removed. Furthermore, on several occasions both nyala and impala were observed browsing seedlings at Abu Madi (personal observation). Woody seedlings can show resistance to herbivory already at early stages of development (Story 1952), and exhibit improved survival after two or so months (Seif El Din & Obeid 1971). As woody seedlings are more vulnerable to defoliation than older plants (Seif El Din & Obeid 1971; Sweet & Mphinyane 1986; Cooper & Owen-Smith 1986; Brown & Archer 1989), it is suggested that once a woody plant has attained a certain size, it is more tolerant of herbivory and thus has a greater chance of survival. Juvenile plants are capable of at least some recovery from dormant axillary buds in response to defoliation, whilst such recovery is very limited in young seedlings (Auld 1994). Protection from defoliation therefore afforded seedlings a window of opportunity during which to attain this critical size.

The postulation that the effect of herbivory on woody seedling growth would be determined by herbivore composition was upheld. A striking difference between Abu Madi and Weenen is the complement of herbivores stocked at either site. The dichotomy lies in that Abu Madi had a high concentration of small-mouthed herbivores, which browsed unprotected seedlings, whilst Weenen Nature Reserve did not (Table 3.1, 3.2). The large-bodied herbivore populations at Weenen made no significant impact on woody seedling growth (Figure 4.7) whilst the suite of small-bodied herbivores at Abu Madi made a negative impact (Figure 4.4). This is consistent with findings that a reduction in the population of small-mouthed browsers benefits woody seedling recruitment (Prins & Vander Jeugd 1993). Furthermore, herbivory did not affect seedlings at the emergence phase, and the impact of herbivory on seedling establishment in primarily a consequence of the effect of herbivory on seedling survival and growth. Although small-mouthed browsers can retard the establishment of juvenile woody plants (Belsky 1984), very few studies have focused on seedlings in their first year of growth, drawing no distinction between seedlings and juvenile plants. At the beginning of the growing season at Abu Madi, herbivory negatively affected seedling growth only in open areas, whereas at the end of the season, when conditions became more arid, herbivory also made an impact in grass areas. This suggests that during dry periods, when

other forage becomes scarce, vertebrate grazing on *Acacia* species seedlings will be higher, perhaps as herbivores must search further afield for suitable material. Furthermore, the dicotyledonous content in the diets of impala and nyala (large populations at Abu Madi, Table 3.1) varies seasonally, reaching a peak during the dry season (Van Rooyen 1992). This offers an explanation as to the defoliation of woody seedlings within the grass sward only at the dry end of the experimental period, when the quality of monocotyledons would have declined and browsers may have had to switch to more suitable forage.

At Abu Madi seedlings not protected from herbivory displayed greater leaf-to-height ratios than protected seedlings. This effect was however only seen in 'open areas', areas heavily utilized by nyala and impala populations, where seedlings were more likely to be encountered by herbivores, and consequently more likely to be selected. This suggests compensatory leaf growth in response to defoliaton of woody seedlings, which has been reported for older individuals (Teague & Walker 1988; Du Toit *et al.* 1990; Gowda 1997), but not for seedlings in their first growing season.

4.4.3 Effect of grass competition on seedling establishment

Species differences in emergence were apparent in their response to grass competition at both Abu Madi and Weenen. *Acacia tortilis* seedlings showed significantly poorer emergence than *A. nilotica* seedlings only when exposed to grass competition and not when in open areas, which may be related to the documented shade intolerance of *A. tortilis* (Smith & Goodman 1986; Smith & Shackleton 1988; Belsky 1994). Whilst *A. nilotica* has also been described as heliophytic (Smith & Goodman 1986) this study indicates a relative advantage of *A. nilotica* over *A. tortilis*. At Weenen the effect of competition on seedling emergence varied in relation to the interaction of species and fire. Grass had an obvious negative effect for both *A. karroo* and *A. nilotica* in unburned conditions, but the scale of this negative effect was greater for *A. karroo*. However, whilst *A. nilotica* had a relative advantage in grass competition, a greater total number of *A. karroo* seedlings emerged. Seedling emergence was similar in burnt areas regardless of grass competition, suggesting that burning may ameliorate conditions for seedling emergence. Most studies on the influence of grass competition on woody seedlings consider the effect of competition post-emergence. There is a dearth of knowledge on woody seedling dynamics at emergence, which must be addressed.

At Abu Madi and Weenen the survival and growth of seedlings over the growing season was lower for seedlings growing in normal grass competition (Figure 4.4 & 4.8), supporting the view that grass competition is detrimental to woody seedling establishment

(Schultz *et al.* 1955; Brown & Booysen 1967; Du Toit 1967; Bush & VanAuken 1995). Differences in seedling establishment due to the grass sward have been attributed to competition for light and moisture between the herbaceous vegetation and brush seedlings (Schultz *et al.* 1955). Whilst above-ground grass competition was eliminated at both Abu Madi and Weenen, the natural patch structure at Abu Madi allowed for planting of seeds in areas considered virtually devoid of below-ground competition, whilst the artificially modified conditions at Weenen would not have reduced below-ground competition comparably. Yet seedlings fared better in open areas at both Abu Madi and Weenen, suggesting that below-ground competition may not be the determining factor in seedling survival over this experimental period. However, this serves as a suggestion for further research, as no direct measures were taken of below-ground competition.

Seedlings planted in the grass sward at Abu Madi and Weenen were subject to above-ground competition by the grass sward, and to a small degree by tree canopies at Abu Madi. A number of studies have reported better seedling establishment as a result of increased irradiance, including studies of *A. tortilis* and *A. nilotica* (Walter 1971; Milton 1982; Knoop & Walker 1985; Smith and Goodman 1987; Smith and Shackleton 1988; Mwalyosi 1990). Whilst Brown & Archer (1989) have shown that only at very high levels of herbaceous litter is there a negative impact on emergence and establishment of woody species, this was very plausible as fire had been excluded for a period of at least four years at Abu Madi, and two years at Weenen. The effect of shade on seedlings was evident in greater etiolation exhibited by seedlings growing in the grass sward at Abu Madi and Weenen seedlings, having a lower leaf-to-height ratio than seedlings growing in the open. At Weenen a difference in leaf-to-height ratio was further expressed between burnt and unburnt areas, suggesting that the temporary removal of the grass cover resulted in increased irradiance, which elicited a higher leaf-to-height ratio on burnt than on unburnt areas.

Grass competition affected seedling establishment throughout the growing season. Mortality was higher, and growth poorer, for seedlings exposed to grass competition from emergence through to the end of the growing season.

4.4.4 Effect of fire on seedling establishment

It was hypothesized that fire, by destroying most of the above-ground grass biomass, can temporarily reduce the effect of the herbaceous sward on woody seedlings, thereby improving their emergence and survival. Whilst seedling emergence on unburnt areas was significantly

greater in open areas, it was not on burnt areas, suggesting that fire in some way negated the poorer emergence of seedlings in the grass sward.

Whilst fire appeared to improve conditions for seedlings emerging in the grass sward relative to seedlings in the open, overall emergence was nevertheless lower in burnt than unburnt areas (Table 4.7). As seeds were shown to germinate in response to sufficient moisture in the laboratory experiments, differences in emergence may be determined by water. Burnt areas have been reported to have lower soil moisture than unburnt areas (Anderson 1965), which can be attributed to significant increases in soil temperature (Savage & Vermeulen 1983, Heady & Child 1994) after burning. The soil water status in burnt areas may also be less favourable for plant growth than in unburnt areas and is subject to wider fluctuations (Cass *et al.* 1984). Other possible factors, such as above-ground competition for light and nutrient availability, were unlikely to influence the emergence stage in burnt areas. Seedlings have been shown to be fully dependent on cotyledons for nearly all of their nutrient requirements during the first weeks after germination (Ernst 1988), and nutrient availability has rarely been found to increase the survival of *Acacia* species (Cohn *et al.* 1989; Brown *et al.* 1998). Furthermore, fire can increase nutrient availability in the short term (Heady & Child 1994, Ojima *et al.* 1994; Monleon *et al.* 1997).

However, seedling survival and growth were better in burnt areas (Table 4.10, Figure 4.7). As grass biomass is lower after burning (Grossman *et al.* 1981), woody seedlings may have benefitted from less grass competition for below-ground resources, and competition for light (Van Auken & Bush 1991). The latter was witnessed in a greater leaf-to-height ratio of seedlings growing on burnt areas as opposed to unburnt areas (Figure 4.7).

The interactive effect of fire and the grass sward on woody seedling emergence merits further investigation to determine which factors result in lower emergence at this stage, especially as the survival and growth of seedlings that emerged on burnt areas was superior to that of seedlings on unburnt areas.

4.4.5 The relationship of herbivory, grass competition and fire

The dominant influence on seedling establishment at Weenen was burning. Burning interacted with grass competition to determine patterns of seedling emergence, and had a greater influence than grass competition on seedling survival. Both grass competition and burning influenced seedlings growth. Although the beneficial effect of burning in reducing

above-ground grass biomass is recognised, burning appears to have contributed to seedling success by other means also. This was recognised in that seedlings in the open in burnt areas fared better than seedlings in the open in unburnt areas.

The influence of grass competition on seedling establishment was greater than that of herbivory at Abu Madi. Firstly, grass competition influenced seedling emergence, whilst herbivory did not. Secondly, although seedlings in open patches were more visible and more accessible to herbivores than seedlings in the grass layer, survival was better in open patches, irrespective of protection from herbivory. Unprotected seedlings in the open fared better than protected seedlings in the grass layer. Furthermore, although both herbivory and grass competition negatively influenced the growth of seedlings, the affect of herbivory in the grass layer only became apparent later in the growing season.

4.4.6 Management implications

As herbivory by small mammals was shown to retard the growth and survival of *Acacia* seedlings, whilst large herbivores did not, an increase in woody plant density is predicted at Weenen because of the absence of small herbivores. Woody seedlings are also expected to fare better in conditions of reduced grass competition. In this regard the application of periodic fires appears to have improved conditions for seedling survival and growth. However, the negative impact of fire on established seedlings is well documented in the literature, and fire therefore does not necessarily result in an increase in woody seedling density. In the light of consistently better seedling survival and growth in areas of reduced grass biomass, the direct impact of the removal of the grass layer by fire on seedling emergence merits more attention.

In the event of a major decrease in numbers of small-bodied herbivores at Abu Madi, successful recruitment of woody seedlings is predicted in bare patches. As herbivory was concentrated mostly on seedlings in bare patches, where seedlings displayed better survival and growth than in the grass areas, it is anticipated that seedlings establishing within bare patches would show markedly improved growth in response to a release from herbivore pressure. A change in character of the savanna would be anticipated, with a gradual increase in the density of woody plants and the elimination of the current patch structure.

CHAPTER 5

THE EFFECT OF LIVESTOCK TYPE AND GRAZING SYSTEM ON THE ESTABLISHMENT OF *ACACIA KARROO*, *ACACIA NILOTICA* AND *ACACIA SIEBERIANA* SEEDLINGS

5.1 Introduction

An analogy to the removal of small-mouthed herbivores from wildlife systems, and the subsequent dominance of large-mammals in savannas, is found in domestic systems where there has been a shift of production systems from sheep or cattle and sheep together to cattle only. The mixed system incorporates small- and large-mouthed herbivores whilst the latter involves only a large-mouthed grazer. The loss of the small-mouthed herbivore component in a domestic system could possibly promote the recruitment of woody individuals in a savanna system, as has been show under natural conditions (Prins & Van der Jeugd 1993). It is with this in mind that domestic systems were investigated by looking at the effect of sheep and cattle on woody seedling recruitment after fire.

The ingestive behaviour of cattle and sheep is important for their potential impact on woody seedling recruitment. Cattle and sheep engender and maintain distinct patterns of height variation within grass swards through selective grazing (Hardy 1995; Morris *et al.* 1999), the height of tall areas of the sward increasing over time as grazing becomes increasingly concentrated on the short patches (Morris *et al.* 1999). The higher relative energy demand of sheep (Mentis 1981) requires that sheep graze more selectively than cattle. Since cattle and sheep have different grazing habits and forage requirements (Nolan & Conolly 1977), they are expected to impact differently on sward structure. Importantly, although both cattle and sheep form patches, sheep graze patches very severely at low and high stocking rates, whilst cattle at high stocking rates increase the size of patches (Morris *et al.* 1999). This suggests that under extremely high stocking rates the formation of 'grazing lawns' may be possible where all grass species, including the less palatable species, are consumed.

The increase of woody vegetation in semi-arid ecosystems is largely attributed to reduced grass competition because of over-utilization by grazers (Skarpe 1990). The removal of the grass layer by grazing may improve conditions for the establishment of woody seedlings, which benefit from an increase in the availability of soil water (McNaughton *et al.* 1983) and a decrease in grass competition (Knoop & Walker 1985; Cohn *et al.* 1989; Bush &

Van Auken 1990; Bush & VanAuken 1995). Sustained heavy grazing of grasses can reduce their above- and below-ground biomass, and resource use (Ellison 1960; Holland & Detling 1990), which may promote the establishment of woody seedlings because of increased irradiance at ground level and increased availability of below-ground resources (Caldwell *et al.* 1987). Therefore, intensive utilization of the vegetation within these patches, low utilization outside of these patches, and related reductions in grass competition, may significantly influence woody seedling recruitment. Furthermore, the positive effects of a reduction in grass competition may be modified by increased pressure by livestock, due to trampling and browsing pressure on woody seedlings, either by direct selection by sheep, or by incidental grazing by cattle. These effects are likely to increase with an increase in stocking pressure, as has been shown with trampling by cattle (Pitt *et al.* 1998). Consequently, woody seedlings may have an opportunity to escape defoliation outside of these patches but not within, whilst woody seedlings inside these patches may benefit from reduced grass competition.

Another change in domestic systems has been from continuous to rotational grazing systems. As woody plants are most vulnerable to defoliation in the first few weeks following germination (Story 1952; Seif El Din & Obeid 1971), it may be possible that a seedling is afforded sufficient time to attain a size which renders it tolerant of at least one defoliation in the case of a rotational grazing system, if the rotation (defoliation absent) is in synchrony with its emergence. Under continuous grazing, the probability of a seedling being missed before it has attained sufficient size may be low if the stocking rate is sufficiently high to force cattle and sheep to graze all the available herbage.

An experiment was designed to test (a) cattle versus sheep, and (b) continuous versus rotational grazing, to examine the beliefs for the eastern seaboard of South Africa that the change from sheep plus cattle to cattle only production systems, and the change from continuous to rotational grazing systems, has promoted the recruitment of *A. karroo, A. nilotica* and *A. sieberiana* seedlings. Furthermore, the study aimed to describe and relate the influence of grass sward structure, as modified by livestock type and grazing system, on woody seedling establishment. It was expected that sheep grazing and continuous grazing systems would negatively impact on woody seedling emergence, survival and growth. Furthermore, it was expected that sheep and continuous grazing systems would promote the formation of a heterogenous grass sward to a greater degree than cattle and rotational grazing systems, and that heterogenous grass swards would be advantageous for woody seedlings. Finally, it was expected that woody seedlings would perform better under conditions of grass

defoliation. Therefore, it was impossible to give a clear prediction of the overall outcome as both negative and positive effects were expected due to sheep and continuous grazing.

5.2 Materials and Methods

5.2.1 Preliminary study - 1996

An experiment, consisting of 8 paddocks, was conducted from September 1996 until July 1998. There were two fenced paddocks per treatment of the following four treatments: (1) paddock 1 (0.5800 ha) and 4 (0.7860 ha) for cattle rotational grazing, (2) paddock 2 (0.6545 ha) and 3 (0.8355 ha) for cattle continuous grazing, (3) paddock 6 (0.7308 ha) and 7 (0.7824 ha) for sheep rotational grazing, and (4) paddock 5 (0.7790 ha) and 8 (0.7700 ha) for sheep continuous grazing. There was insufficient infrastructure for a cattle plus sheep treatment. One weaner was placed in each of the cattle paddocks, 2 sheep were placed in each of the rotational grazing paddocks, and one sheep in each of the continuous grazing paddocks. The stocking rates and pattern of grazing for each paddock are illustrated in Appendix 1.

Acacia karroo, A. sieberiana and *A. nilotica* seeds were planted in mid-September 1996 (before the first rains) every 0.5 m between two marked points on opposite sides of the paddock such that the seedlings could be relocated using a tape measure. The number of seeds planted were 520, 680, 690, 520, 600, 660, 600 and 516 seeds in paddocks 1 to 8 respectively. The seeds were first scarified in boiling water, and planted randomly at 0.5m intervals in between grass tussocks at a depth of about 2 cm below the soil surface to ensure good contact between the soil and the seed testa (Brown & Booysen 1967).

Seedlings were monitored in October 1996, May 1997, October 1997 and July 1998. Seedling height and the number of leaves per seedling were measured, and it was recorded whether or not defoliation had occurred.

5.2.2 Experimental study - 1997

The above experiment was repeated after these paddocks were burnt in August 1997, in order to monitor seedling recruitment throughout the 1998 growing season. The fuel load was estimated using a disc pasture meter (Appendix 2). The paddocks were allocated treatments randomly in 1997. The stocking rates in 1996 were too low to significantly impact the vegetation, and consequently stocking rates were increased in 1997 (Appendix 1), assuming that this would increase the probability that differences in treatment type would be expressed

in the response of the woody and the herbaceous components. Two weaners were placed in each of the cattle paddocks, and 6 sheep were placed in each of the sheep paddocks. After 4th December 1997 sheep were lost due to a roundworm outbreak; consequently there was 1 sheep less per paddock except for paddock 1, where there were two sheep less. Cattle number also declined in paddock 8 on 20th December 1997 due to stock theft. As a result the stocking rate changed during the course of the season (Appendix 1). It was endeavoured to keep the livestock in the paddocks for as long as possible. However, there were periods when the cattle and/or sheep had to be removed from the paddocks due to a lack of forage.

The seeds were planted on the 22 September 1997 after rainfall (8.5 mm) a day after the livestock were put into the paddocks. Seeds were planted systematically between markers for purposes of identification (*A. karroo*, *A. nilotica*, and *A. sieberiana* - 0.5, 1.0, 1.5 and so on respectively).

5.2.3 Seed preparation

A different method of seed scarification was used owing to the low germination of seeds scarified in boiling water the previous season (1996). *Acacia karroo* was soaked in 1 M sulphuric acid for 45 minutes, whilst *A. nilotica* and *A. sieberiana* were soaked for 60 minutes to make the seed coat water-permeable (Brown & Booysen 1967, 1969), and then washed and allowed to dry at room temperature. The effectiveness of scarification by acid was tested in the laboratory. Seeds were scarified and planted in pots. Seedling germination was recorded, and seedlings not germinating within 21 days of planting were tested for viability using tetrazolium chloride.

5.2.4 Monitoring of seedlings

Emergence (first recorded 14 days after planting), defined as the appearance of cotyledons above ground, and survival and growth of seedlings through to the end of the growing season were monitored from the 1st October to the 30th April (14, 54, 97, 129, 180 and 225 days), measuring leaf number and plant height.

5.2.5 Veld Condition

At the end of the growing season treatment differences in the compressed sward height of grass was measured using a disc pasture meter (Bransby & Tainton 1977) for the purpose of estimating herbage mass accumulation (Appendix 2) and sward structure. Species composition and structure were determined by distance to, and the height of, the grass species nearest to a woody seedling surviving by the 225th day (78, 174, 173, 112, 118, 160, 75, 66 points for paddocks 1 to 8 respectively). Furthermore, grass cover was ranked in a 0.5 m diameter around each woody seedling using Walker's scale (1976). Compositional difference among paddocks were examined with correspondence analysis (CA) using the CANOCO package (Ter Braak & Smilauer 1998) in order to establish paddock similarity.

5.2.6 Analysis

Comparisons of the proportion of individuals emerging in a treatment were conducted using an analysis of variance (Genstat 5 Committee 1987), looking at the effects of *Acacia* species, livestock type, and grazing system, and differences in means were illustrated graphically using least significant differences ($p < 0.05$). Seedling emergence was tested for seedlings that had emerged by the 14th day since planting, and for the total number that emerged over the entire season.

The relationship between treatment and seedling survival or mortality over the growing season was investigated with the use of a generalized linear model (GLM), and a logistic model (Genstat 5 Committee 1987) was used to describe the binomial data, which recorded the presence (1) or absence (0) of seedlings at each recording interval. Seedling survival was tested for the seedling cohort that had emerged by the 14th day after planting, and the total number of seedlings that emerged over the growing season. The survival of the 14th day cohort of seedlings was examined in two ways; firstly, by testing the survival of seedlings at each recording interval relative to the original number of seedlings that emerged in that cohort, and secondly, by examining survival and mortality between recording intervals. The survival of the total number of seedlings that emerged over the entire season was tested relative to the survival at the end of the season. The standard errors of the predictions were used to illustrate differences in treatment combinations in terms of survival.

A residual maximum likelihood (REML) analysis was undertaken to test for significant differences in the growth of seedlings over the growing season in terms of mean leaf number, seedling height and leaf-to-height ratios per treatment combination (Genstat 5

Committee 1987). Differences in the means of seedling growth in response to treatment over the growing season were illustrated by plotting their means and 95 % confidence limits.

Sward composition (relative abundance and presence/absence) was compared among paddocks, which would indicate how similar paddocks were (which was important in assuming seedling responses to be the result of treatment and not paddock characteristics), and secondly, changes in the sward structure, which would have arisen as a consequence of treatment type. The latter was deemed important as it offered an opportunity to relate changes in veld condition, which were the result of differences in livestock type and grazing system, to differences in seedling growth and survival. The grass sward was examined on paddock scale, and at a seedling scale (to test for direct links between the grass sward and seedling survival and growth).

Simple sward parameters, such as mean sward height, are insufficient for the description of complex sward structures unless complemented by measures of structural variation. Further, because sward height data are often not normally distributed, statistics such as the mean and standard deviation give unrealistic impressions of the sward. An algorithm (Morris *et al.* 1999) was therefore applied to the compressed sward heights at Ukulinga in order to identify the 'short' and 'tall' patches in the paddocks, and to describe the variation of heights within each patch type and their relative proportions in the sward. This analysis gives an indication of the homogeneity of the grass sward. As the variation in height in all paddocks was bimodally distributed, the means of the short and tall components could be tested for by analysis of variance. The proportion of tall and short grass components in each paddock was tested by analysis of variance. Common height categories had to be chosen, so that comparisons could be made across treatments. The categories chosen were: 1 - 10 cm, 11 - 30 cm, and 31 cm.

Disc pasture readings were carried out on the grass component immediately adjacent to each seedling surviving at the end of the experimental period. Differences among treatments in the mean distance to the nearest grass plant and the height of this grass plant were analysed by an ANOVA, and differences among paddocks were illustrated using 95 % confidence limits. The relationship of compressed sward height adjacent to a seedling, mean distance to the nearest grass plant, and height of this grass plant, to woody seedling growth was tested for by regression analysis.

5.3 Results

The 1996 study offered very little data as seedling germination was too poor to analyze statistically. Therefore, only the results from the 1997 study were analyzed.

5.3.1 Laboratory work

Differences between species in terms of seed viability were reflected in germination results (Table 5.1). All three species had fairly high germination success, whilst the best results were obtained for *A. karroo*, followed by *A. nilotica*, with *A. sieberiana* showing the poorest viability and germination. Seedling emergence in the field observed a similar pattern, albeit at much lower percentages (Figure 5.1).

Table 5.1 Percentage germination and viability of scarified *A. karroo*, *A. nilotica* and *A. sieberiana* seeds taken from Ukulinga Research Farm in 1997

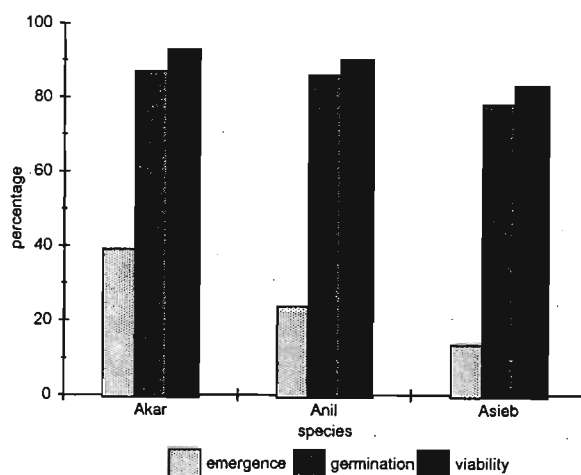| Species	Germination (%)	Viability (%)
A. karroo	87	93
A. nilotica	86	90
A. sieberiana	78	83

Figure 5.1 Laboratory germination and viability *versus* emergence in the field for seeds collected at Ukulinga Research Farm.

5.3.2 Seedling emergence

Most (80.2 %) of the seedlings had emerged by the 14th day after planting, whilst an additional 17.1 % and 2.7 % had emerged by day 54 and 97, respectively. Emergence patterns were similar for seedlings that had emerged by the 14th day since planting, and for the total number that emerged over the entire season.

Considering each *Acacia* species independently, there were no differences solely due to animal type, whilst the impact of grazing system on seedling emergence was subject to livestock type (Table 5.2). Seedling emergence was consistently greater for cattle in rotational systems, and for sheep in continuous systems. (Table 5.3 & 5.4). However, the difference between the aforementioned was the greatest for *A. karroo*. *Acacia karroo* nevertheless had significantly greater emergence than *A. sieberiana* across all treatment combinations, and *A. nilotica* in cattle rotational and sheep continuous paddocks.

Whilst complex interactions appear to exist, a few general trends can be extracted. A significantly greater proportion of *A. karroo* than *A. nilotica* seedlings emerged, whilst the latter exhibited significantly higher emergence than *A. sieberiana* (Table 5.3 & 5.4). As defoliation of woody seedlings was not noted at this stage, the emergence patterns were not likely to reflect selection of woody species by herbivores. Indirect effects were more likely to have been responsible for differences among treatments. The differences in emergence found between species mirrored the laboratory findings.

Table 5.2 ANOVA table of the proportion of *A. karroo*, *A. nilotica* and *A. sieberiana* seedlings that had emerged by the (a) 14th day since planting and (b) over the entire season at Ukulinga Research Farm

Source	Degrees of freedom	(a) P>F	(b) P>F
rep × wholeplot stratum	1	NS	NS
livestock type	1	0.780	0.858
system	1	0.834	0.388
livestock type × system	1	0.090	0.129
Residual	3		
rep × wholeplot × species stratum			
species	2	<0.001	<0.001
species × livestock type	2	0.009	0.008
species × system	2	0.744	0.882
species × animal × livestock type	2	0.002	0.006
Residual	8		
Total	23		

Table 5.3 The percentage, number and least significant differences (5% level) of means of *A. karroo, A. nilotica* and *A. sieberiana* seedlings that had emerged by the 14th day since planting, in all treatment combinations at Ukulinga Research Farm

Treatment	A. karroo			A. nilotica			A. sieberiana ⸳		
	number	%	LSD	number	%	LSD	number	%	LSD
Species	628	39.0	3.8	381	23.6	3.8	215	13.4	3.8
Cattle paddocks	321	39.2	10.8	173	21.3	10.8	142	17.5	10.8
Sheep paddocks	307	38.8	10.8	208	26.0	10.8	73	9.3	10.8
Rotational systems	330	40.0	10.8	190	22.8	10.8	106	12.8	10.8
Continuous systems	298	39.5	10.8	191	24.5	10.8	109	14.0	10.8
Cattle in rotational systems	208	48.5	15.3	106	25.0	15.3	73	17.0	15.3
Cattle in continuous systems	113	30.0	15.3	67	17.5	15.3	69	10.0	15.3
Sheep in rotational systems	122	30.0	15.3	84	20.5	15.3	33	8.5	15.3
Sheep in continuous systems	185	47.5	15.3	124	31.5	15.3	40	18.0	15.3

Table 5.4 The percentage, number and least significant differences (5% level) of means of *A. karroo, A. nilotica* and *A. sieberiana* seedlings that emerged over the entire season, in all treatment combinations at Ukulinga Research Farm

Treatment	A. karroo			A. nilotica			A. sieberiana		
	number	%	LSD	number	%	LSD	number	%	LSD
Species	780	48.4	3.8	474	29.5	3.8	265	16.3	3.8
Cattle paddocks	392	47.9	10	217	26.7	10.1	168	20.6	10.1
Sheep paddocks	388	48.8	10	257	32.2	10.1	97	12.1	10.1
Rotational systems	393	46.6	10	228	27.3	10.1	127	15.0	10.1
Continuous systems	387	50.1	10	246	31.6	10.1	138	17.6	10.1
Cattle in rotational systems	232	53.4	14	121	28.3	14.3	82	19.0	14.3
Cattle in continuous systems	160	42.4	14	96	25.2	14.3	86	22.2	14.3
Sheep in rotational systems	161	39.8	14	107	26.4	14.3	45	11.1	14.3
Sheep in continuous systems	227	57.9	14	150	38.1	14.3	52	13.1	14.3

5.3.3 Seedling survival

Fitting a logistic regression model to seedling survival at each recording interval, relative to the original cohort of seedlings at day 14, the addition of time, species, livestock type and grazing system to the model significantly reduced the deviance of the model, accounting for 69.9 % of the deviance. Interaction terms did not significantly influence the regression model. Only the following times significantly influenced the regression model and its predictions: 54 days, 129 days, 180 days and 225 days, and were incorporated into the model. As indicated by the estimates of the parameters (Table 5.5), *A. nilotica* and *A. sieberiana*, all relevant times, grazing by sheep, and rotational grazing systems negatively influenced seedling survival relative to seedlings that had emegred by day 14. Predictions from the model illustrated these findings (Figure 5.2).

Reductions in seedling survival were most pronounced at the beginning of the season between day 14 and 54. After a large initial decrease, survival improved until the later stages of the growing season, when predicted seedling survival declined similarly for all treatments. By the 54th day, seedlings exposed to cattle grazing and continuous grazing systems had established superior survival over seedlings exposed to sheep grazing and rotational grazing systems, respectively, an advantage which was maintained throughout the rest of the growing season. Furthermore, livetock type exerted a greater effect on seedlng survival than did grazing system. Differences in seedling survival in response to treatment were exhibited by all the woody species. However, *A. karroo* showed significantly higher survival than *A. nilotica*, and the latter showed significantly higher survival than *A. sieberiana*, for each treatment.
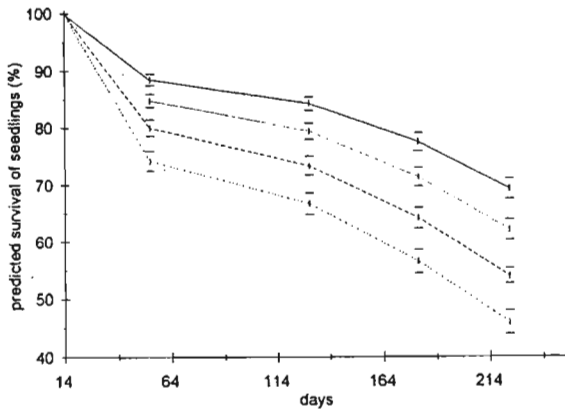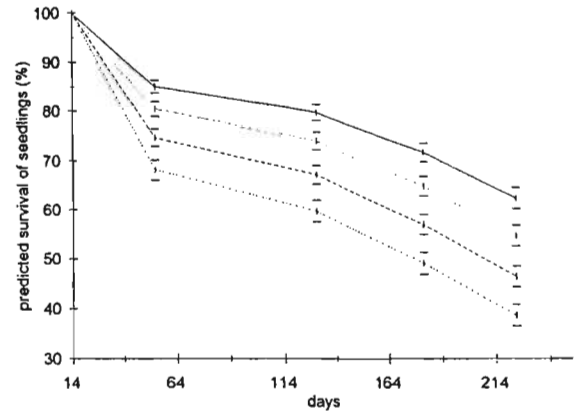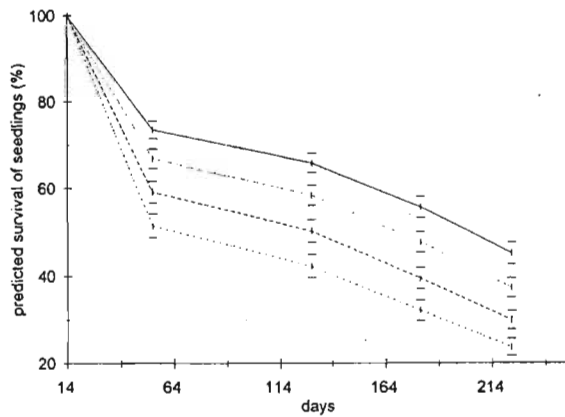
Acacia karroo

Acacia nilotica

Acacia sieberiana

Figure 5.2 Differences in predicted survival at Ukulinga Research Farm of the original 14th day cohort of seedlings of *A. karroo*, *A. nilotica* and *A. sieberiana* surviving over time, comparing continuous cattle (solid line), rotational cattle (——), continuous sheep (···) and rotational sheep (—·—·) respectively (bars are standard errors).

Table 5.5 Estimates of the parameters of the logistic regression model for the survival of seedlings of *A. karroo*, *A. nilotica* and *A. sieberiana* that had emerged by the 14th day since planting at Ukulinga Research Farm

Treatment	estimate	se	t(*)	t pr.
Constant	2.0290	0.0966	21.00	<0.001
A. nilotica	-0.2990	0.0714	-4.19	<0.001
A. sieberiana	-1.0066	0.0854	-11.78	<0.001
Time 4	-0.3643	0.0946	-3.85	<0.001
Time 5	-0.7975	0.0920	-8.66	<0.001
Time 6	-1.2213	0.0912	-13.39	<0.001
Sheep grazing	-0.6510	0.0654	-9.95	<0.001
Rotational grazing	-0.3199	0.0643	-4.96	<0.001

A logistic regression model was fitted to age-specific survival of seedlings from the cohort of seedlings that had emerged by day 14. The addition of time, species and livestock type to the model significantly reduced the deviance of the model, accounting for 53.8 % of the deviance. Interaction terms did not significantly influence the regression model. All times could be incorporated into the model, indicating that age-specific survival varied significantly over time. *Acacia karroo* and *A. nilotica* did not exhibit significantly different impacts on the model and were therefore considered together in the model. As indicated by the estimates of the parameters (Table 5.6), *A. sieberiana*, all times throughout the growing season and grazing by sheep negatively influenced seedling survival. Grazing system did not have a significant effect. Clearly survival prospects improved from day 54 to day 97 (Figure 5.3 a), after which the probability of survival remained fairly constant, before decreasing in the later stages of the growing season. The probability of seedlings surviving at the end of the season was nevertheless higher than within the first 54 days after planting. The prospects for survival were poorer for seedlings growing in sheep paddocks than in cattle paddocks. Age-specific mortality revealed the same trend, being the reciprocal of age-specific survival (Figure 5.3 b).
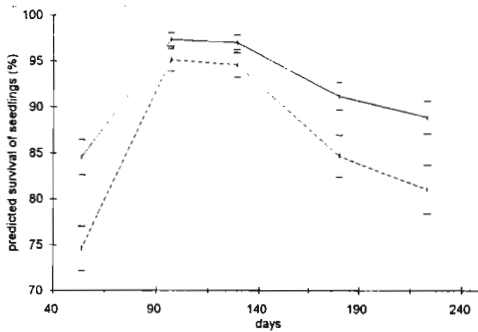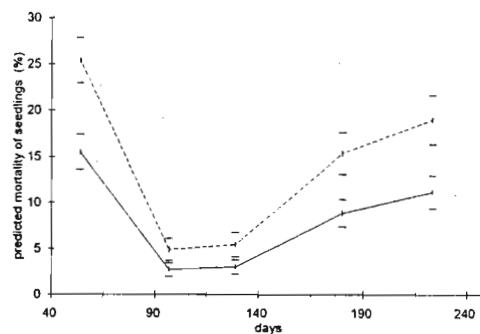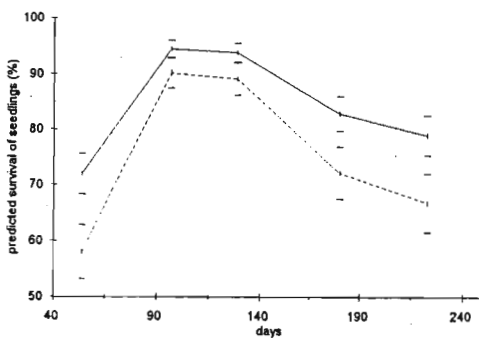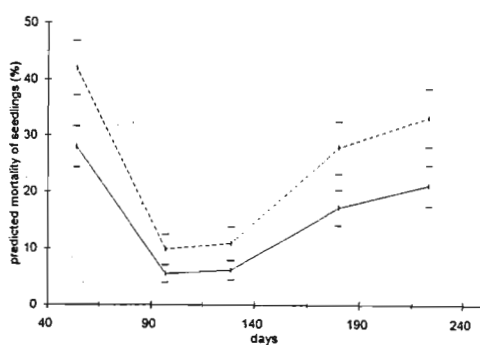
(a) *Acacia karroo & Acacia nilotica*　　　　　(b) *Acacia karroo & Acacia nilotica*

(a) *Acacia sieberiana*　　　　　(b) *Acacia sieberiana*

Figure 5.3 Differences in predicted age-specific (a) survival and (b) mortality of *A. karroo* and *A. nilotica,* and *A. sieberiana* seedlings from the 14th day cohort at Ukulinga Research Farm, comparing paddocks grazed by cattle (solid line) and by sheep (---).

Table 5.6 Estimates of the parameters of the logistic regression model for age-specific survival of seedlings of *A. karroo*, *A. nilotica* and *A. sieberiana* that had emerged by the 14th day since planting at Ukulinga Research Farm

Treatment	estimate	se	t(*)	t pr.
Constant	1.698	0.145	11.67	<0.001
A. sieberiana	-0.755	0.179	-4.22	<0.001
Time 3	1.889	0.276	6.85	<0.001
Time 4	1.777	0.271	6.57	<0.001
Time 5	0.630	0.193	3.27	<0.001
Time 6	0.375	0.191	1.96	0.052
Sheep grazing	-0.620	0.146	-4.24	<0.001

For the logistic regression model fitted to the total number of seedlings that emerged relative to survival at the end of the season, the addition of time, species and livestock type to the model significantly reduced the deviance of the model, accounting for 39.2 % of the deviance. Interaction terms did not significantly influence the regression model. *Acacia karroo* and *A. nilotica* were not significantly different and were therefore considered together in the model. As indicated by the estimates of the parameters (Table 5.7), *A. sieberiana*, time and grazing by sheep negatively influenced seedling survival (Table 5.8). The negative influence of time in this model represented one time interval, a comparison of seedling survival at the end of the season relative to the total number of seedlings that had emerged.

Table 5.7 Estimates of the parameters of the logistic regression model for survival of seedlings of *A. karroo*, *A. nilotica* and *A. sieberiana* that emerged over the whole season at Ukulinga Research Farm

Treatment	estimate	se	t(*)	t pr.
Constant	10.840	2.560	4.24	<0.001
Time 6	-10.210	2.550	-4.00	<0.001
A. sieberiana	-0.913	0.143	-6.37	<0.001
Sheep grazing	-0.739	0.107	-6.91	<0.001

Table 5.8 Differences in predicted age-specific survival and mortality of *A. karroo* and *A. nilotica* versus *A. sieberiana* seedlings that emerged over the entire season at Ukulinga Research Farm

species	livestock type	survival (%)		motality (%)	
		mean	standard error	mean	standard error
A. karroo and *A. nilotica*	cattle	65.3	1.85	34.7	1.85
	sheep	47.3	1.90	52.7	1.90
A. sieberiana	cattle	43.0	3.27	57.0	3.27
	sheep	26.5	2.89	73.5	2.89

Rainfall over the 1997/1998 experimental period was generally above average, yet unlikely to result in waterlogging (Figure 3.1). Therefore, mortality of seedlings was not the consequence of abnormal moisture conditions, and represented natural responses for that area.

Whilst animal type significantly influenced age-specific survival and survival over the whole season, grazing system did not. On these grounds, the hypothesis that sheep grazing would negatively impact on woody seedling survival was not rejected, whilst the hypothesis that seedlings exposed to rotational grazing would fare better than seedlings exposed to continuous grazing was rejected. Clearly, *A. karroo* and *A. nilotica* were far more successful than *A. sieberiana*.

5.3.4 Seedling growth

Leaf growth and plant height reached a maximum 180 days after emergence (Figure 5.4), after which seedlings generally maintained their height but experienced substantial leaf dehiscence. Leaf numbers at the end of the season were generally similar to those exhibited 54 days after planting. This trend reflects the rainfall pattern over the 1997/98 growing season (Figure 3.1). Species differences were expressed in leaf number, plant height and the leaf-to-height ratio (Table 5.9, Figure 5.5). *Acacia nilotica* produced the most leaves per seedling and had the greatest leaf-to-height ratio of all three species. *Acacia karroo* was in turn superior to *A. sieberiana* in the abovementioned growth characteristics. However, *A. sieberiana* grew the tallest, followed by *A. nilotica* and lastly *A. karroo.*

Livestock type was a factor that influenced the growth of seedlings (Table 5.9), and seedlings growing in cattle areas exhibited greater leaf numbers, seedling height and leaf-to-height ratios than seedlings growing in sheep areas (Figure 5.5 (1)). Leaf number and leaf-to-height ratio were furthermore influenced by grazing system, especially towards the later stages of the growing season (Table 5.9 (a) and (c), Figure 5.5 (2)). Seedlings exposed to rotational grazing generally showed more growth than those exposed to continuous grazing. Species, livestock type and grazing system interacted significantly at various stages during the growing season. These interactions were however inconsistent and generalities could not be drawn from them.

These results support the hypothesis that sheep grazing would negatively impact seedling growth, whilst woody seedlings would benefit from rotational grazing systems.

Figure 5.4 Differences of means (± 95 % confidence limits) in (a) leaf number per plant, (b) height per plant and (c) leaf-to-height ratio for *A. karroo*, *A. nilotica* and *A. sieberiana*, comparing the growth of seedlings in cattle areas under rotational grazing systems (solid line) and continuous grazing systems (——), and comparing the growth of seedlings sown in sheep areas under rotational grazing systems (····) and continuous grazing systems (—·—·).
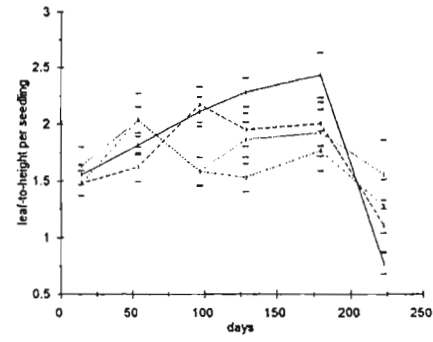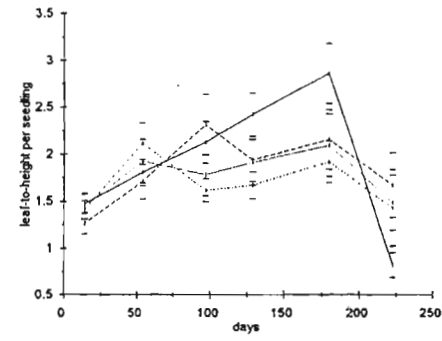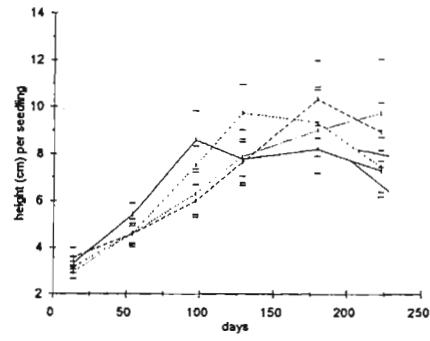
(a) Leaf number
Acacia karroo

(b) height

(c) leaf-to-height

Acacia nilotica

Acacia sieberiana

78
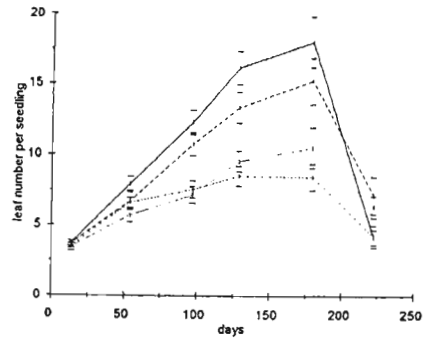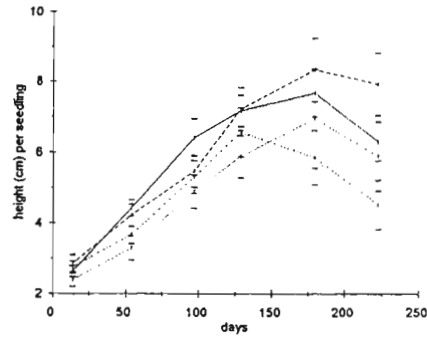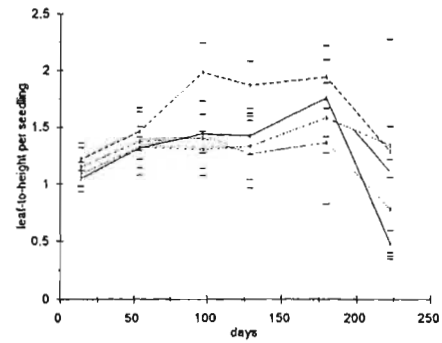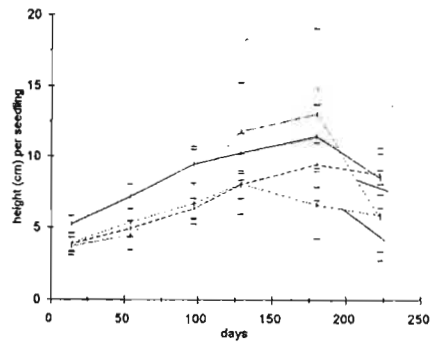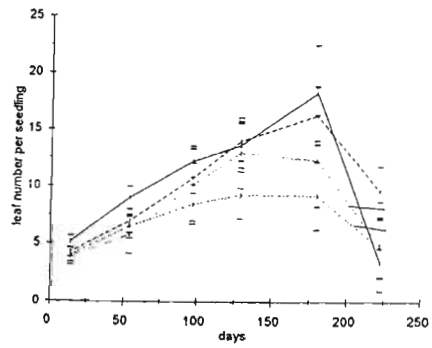
Figure 5.5 Differences of means (± 95 % confidence limits) in (a) leaf number per plant, (b) height per plant and (c) leaf/height per seedling for *A. karroo*, *A. nilotica* and *A. sieberiana*, comparing (1) the growth of seedlings in cattle areas (solid line) and sheep areas (---), and (2) the growth of seedlings sown in rotationally grazed areas (solid line) and continuously grazed areas (---).

(1)

(a) Leaf number

(b) height
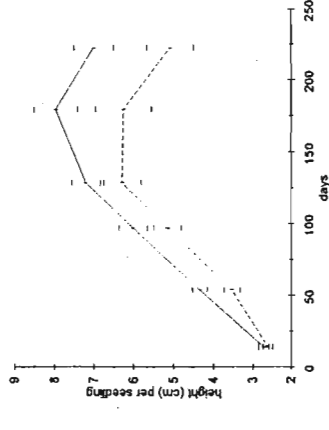
(c) leaf-to-height
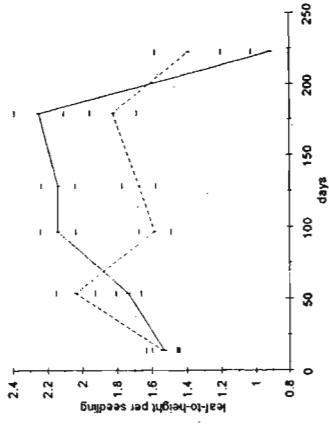
Acacia karroo
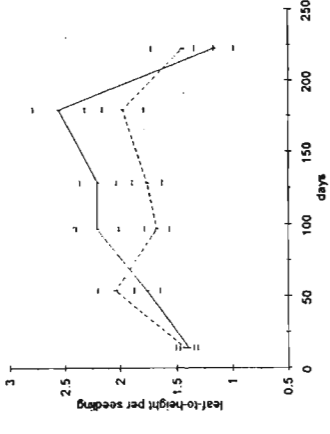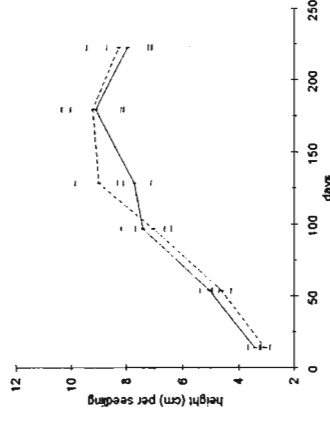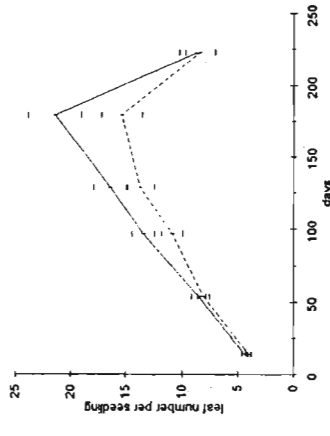
Acacia nilotica

Acacia sieberiana

(2)
(a) Leaf number
Acacia karroo
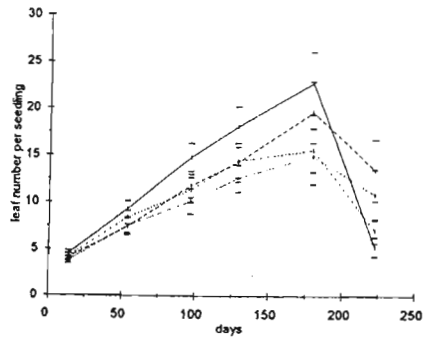
(b) height

(c) leaf-to-height

Acacia nilotica

Acacia sieberiana

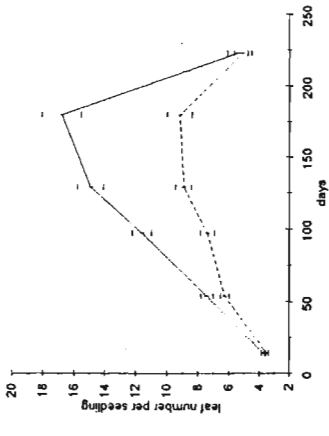## 5.3.5 Veld condition assessment

5.3.5.1 Species composition

Relative species abundance varied across paddocks (Table 5.10), with paddocks 1 and 4 being the most different from the other paddocks as shown in the correspondence analysis (Figure 5.6). In comparison with other paddocks, Paddock 1 tended to have high relative abundances of *Sporobolus pyramidalis*, and *Eragrostis plana*, whilst paddock 4 had high relative abundances of *Digitaria eriantha*, *Bothriochloa insculpta*, *Cymbopogon excavatus* and *Aristida junciformis*. The rest of the paddocks had similar patterns of species abundance, with *Sporobolus africanus*, *Paspalum dilatatum*, *Chloris gayana*, *Hyparrhenia hirta*, *Panicum maximum*, *Cynodon dactylon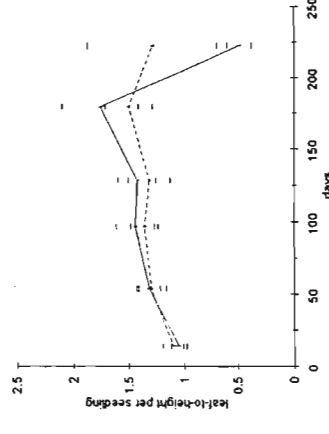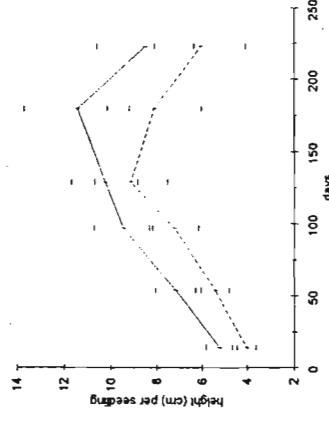* and *Eragrostis curvula* dominating. Paddock 4 was most different to the rest of the paddocks, evident by its separation along axis 1, which accounted for 46.3 % of the variance. Axis 2 accounted for 26.3 %, axis 3 for 15 % and axis 4 for 2.4 %. This difference could be attributed to the large component of *Digitaria eriantha* in this paddock, which had encroached from a neighbouring *Digitaria* pasture. Paddock 1 was adjacent to a farm road, which may have influenced conditions in this site. Paddock 8, which was also adjacent to the farm road and at the same position on the slope, was most similar to paddock 1, lending support to the above argument. Although paddocks 1 and 4 were quite distinctly separated from the other paddocks in terms of relative abundance, comparison of presence/absence of species across paddocks (Table 5.10) indicated that the paddocks were nevertheless fairly similar. All paddocks contained substantial numbers of *Eragrostis* and *Sporobolus* species and *Chloris gayana*, and were to a lesser degree commonly represented by numerous other species. Consequently, paddocks were considered to be similar and differences in the success of *Acacia* seedlings among paddocks were assumed to be the result of treatment differences. Furthermore, at the beginning of the growing season the above-ground biomass was removed by burning, creating uniform sward conditions across all paddocks.

Table 5.10 Relative (a) abundance and (b) presence/absence of grass species in each paddock at Ukulinga Research Farm. Key to species: AJU = *Aristida junciformis*, BIN = *Bothriochloa insculpta*, CDA = *Cynodon dactylon*, CEX = *Cymbopogon excavatus*, CGA = *Chloris gayana*, DER = *Digiteria eriantha*, ECU = *Eragrostis curvula*, EPL = *Eragrostis plana*, ERA = *Eragrostis racemosa*, HHI = *Hyparrhenia hirta*, PAS = *Paspalum dilatatum*, PMA = *Panicum maximum*, SAF = *Sporobolus africanus*, SPY = *Sporobolus pyramidalis*, TTR = *Themeda triandra*

(a)

Paddock	AJU	BIN	CDA	CEX	CGA	DER	ECU	EPL	ERA	HHI	PAS	PMA	SAF	SPY	TTR
1	2.9	0.0	1.0	0.3	6.5	0.0	12.8	5.4	0.0	8.8	0.0	0.3	11.3	50.7	<0.1
2	2.0	0.1	1.5	1.4	21.0	0.0	36.3	2.2	0.0	13.5	3.9	1.8	8.8	7.4	0.0
3	11.3	0.0	0.2	18.1	2.4	0.0	34.7	0.3	<0.1	14.2	7.7	0.1	8.7	2.2	<0.1
4	20.3	0.6	<0.1	23.9	1.8	27.0	9.0	0.0	0.0	0.0	0.1	0.0	14.5	2.9	0.0
5	1.2	0.2	0.6	4.6	37.2	0.0	16.5	0.3	0.0	3.9	5.5	1.0	21.6	7.3	0.0
6	0.1	0.0	2.4	5.9	13.3	1.1	71.4	0.1	0.1	0.9	0.3	<0.1	2.3	1.9	0.0
7	1.1	0.1	2.1	1.3	5.4	0.0	67.7	2.0	0.0	6.0	0.9	2.8	30.	7.6	0.0
8	0.1	0.0	1.0	0.0	20.0	0.0	37.4	1.3	0.0	3.5	0.4	0.6	17.5	18.2	0.0

(b)

Paddock	AJU	BIN	CDA	CEX	CGA	DER	ECU	EPL	ERA	HHI	PAS	PMA	SAF	SPY	TTR
1	1.3	0.0	3.0	0.8	16.0	0.0	9.7	11.8	0.0	14.8	0.0	3.0	9.7	29.5	0.4
2	3.3	0.7	4.1	2.1	18.8	0.0	21.4	6.5	0.0	11.4	10.0	2.0	11.3	8.5	0.0
3	9.8	0.0	0.4	17.5	4.6	0.0	26.7	1.0	0.8	15.6	9.0	0.2	9.6	4.6	0.2
4	19.4	0.9	0.4	18.5	4.9	9.3	19.8	0.0	0.0	0.0	2.2	0.0	20.7	4.0	0.0
5	2.1	0.4	1.4	3.2	34.1	0.0	20.6	1.4	0.0	4.6	5.3	0.7	19.9	6.4	0.0
6	0.4	0.0	7.2	4.9	15.2	0.8	52.9	1.1	0.8	1.5	1.9	0.8	7.2	5.3	0.0
7	5.5	0.5	4.5	0.5	13.4	0.0	33.3	4.5	0.0	7.5	3.0	9.5	7.5	10.5	0.0
8	1.0	0.0	2.1	0.0	19.2	0.0	28.2	3.7	0.0	5.9	3.2	4.3	11.2	21.3	0.0
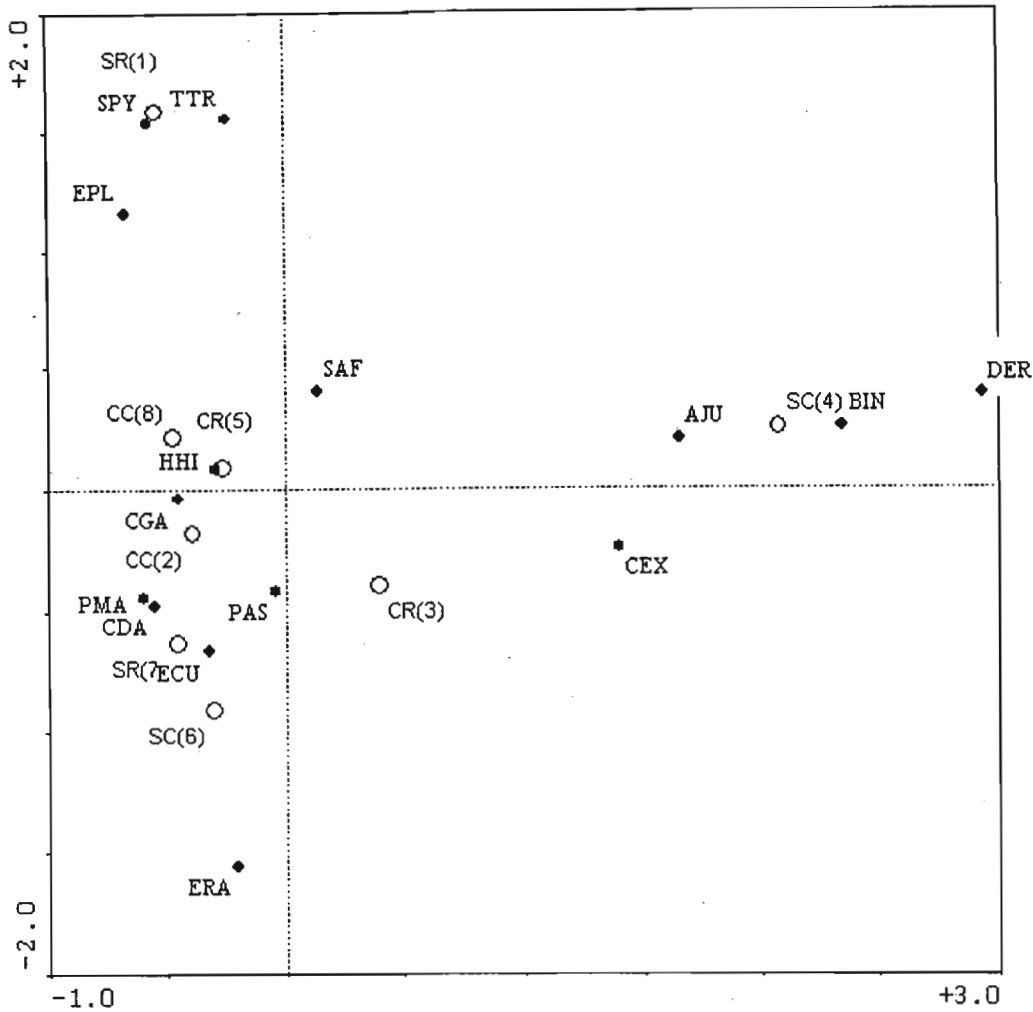
Figure 5.6 Correspondence analysis of sites and species composition data collected at Ukulinga Research Farm. Key to species: AJU = *Aristida junciformis*, BIN = *Bothriochloa insculpta*, CDA = *Cynodon dactylon*, CEX = *Cymbopogon excavatus*, CGA = *Chloris gayana*, DER = *Digiteria eriantha*, ECU = *Eragrostis curvula*, EPL = *Eragrostis plana*, ERA = *Eragrostis racemosa*, HHI = *Hyparrhenia hirta*, PAS = *Paspalum dilatatum*, PMA = *Panicum maximum*, SAF = *Sporobolus africanus*, SPY = *Sporobolus pyramidalis*, TTR = *Themeda triandra*; treatment description: SR = sheep rotational, SC = sheep continuous, CC = cattle continuous, CR = cattle rotational; paddock number: in brackets after the treatment description.

5.3.5.2 Sward structure

The distance to the nearest grass plant from a woody seedling, and the height of the nearest grass plant, varied similarly across paddocks. Tall grass plants were characteristic of paddocks that had larger distances between plants, and short grass plants were found in paddocks with shorter distances between plants (Figure 5.7).

Analysis of variance revealed that height of the nearest grass plant was greater under continuous than rotational systems (albeit at the 10 % level), whilst there was no difference in terms of distance to the nearest grass plant between systems (Table 5.11 & 5.12). The height and distance of the nearest grass plant from a woody seedling was significantly greater in sheep than cattle paddocks (Table 5.11 & 5.12).

Cattle and rotational grazing resulted in a denser, shorter grass sward than sheep and continuous grazing. Whilst grass plants were unable to grow tall in cattle-grazed paddocks, low utilization by sheep allowed them to grow into a tufted from.
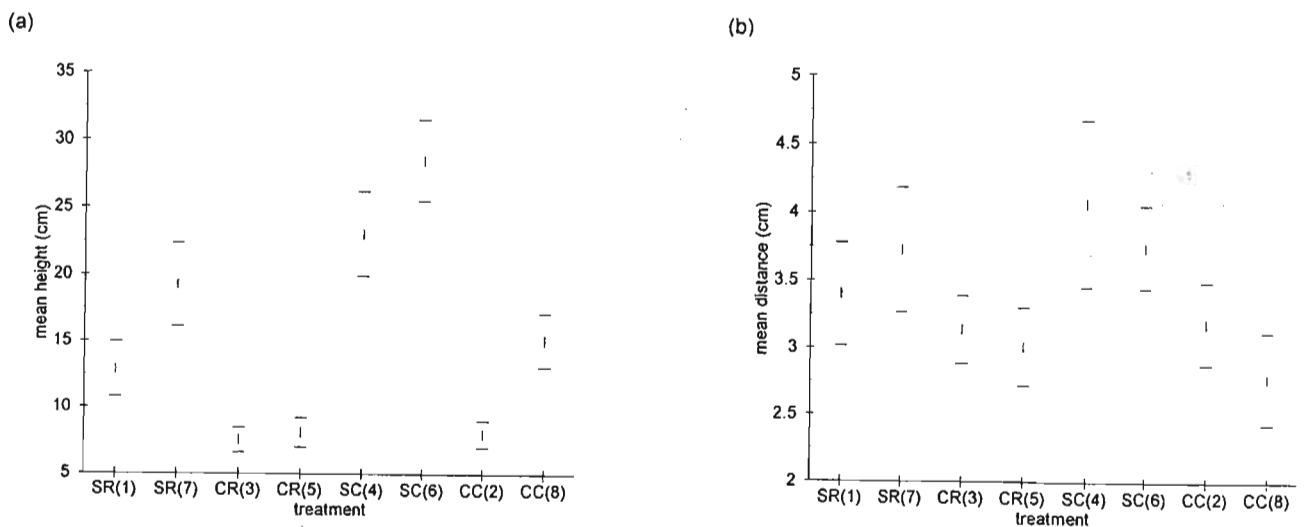
Figure 5.7 Graph illustrating (a) mean height of grass plants and (b) mean distance between grass plants per treatment at Ukulinga Research Farm (bars are 95% confidence limits). Key to treatments: SR = sheep rotational, CR = cattle rotational, SC = sheep continuous, CC = cattle continuous; paddock numbers are in brackets.

Table 5.11 ANOVA table of the means among treatments of (a) the height of the nearest grass plant, and (b) distance to the nearest grass plant at Ukulinga Research Farm

Source	Degrees of freedom	(a) P>F	(b) P>F
animal	1	0.015	0.011
system	1	0.071	0.472
animal × system	1	0.339	0.233
Residual	4		
Total	7		

Table 5.12 The means of (a) the height of the nearest grass plant, and (b) distance to the nearest grass plant, including least significant differences (5% level), in all treatment combinations at Ukulinga Research Farm

Grazing system	(a) height		(b) distance	
	mean	LSD	mean	LSD
cattle	9.68	7.64	3.025	0.4337
sheep	20.90	7.64	3.732	0.4337
continuous	18.65	7.64	3.440	0.4337
rotational	11.93	7.64	3.316	0.4337
cattle × continuous	11.55	10.81	2.977	0.6134
cattle × rotational	7.82	10.81	3.072	0.6134
sheep × continuous	25.75	10.81	3.903	0.6134
sheep × rotational	16.04	10.81	3.560	0.6134

A double normal distribution gave a better fit than a single normal distribution for the compressed sward height and dry matter data in every paddock. The proportion of 'tall' and 'short' grass components, and the difference in the means of the modals, were examined (Table 5.13, 5.14).

Analysis of variance revealed that cattle grazing resulted in a greater proportion of short plants (1 - 10 cm), sheep in a greater proportion of intermediate plants (11 - 30 cm), and there was no difference between animal type in the tall grass category (31 cm). The tall grass category represented a very small proportion of the grass sward, and was very variable. The proportion of short, intermediate and tall grass plants did not vary between grazing systems.

The tall and short means of the bimodal distributions were greater for sheep than for cattle treatments. Cattle utilized more of the available herbage, whilst sheep concentrated their efforts on smaller patches, ignoring much of the vegetation (Table 5.13, 5.14). There was no difference among grazing system for tall and short means.

Grazing by cattle appeared to make the greatest impact on the grass sward, which was consistent with the preceeding analysis of variance (Table 5.11 & 5.12).

Table 5.13 ANOVA tables of the proportion of (a) short plants (1 - 10 cm), (b) intermediate plants (11 - 30 cm), and (c) tall plants (> 31 cm), and the (d) tall and (e) short means of the bimodal distributions among treatments at Ukulinga Research Farm

Source	Degrees of freedom	(a) P>F	(b) P>F	(c) P>F	(d) P>F	(e) P>F
animal	1	0.051	0.064	0.305	0.004	0.004
system	1	0.169	0.244	0.352	0.320	0.628
animal × system	1	0.539	0.368	0.406	0.082	0.154
Residual	4					
Total	7					

Table 5.14 The proportion of (a) short plants (1 - 10 cm), (b) intermediate plants (11 - 30 cm), and (c) tall plants (> 31 cm), and the (d) tall and (e) short means of the bimodal distributions, including least significant differences (5% level), in all treatment combinations at Ukulinga Research Farm

Grazing system	(a) 1-10 cm mean	LSD	(b) 11 -30 cm mean	LSD	(c) > 31 cm mean	LSD	(d) tall mean	LSD	mean	LSD
cattle	0.677	0.3724	0.318	0.3562	0.000	0.1121	34.3	14.81	17.8	6.21
sheep	0.307	0.3724	0.642	0.3562	0.050	0.1121	66.6	14.81	31.5	6.21
continuous	0.380	0.3724	0.567	0.3562	0.048	0.1121	47.4	14.81	25.2	6.21
rotational	0.605	0.3724	0.392	0.3562	0.010	0.1121	53.5	14.81	24.0	6.21
cattle × continuous	0.520	0.5266	0.470	0.5038	0.010	0.1586	37.5	20.94	20.3	8.78
cattle × rotational	0.835	0.5266	0.165	0.5038	0.000	0.1586	31.1	20.94	15.2	8.78
sheep × continuous	0.240	0.5266	0.665	0.5038	0.090	0.1586	57.4	20.94	30.1	8.78
sheep × rotational	0.375	0.5266	0.620	0.5038	0.010	0.1586	75.8	20.94	32.9	8.78

The degree of patchiness depends on the proportion of each component in the sward, and the variation in heights of each component. For example, rotational grazing by sheep appears to have created heterogenous grass swards with patches that vary tremendously in height (Figure 5.14). However, Figure 5.8 reveals that the 'tall' component covers a very small proportion of the grass sward and the paddocks were very homogenous. Figure 5.10 lends further support to this explanation; the means for all the measurements taken in these paddocks lie at almost exactly the level of the 'short' grass component (Figure 5.9). However, as the short grass component had means greater than 30 cm, which is not characteristic of sheep grazing, most of the vegetation had not been utilized. This indicates that sheep managed in a rotational grazing system, with exceptionally high stocking rates

(Appendix 1), do not impact greatly on the grass sward. Continuous grazing by sheep resulted in less utilization of the grass sward than rotational grazing. Although the means of the 'tall' and 'short' components in these paddocks were very different, the bulk of the grass heights were similar. Patches that formed in sheep paddocks were too few and too small to make an impression on the sward structure analysis.

One important consideration is the unavoidable variation in disc meter reading due to irregularities on the soil surface. This problem was especially relevant in very short grass swards, where a difference of 5 cm can in some cases double the size of the plant. Therefore, paddocks 2,3 and 5 (grazed by cattle) were considered to be homogenous as the difference between the 'tall' and the 'short' components in these paddocks was less than 7 cm. Heavy utilization of the grass sward in these paddocks resulted in the veld assuming the appearance of a 'grazing lawn', although almost all the species were bunchgrasses. Stocking rates for these paddocks were set at abnormally high levels to maximize animal impact on the vegetation (Appendix 1), resulting in complete utilization of the available herbage, regardless of stocking system. Even unpalatable species such as *C. excavatus* and *A. junciformis* were consumed. Consequently, the effect of trampling was expected to have been far greater in cattle areas.

Grazing by cattle under a continuous grazing system in paddock 8 resulted in a fairly homogenous grass sward, but did not result in the formation of grazing 'lawns' as in the other cattle paddocks. Stocking rates of paddocks within a livestock type were relatively comparable at the start of the experiment and differences found between treatments were not expected to be as a result of differences in stocking rate. However, the stocking rate in paddock 8 was set lower than that in paddock 2 (a paddock grazed by cattle under a continuous system), and was further decreased as a result of stock theft (20th December 1997). This offers an explanation for differences between the two paddocks, also expressed in dry matter production at the end of the growing season (Appendix 2).

Trends in dry matter production (Appendix 2) support differences shown in sward structure between paddocks. After the growing season paddocks grazed by cattle had lower residual dry matter than paddocks grazed by sheep, whilst rotationally grazed systems were more heavily utilized than continuously grazed systems.

(a)

(b)
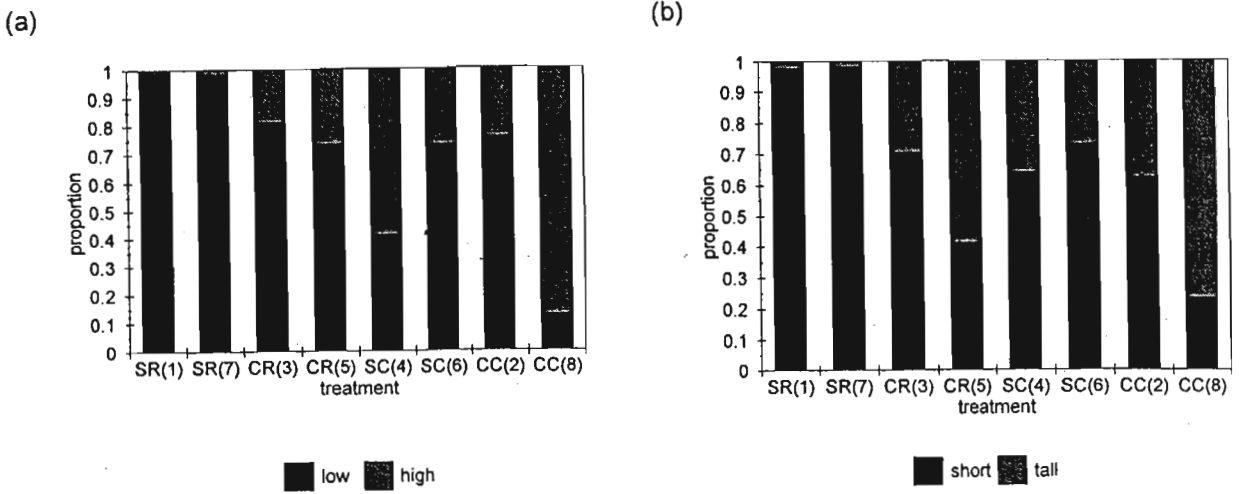
Figure 5.8 The proportion of 'tall' and 'short' grass components per paddock at Ukulinga Research Farm when considering (a) dry matter and (b) compressed sward height. Key to treatments: SR = sheep rotational, CR = cattle rotational, SC = sheep continuous, CC = cattle continuous; paddock numbers are in brackets.
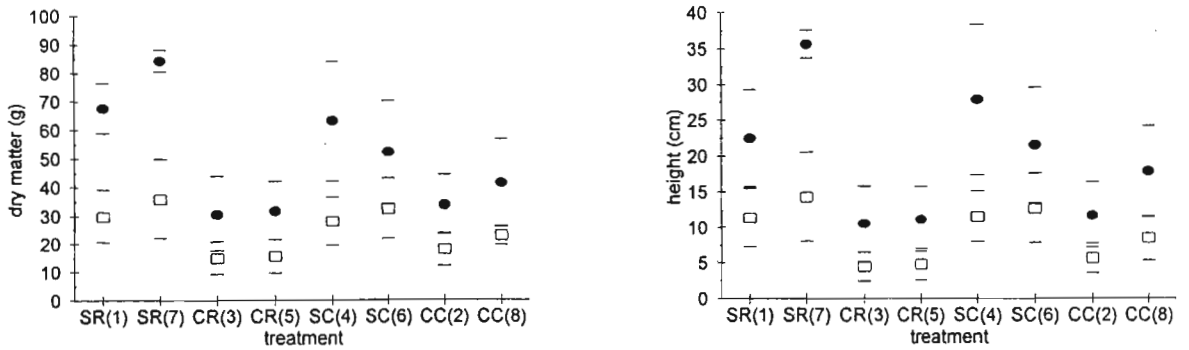
Figure 5.9 The upper ('tall grass') and lower ('short grass') means of the bimodal distribution in each paddock at Ukulinga Research Farm for (a) dry matter and (b) compressed sward height readings per paddock (bars are 95% confidence limits). Key to treatments: SR = sheep rotational, CR = cattle rotational, SC = sheep continuous, CC = cattle continuous; paddock numbers are in brackets.
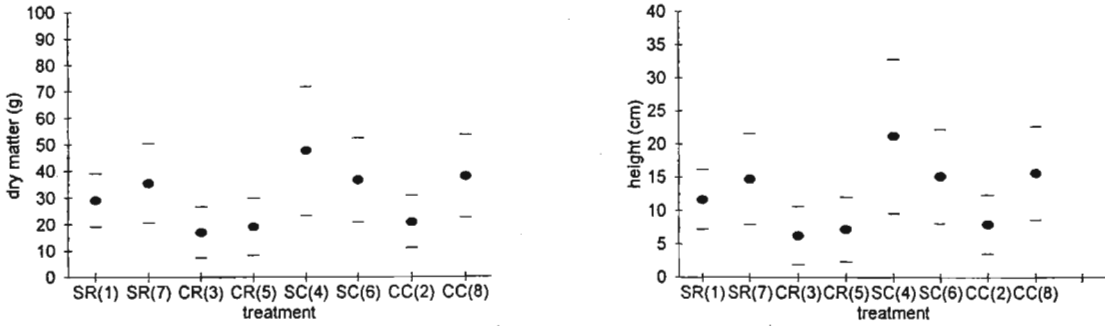
Figure 5.10 The means for (a) dry matter and (b) compressed sward height readings when considering all measurements per paddock at Ukulinga Research Farm (bars are 95% confidence limits). Key to treatments: SR = sheep rotational, CR = cattle rotational, SC = sheep continuous, CC = cattle continuous; paddock numbers are in brackets.

5.3.5.3 The interaction of woody seedling and grass sward

As woody seedling growth and survival reacted positively to cattle grazing and rotational grazing systems, which are related to greater grass defoliation, it was tempting to infer a relationship between grass biomass and woody seedlings. However, no direct relationship could be established between seedling height, leaf number or leaf-to-height ratio, and distance to the nearest grass species, height of the nearest grass species, and the disc pasture meter measurement corresponding to the seedling.

5.4 Discussion

5.4.1 General trends

Although a large proportion of the seedlings that emerged over the entire season emerged soon after planting (80.2 %), a substantial proportion (17.1 %) emerged between 2 and 7 weeks after planting. However, the latter were assumed to have emerged soon after the first recording date as, firstly, their leaf numbers and heights when first recorded were similar to those of seedlings that had germinated by the first recording date, and secondly, the cotyledons had wilted and/or fallen off. Most seeds therefore germinated soon after sufficient rainfall, a sign that scarification by sulphuric acid was effective in releasing viable seeds from dormancy. Woody seedling emergence took place in a post-burn environment immediately after substantial rainfall, coinciding with a spring flush in the herbaceous layer. Grazing pressure would not have been intense as forage was not limiting at this stage. Furthermore, for reasons explained in section 4.4.1 the likelihood of seedlings being encountered within this period was considered small. Patterns in seedling emergence, relative to grazing system and animal type, were confounding, limiting the interpretation to species differences.

Species differences in emergence mirrored differences in seed viability, albeit at much lower percentages, in decreasing order as *A. karroo*, *A. nilotica* and *A. sieberiana*. *Acacia karroo* has been described as an important woody invader of grassland in South Africa (O'Connor 1995), which is easily conceiveable as this species showed superior emergence and survival over *A. nilotica* and *A. sieberiana*. Although the latter two species exhibited better above-ground growth than *A. karroo*, below-ground growth was not examined. However, these trends were not reflected in the adult population at Ukulinga, which was dominated by *A. nilotica*, followed by *A. sieberiana* and lastly *A. karroo*. This suggests that differences among species during the first growing season do not determine woody plant recruitment in this system.

Highest seedling mortality occurred at the beginning of the season, irrespective of treatment, becoming less thereafter and showing a slight increase at the end of the growing season. This was an unexpected result for reasons explained in section 4.4.1. Moisture stress at the end of the growing season was probably responsible for seedling mortality, as surviving seedlings had lost most of their leaves due to wilting. More intensive monitoring is necessary to discover which factors are responsible for initial mortality of seedlings.

5.4.2 The effect of animal type and grazing system on seedling establishment

Whilst trampled plants were encountered in cattle grazed paddocks, trampling being identified as a break of the seedling stem, trampling to this degree was never witnessed in sheep camps. As high stocking pressures of cattle increase the effect of trampling on tree seedlings (Pitt *et al.* 1998), seedlings in cattle paddocks at Ukulinga are likely to have been affected by trampling. It was difficult to determine whether damage to a seedling was the result of less severe trampling or herbivory. Nevertheless, on occasion, damage could with a reasonable degree of certainty be attributed to herbivory by sheep, whilst this was not the case for cattle.

Seedling emergence had consistent patterns for all *Acacia* species examined. Whilst emergence in cattle treatments was greater for seedlings in rotational systems, emergence in sheep treatments was greater in continuous systems. Furthermore, there were no differences between the aforementioned treatment combinations. Although reasons for these patterns could not be established, consistency across species sanctions further investigation.

Whilst there was no significant difference in seedling emergence solely due to animal type, seedling survival and growth was greater in cattle than in sheep paddocks (Figure 5.3 & 5.5), which is consistent with the belief that woody seedlings are adversely affected by small-mouthed herbivores. Differences in feeding ecology between large and small ruminants has been widely documented (Illius & Gordon 1987; Heady & Child 1994; Owen-Smith 1999), which may largely be explained in terms of the different constraints under which animals of different body size are forced to operate. As sheep have narrower muzzles than cattle, the latter cannot exercise a fine degree of selection as the former, and consequently are unlikely to select woody seedlings. In situations where stocking rates are abnormally high, as in this study, livestock exert more pressure on the available vegetation (Acocks 1966), and selectivity is diminished (Van Soest 1982). The recommended stocking rate (Smith 1998) for the experimental area was calculated at 0.376 AU/ha, which was much lower than the stocking rate applied to the paddocks and, moreover, livestock were kept on the veld for as long as possible (Appendix 1). The effect of such high stocking pressures resulted in heavy utilization of the veld and extremely high grazing pressure. The probability of sheep selecting out woody seedlings was likely to increase under these conditions, which therefore favoured seedling survival in cattle areas. The relative importance of seedling growth and survival in determining woody seedling establishment was unclear in this context, as herbivory impacted negatively on both.

There was no significant difference in seedling emergence solely due to grazing system, and grazing system did not influence seedling survival. However, in terms of growth, seedlings fared better in rotationally grazed paddocks than in continuously grazed paddocks, suggesting that seedlings benefitted from the period of rest between rotations. A switch from continuous to rotational grazing appears to have given woody seedlings a distinct opportunity for growth, a finding consistent with the belief that seedlings in rotational systems are favoured by having sufficient time to grow between rotations to attain a size rendering the seedling tolerant of at least one defoliation. The absence of defoliation would have provided an opportunity for greater leaf production and growth in plant height, important for dry season survival (O'Connor 1995). This was true for seedlings in cattle and sheep paddocks, which implies that cattle do exert an impact on woody seedlings, albeit it indirectly. However, regardless of grazing system, seedling growth was still poorer in sheep paddocks, indicating that sheep grazing of seedlings had a more pronounced effect than indirect effects due to cattle grazing. The influence of grazing system on seedling establishment at this site, and ultimately bush encroachment, appears to be determined by its effect on seedling growth.

The influence of animal type on seedling establishment was deemed more important than grazing system as grazing system, whilst influencing seedling growth, did not affect seedling survival. Ultimately the combination of cattle and rotational grazing was best for seedling establishment.

5.4.3 The effect of veld condition on seedling establishment

No direct relationship was found linking seedling establishment to veld condition. However, variation in veld condition provided useful information on the effect of animal type and grazing system on grass sward structure.

As a result of abnormally high stocking rates cattle utilized all of the available herbage in the paddocks, including unpalatable species such as *Cymbopogon excavatus* and *Aristida junciformis*, resulting in homogenous grass swards. Continuous grazing resulted in greater utilization than rotational grazing. Sheep did not utilize much of the grass sward, suggesting that high stocking rates resulted in greater intensity of patch utilization. Patterns of selectivity by sheep and cattle were consistent with studies on their feeding behaviour (Hardy 1995; Morris *et al.* 1999). Examination of seedling establishment relative to veld heterogeneity could not be tested as the disc pasture method was not sensitive enough for detecting patches.

The greater leaf-to-height ratio of seedlings growing in cattle and rotational paddocks as compared with sheep and continuous paddocks was attributed to lower grass biomass, which increases light availability (Van Auken & Bush 1991; Fahnstock & Knapp 1994). Shading is a major factor limiting *Acacia* seedling growth (Smith & Shackleton 1987), and an increase in light levels can promote aerial growth (Fahnstock & Knapp 1994) and result in an increase in the leaf-to-height ratio of *Acacia* species (Milton 1982; O'Connor 1995).

Although grazing has been reported as a key determinant of shrub dynamics (Roques *et al.* 2001), this study could not determine a direct link between grass sward structure, as modified by grazing system and livestock type, and woody seedling dynamics. However, this study provides evidence suggesting that grass interference with irradiance affects woody seedlings. This was in turn subject to influence from livestock type and gazing system.

5.4.4 Management implications

The success of a cohort of woody seedlings in its first growing season was largely determined by livestock type and grazing system, which highlights the importance of correct agricultural management practices addressing woody seedling dynamics. A switch from continuous to rotational grazing, and more importantly from sheep to cattle grazing, appears to promote woody seedling encroachment. Furthermore, stocking rate has an overriding effect on grazing system in terms of veld condition. Decreases in grass biomass may improve seedling establishment, both by a reduction in grass competition and a decrease in fuel load for fires. Incorrect stocking could promote seedling establishment.

CHAPTER 6

THE EFFECT OF FIRE INTENSITY AND FIRE TYPE ON GERMINATION AND MORTALITY OF SEEDS OF *ACACIA KARROO*, *ACACIA NILOTICA* AND *ACACIA SIEBERIANA*

6.1 Introduction

The success of *Acacia* species in savannas can be attributed in part to the production of substantial quantities of seeds, which abets seed mortality due to the high rate of infestation by bruchid beetles (*Bruchidus* spp.) and other environmental uncertainties (Sabiiti & Wein 1987). A general survival 'strategy' is to accumulate large quantities of viable but dormant seeds in the soil during the intervals between fires (Meney *et al.* 1994), whose germination can be stimulated by heat from fires (Portlock *et al.* 1990). Whilst the impact of a fire on the fate of woody seeds is related to fire intensity, maximum fire temperature and duration of exposure (Gill 1981; Pieterse & Cairns 1987; Mucunguzi & Oryem-Origa 1996), the passage of fire can enhance the germination of legume species (Shea McCormick & Portlock 1979; Cavanagh 1980; Hill 1982; Sabiiti 1983; Auld 1986; Hodgkinson 1991; Bell *et al.* 1995; Bradstock & Auld 1995). Other factors related to fire that affect seed germination of *Acacia* species are thickness of testa (Mucunguzi 1995), insect damage (Mucunguzi 1995), burial depth (Auld 1986) and water availability.

Fire interacts with insect damage since fire can increase temperatures beyond a level acceptable for bruchid beetle survival, whilst the embryo shows relatively less sensitivity to increased temperatures (Sabiiti & Wein 1987). In the case of depth of seed burial, the recruitment of shrubs and the number of seedlings present has been found to be dependent on the depth at which the seed was buried in the soil as fire moderates soil temperatures (Auld 1986; Hodgkinson 1991; Portlock *et al.* 1990; Bradstock & Auld 1995; Tozer 1998). The finding that depth of seed burial is important for obtaining favourable temperatures for seed germination, by creating a range of temperatures in the soil, supports studies concluding that a critical temperature exists for both germination and seed mortality (Hodgkinson & Oxley 1990; Portlock *et al.* 1990; Auld & O'Connell 1991). Although heat from fire or solar irradiance is an important natural agent for breaking dormancy of seeds with thick seed coats, the supposed benefits obtained from temperatures high enough and exposures long enough to remove seed coat impermeability may in fact lead to deterioration of seed vigor or even seed embryo death (Portlock *et al.* 1990).

The size of the seed and thickness of the testa can determine the temperature at which dormancy is broken. Whilst moderate temperatures were found to promote the germination of *A. gerrardii* seeds, and higher temperatures caused high seed mortality, the larger seeded *A. sieberiana* seeds had a higher heat resistance than *A. gerrardii* (Mucunguzi & Oryem-Origa 1996). Similarly, Babalwa & Witkowski (1997) reported that larger *A. karroo* seeds maintained better viabilities than relatively smaller *A. tortilis* seeds.

The effect that fire has on woody seeds varies according to the application of a head or a back fire. Although head fires have a greater overall fire intensity than back fires (Trollope 1978), back burns concentrate their maximum heat closer to the ground than head burns (Bailey & Anderson 1980; Trollope 1983, 1984 c), exposing seeds on the soil surface to higher temperatures. As a back burn advances against the direction of the wind, the passage of fire is slower than for a head burn, which advances in the same direction as the wind. Consequently the duration of the fire at any specific point in the grass sward must generally be longer in a back burn than a head burn (Trollope 1974), exposing seeds to fire for a longer time.

Acacia karroo, A. nilotica and *A. sieberana* are three leguminous tree species which have evolved in conditions of fairly frequent fires, and are successful colonizers of such areas. In fact, the passage of fire has been shown to release seeds of *A. karroo* (Babalwa *et al.* 1997), *A. sieberiana* (Sabiiti & Wein 1987; Mucunguzi & Oryem-Origa 1996), and numerous other *Acacia* species (Hill 1982; Hodgkinson & Oxley 1990; Auld & O'Connell 1991; Bradstock & Auld 1995; Teketay 1996) from dormancy. It is likely that variations in the fire regime, especially fire intensity, through its interaction with differential sensitivity to heat in seeds of various species, may play a role in determining population and community structure. It was with this in mind that the relationship between seeds of the abovementioned species and a variety of fires was investigated to determine how fire characteristics affect germination and mortality of these species.

The experiments were set up to address the following objectives:

1) Determine which species demonstrated changes in germination and viability after fire.
2) Quantify the relationships between fire intensity and seed germination and viability.
3) Determine the influence of fire type on seed germination and viability.
4) Identify if the responses of 1, 2 and 3 are affected by seed size.

6.2 Materials and methods

The experiments took place during veld burning on 29 June 1997 and 28 August 1998. Fire characteristics were determined at the micro-site level, with the aim of obtaining an accurate description of the changes in temperature experienced by a seed at a specific location. The fire temperatures at a micro-site were measured using chromel-alumel (type K) thermocouples and a Campbell 21X datalogger housed in a box. A micro-site was defined as a position between grass tussocks on the soil surface where the seeds were exposed to fire.

The experiments took place in the grass component in a mesic savanna. Fire intensities and maximum temperatures were determined for each micro-site. The 24 gauge (0.51 mm diameter) thermocouple wires were covered with glass braid with an additional outer glass braid cover and were buried at about 80 mm below the soil surface for protection from the fire. Only the measurement points were exposed above the ground, measuring temperatures no more than 10 mm from the soil surface. In order to obtain a representative measure of the fire temperature at each micro-site, four points were welded in parallel per thermocouple with the datalogger measuring the average temperature of the four thermocouples on one datalogger channel (Figure 6.1).

The weld for each thermocouple measurement point was about 3 mm long so as to be of almost the same dimensions as the seeds. Per micro-site, six sets of thermocouples (four points per set) were used in 1997 whilst four sets of thermocouples (four points per set) were used in 1998. The micro-sites were selected in the veld with the intention of obtaining a wide range of fire intensities within the veld. A hundred seeds of each species were exposed to fire at each micro-site. In order to examine the effect of fire type on seeds, two back fires and one head fire were studied in 1997, and in 1998 two back and two head fires.

We used slow (16.67 ms) differential voltage measurements for the temperature measurements and a 0 to 50 mV range. The datalogger was programmed to measure each thermocouple temperature every 0.5 s, each temperature being an average of the four thermocouples connected in parallel (Figure 6.1). Measurements more frequent than 0.5 s were not possible since the datalogger program took just over 0.4 s to execute. An average of the 0.5 s values was performed either every 1 s (for fast moving fires), 1.5 s, 2 s or every 5 s while the surface cooled down. Since the thermocouples were wired in parallel, each measurement was a spatial average of the temperature at four locations. For each set of temperature measurements, the real time was also stored to identify the data. During the fire the recorded temperatures were observed in real-time and the high frequency measurements (every 0.5, 1.5, 2 or every 5 s) initiated just before the arrival of the fire. These procedures

minimized the amount of unnecessary information in datalogger memory. Another datalogger (Campbell Scientific CR500) with normal automatic weather station sensors (solar irradiance using a LI200 pyranometer, Vaisala CS500 air temperature and water vapour pressure sensor housed in a six-plate Gill shield and an RM Young 03001 wind speed sensor) was used to record the local micro-climate during the fire.

The soil water content at the site prior to burning was measured at five different locations using a CS615 soil reflectometer (TDR) sensor. The probe was inserted at an angle into the soil to ascertain the average soil moisture content up to 150 mm. The sensor was attached to a 21X datalogger.
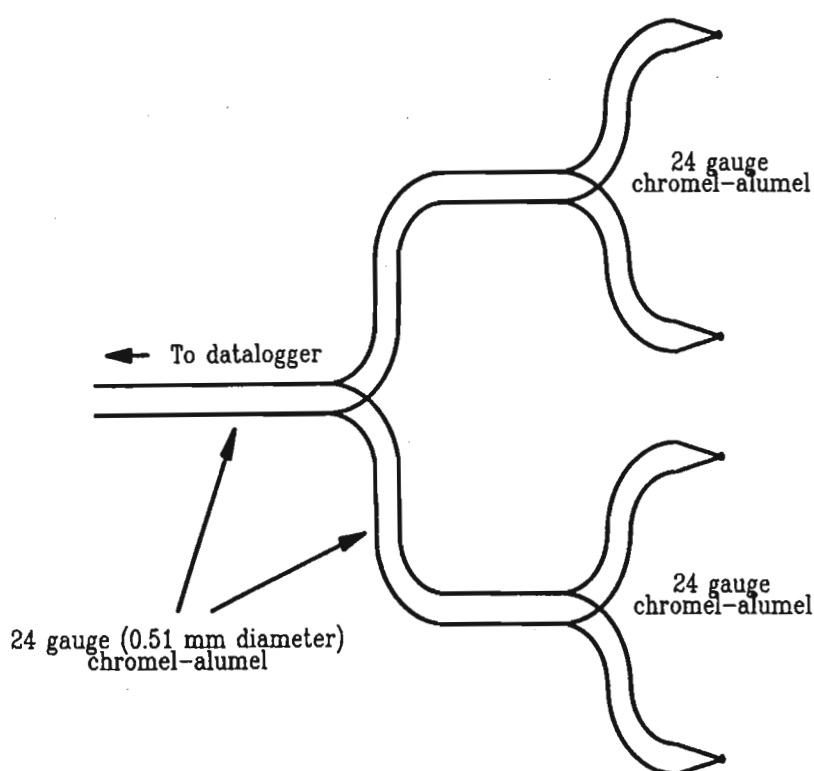
Figure 6.1 Diagram illustrating the experimental design of the thermocouples (from Savage *et al.* 1997)

Before each experimental period, seeds of the experimental species (100 per species) were tested for viability with the use of tetrazolium chloride. After visual examination of the seeds for bruchid infestation, the seed coat was mechanically scarified to allow penetration of the tetrazolium chloride into the embryo. After imbibition the seeds were cut in half and examined for changes in pigmentation which provides evidence of seed viability. *Acacia*

sieberiana seeds were not examined in 1998 owing to the poor viability exhibited by this species in that particular year, which would have confounded results for that year.

A germinability test was conducted on seeds exposed to fire and seeds not exposed to fire (control). Seeds were placed on filter paper in petri dishes in a germination oven (mean temperature of 22 to 25 °C) for a period of 21 days, each day recording how many seeds had germinated on that day. This temperature had been used in similar experiments on *Acacia* seeds (Pieterse 1986; Holmes 1988; Hodgkinson & Oxley 1990). A seed was considered to have germinated when a radicle of 2 mm had emerged. Once a seed had germinated, it was removed. These seeds were then noted both viable and germinable. After 21 days the seeds that had not imbibed water were tested for viability with tetrazolium chloride as described before. The seeds that had imbibed but had not germinated were noted as not viable and not germinable and were discarded. In most cases these seeds were clearly rotten.

6.3 Analysis

Changes in temperature over time, recorded by the datalogger, were plotted on graphs. The intensity of each burn was calculated by determining the area under each temperature *vs* time curve for measured temperatures greater than 25 °C. The area under the curve was calculated for each consecutive times t_1 and t_2 for which the measured temperatures were T_1 and T_2, respectively, as the area of the trapezium formed by the two vertical time lines for t_1 and t_2 and the horizontal temperature lines T_1 and T_2 (Figure 6.2).

The area of the trapezium was calculated as the sum of the:
(i) area of the rectangle: $(t_2 - t_1) \times$ absolute value of $(T_1 - T_n)$, plus
(ii) the area of the triangle: $(t_2 - t_1) \times$ absolute value of $[(T_2 - T_1)/2]$.
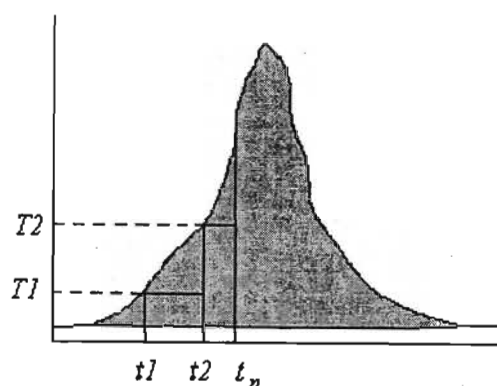
Figure 6.2 Calculation of the area under each temperature vs time curve for calculation of the fire intensity (°C.h) using the temperature before the experiment as a baseline (roughly 25°C).

The total area was calculated as the sum of each incremental area. For each burn, the average and standard deviation of all areas was calculated. Furthermore, the maximum temperature of each fire was determined.

Student t-tests were used to test for differences in fire intensity and maximum temperature of head and back fires. These differences were illustrated graphically with 95 % confidence bars.

The response of seeds to fire was examined by calculating percentage germination and percentage mortality (the sum of the number of seeds that became rotten and the number that did not become rotten but were found to have lost viability after the fire), and plotting these responses relative to fire intensity and maximum temperature. Regression equations were developed for predicting mortality of seed under different fire intensities and maximum temperatures. These were carried out for the pupose of determining critical threshold temperatures and fire intensities for seedling mortality and germination. *Acacia karroo* and *A. nilotica* could be considered over both seasons, whereas *A. sieberiana* could only be examined for the 1997 season.

6.4 Results

6.4.1 Laboratory results

Acacia karroo and *A. nilotica* seeds were found to have high viability, exceeding 90 % in both years, whilst *A. sieberiana* had slightly poorer viability (Table 6.1). In the germination trial (Table 6.2) it was found that very few of the seeds germinated, and that the remaining seeds that did not imbibe generally remained viable. Variations in the response of different *Acacia* species to fire were therefore assumed to be related to seed characteristics.

Seed mass differed significantly among species, with *Acacia sieberiana* the heaviest, followed by *A. nilotica* and lastly *A.karroo* (Table 6.1).

Table 6.1 Mass and percentage viability of *A. karroo*, *A. nilotica* and *A. sieberiana* seeds taken from Ukulinga Research Farm in 1997 and 1998 (n = 100 for each species)

Species	mass (g)		viability (%)	
	mean	standard deviation	1997	1998
Acacia karroo	0.0422	0.0061	94	92
Acacia nilotica	0.1309	0.0107	91	93
Acacia sieberiana	0.1870	0.0335	85	-

Table 6.2 Percentage germination, mortality (seeds rotten and found to be not viable) and viability (seeds that did not germinate but remained viable) of *A. karroo*, *A. nilotica* and *A. sieberiana* seeds (not scarified) taken from Ukulinga Research Farm in (a) 1997 and (b) 1998 (n = 100 for each species)

Species	Germination (%)	Mortality (%)	Viability (%)
(a) 1997			
Acacia karroo	6	8	86
Acacia nilotica	4	13	83
Acacia sieberiana	7	19	74
(b) 1998			
Acacia karroo	4	6	90
Acacia nilotica	1	6	93

6.4.2 Back fires *versus* head fires

Changes in fire temperature over time, as recorded by the datalogger, were illustrated for each micro-site (Appendix 3). The data recorded by the datalogger for back fire 1 micro-site 3 in 1997 had to be rejected as the fire did not pass over these thermocouples. Data received for head fire 1 micro-site 1 also had to be rejected as a rock was discovered in close proximity to the seeds which remained hot for a long period after the fire had passed. For the remaining micro-sites, the means, standard deviations and confidence limits were calculated (Appendix 4) to illustrate (Figure 6.3) differences evident in the t-tests.

Back fires had higher fire intensities and maximum temperatures than head fires in each season, although these differences were not always significant (Figure 6.3). In both seasons, generally head fire intensities remained below 10 °C.h and maximum temperatures remained below 450 °C (Figure 6.4). The four highest maximum temperatures and intensities

achieved by the 1998 head fires were attributable to temperatures obtained by thermocouples placed in a patch dominated by *Cymbopogon excavatus* grass plants, which burned extremely hot (personal observation). Therefore, maximum temperatures and fire intensities of head fire 2 cannot be compared to the other fires in terms of fire type. However, note must be made of the fact that although the *C. excavatus* fire had a far higher maximum temperature than the other sites, it still had a lower fire intensity than back fires in that year.

(a) 1997
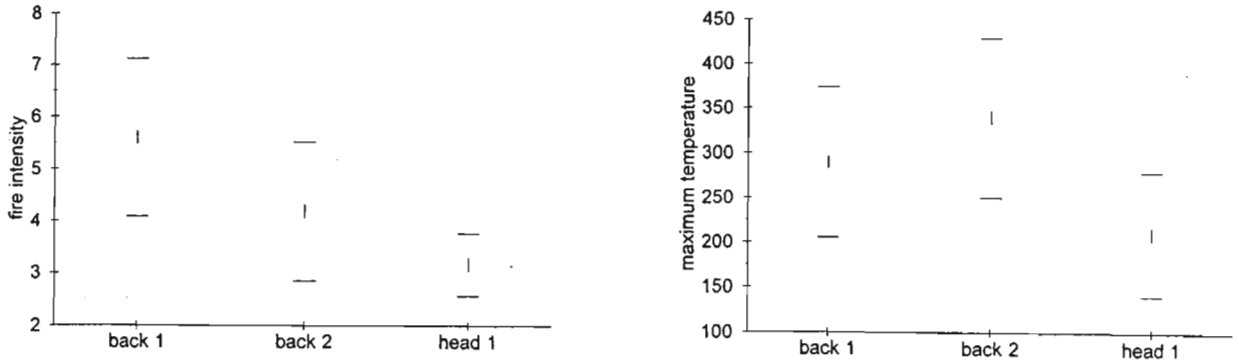
(b) 1998
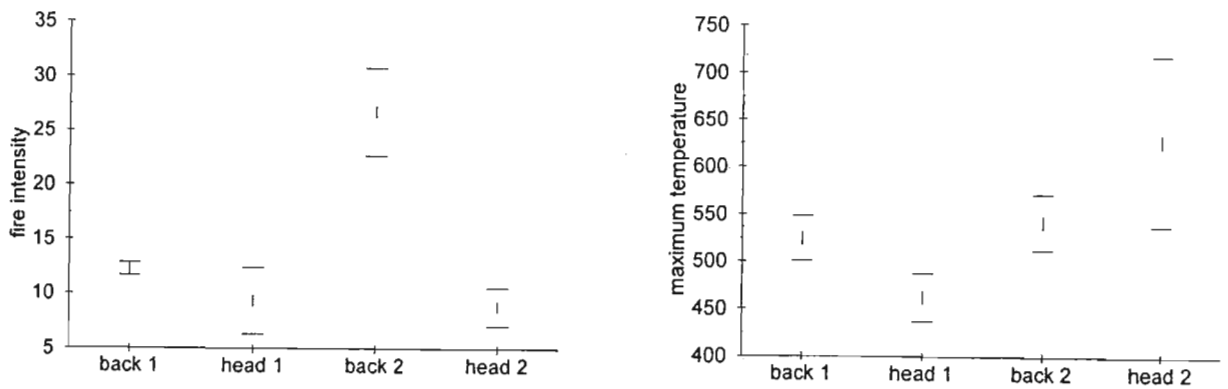
Figure 6.3 Mean fire intensity ($^{\circ}$C.h) and maximum temperature ($^{\circ}$C) of head and back fires in (a) 1997 and (b) 1998 (95% confidence limits)
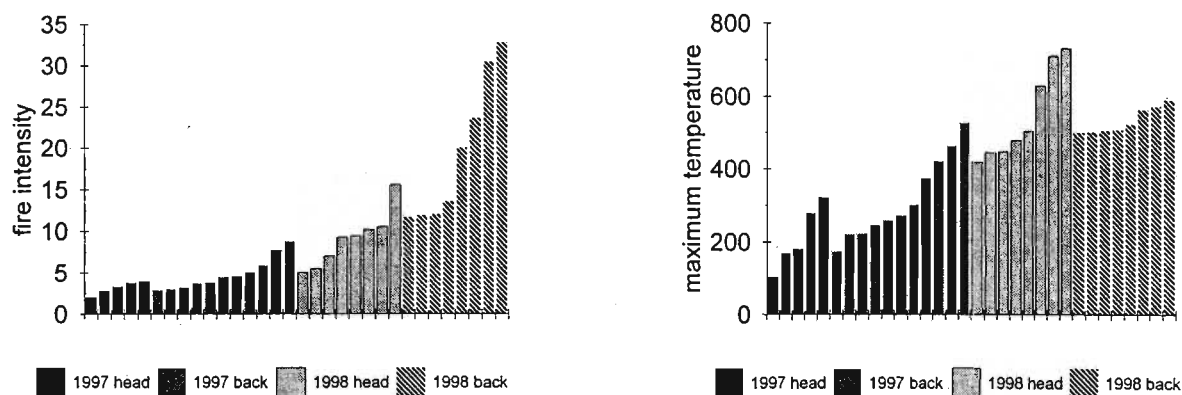
Figure 6.4 Individual (a) fire intensities (°C.h) and (b) maximum temperatures (°C) of head and back fires in 1997 and 1998

6.4.3 Seed germination, mortality and survival

When examining the 1997 and 1998 seasons separately there were no apparent trends in germination and mortality versus fire intensity and maximum temperature. However, when both seasons were considered together a relationship became apparent, although indistinct and very variable (Figure 6.5). Whilst it was impossible to fit curves to germination, which was too variable, it was possible to relate mortality of *A. karroo* and *A. nilotica* to maximum temperature and fire intensity, which accounted for 47.3 % and 53.5 % of the variance respectively, and to relate maximum temperature to mortality of *A. sieberiana*, which accounted for 55.9 % of the variance.

Unfortunately, species differences could not be examined in terms of germination, as the germination response to fire intensity and maximum temperature was too variable. Considering all species together relative to the controls (Table 6.2), seed germination was enhanced in both 1997 and 1998. A fire intensity greater than 15 °C.h yielded less germination than the controls, whilst an intensity of lower than 15 °C.h yielded germination generally comparable to or greater than the controls (Figure 6.5). The relationship of germination and maximum temperature was too vague to draw any reasonable conclusions.

The passage of fire also decreased the potential recruitment of seeds. Control seeds had low mortality during the experiments (Table 6.2), whilst seeds exposed to fire generally experienced between 40 % and 100 % mortality for fire intensities greater than 10 °C.h and

maximum temperatures greater than 450 °C (*A. karroo* and *A. nilotica)*. Below the aforementioned temperatures and fire intensities mortality ranged between 6 and 40 %. A threshold fire intensity and maximum temperature therefore appears to exist, beyond which mortality of *A. karroo* and *A. nilotica* is increased. At higher temperatures *A. karroo* (smaller-seeded) exhibited poorer survival than *A. nilotica* (larger-seeded).

The relationship of fire intensity and mortality of *A. sieberiana* could not be compared to *A. karroo* and *A. nilotica* as fire intensity in 1997 did not exceed 9 °C.h. However, *A. sieberiana* illustrated greater resistance to maximum temperature, with seed mortality less than 60 % for temperatures in excess of 450 °C. The success of *A. sieberiana* must be seen in the light of its relatively poorer viability (19%) than *A. karroo* (8%) and *A. nilotica* (13%).

Acacia karroo, Acacia nilotica
(a) germination

(b) mortality

● 1997 ☐ 1998

● 1997 ☐ 1998

● 1997 ☐ 1998

● 1997 ☐ 1998
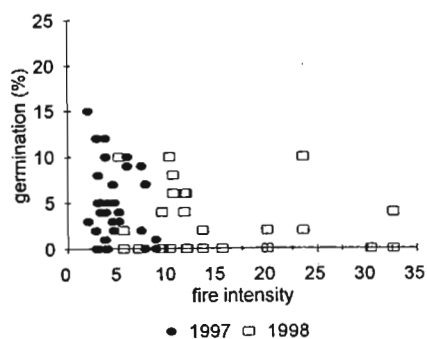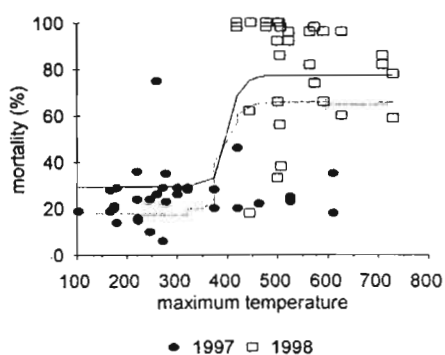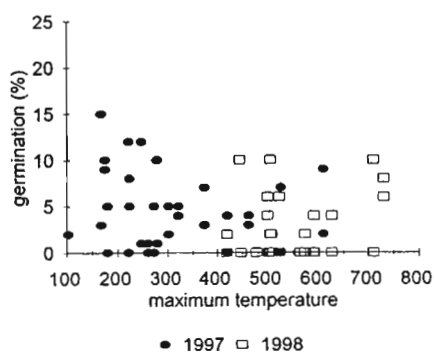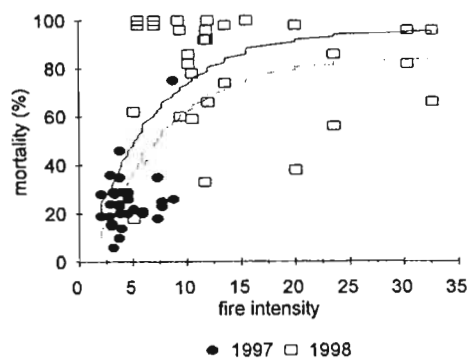
Acacia sieberiana
(a) germination
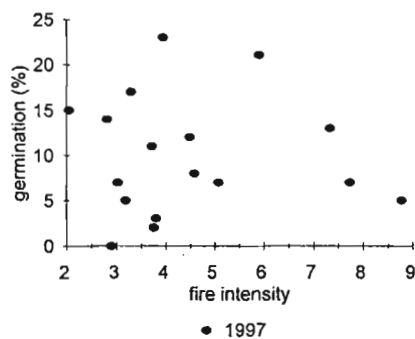
Acacia sieberiana
(b) mortality
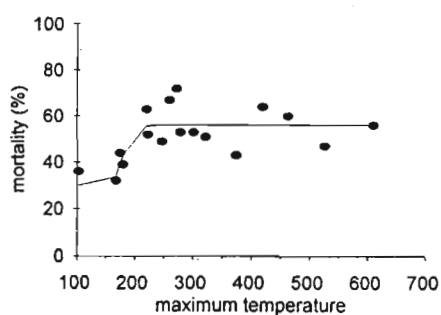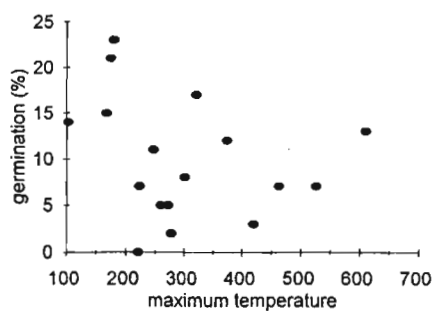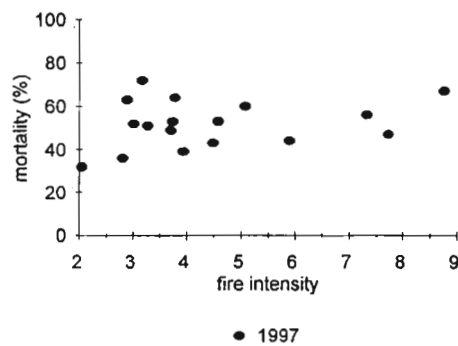
● 1997

Figure 6.5 The effect of fire intensity (^{o}C.h) and maximum temperature (^{o}C) on percentage

seed (a) germination and (b) mortality for *A. karroo* (solid line) and *A. nilotica* ( ), and *A.*

sieberiana.

6.5 Discussion

6.5.1 Germination

The relatively mild fire in 1997 and the much hotter fire in 1998 both increased the germination of *Acacia* seeds relative to the control seeds, although germination was poorer in 1998 than in 1997. The difference in fires was attributed to climatic conditions at the experimental site on the day of burning and differences in biomass between seasons (Appendix 5 and 6). In 1998 the conditions for a hot fire were more favourable than in 1997, as on the day of burning the ambient temperature was higher, fuel moisture lower and a higher fuel load had accumulated in 1998.

Whilst many authors have shown that fire can initiate germination of seeds from dormancy (Sabiiti 1983; Sabiiti & Wein 1987; Portlock *et al.* 1990; Hodgkinson 1991; Bell *et al.* 1995; Bradstock & Auld 1995), fire intensity and maximum temperature determine whether a fire is beneficial or not to the species (Hodgkinson & Oxley 1990; Auld & O'Connell 1991; Babalwa *et al.* 1997). This proposes the existence of a threshold fire intensity and maximum temperature at which seed germination is enhanced, and beyond which seed germination is adversely affected. At Ukulinga the threshold was considered to be 15 °C.h for fire intensity, whilst no relationship was evident for germination *versus* maximum temperature. However, germination remained comparable to that of control seeds across all maximum temperatures, and even exhibited higher germination at temperatures over 700 °C. Studies have shown germination of seeds to be enhanced by relatively lower temperatures, such as temperatures of 55 °C to 60 °C (Portlock *et al.* 1990), 80 °C to 100 °C (Auld & O'Connell 1991), and 60 °C (Hodgkinson & Oxley 1990).

The germination results at Ukulinga were similar to results obtained by Portlock *et al.* (1990), as great variation in germination was witnessed in both studies, and germination was less than 15% after fire temperatures exceeding 200 °C. Nevertheless, seed germination generally remained higher than in the controls. Variability in germination elicits questions as to variation in seed dormancy and heating tolerances within a species.

6.5.2 Mortality

In both seasons the potential of future seedling recruitment declined after a fire, as many seeds were destroyed by the passage of the fire, whilst seeds not exposed to fire (control) retained their ability to germinate at a later stage. The negative impact of intense ground fires

may be the destruction of seeds on or near the soil surface. Maximum temperatures obtained at Ukulinga (ranging from 103 °C to 730 °C) far exceeded temperatures recognized to increase seed mortality. However, a temperature of 450°C and intensity of 10°C.h were considered threshold values, mortality being much greater above this temperature and intensity than below. The lethal threshold has been described to be upwards of temperatures of 70 °C and 80 °C (Hodgkinson & Oxley 1990), and temperatures above 120 °C (Auld & O'Connell 1991). Most authors advocate a lethal threshold of temperatures below 100 °C, but seeds have been found to germinate at temperatures greater than 200 °C (Portlock et al. 1990). However, a large percentage of the soil seedbank is likely to remain dormant after a fire, as was the case with *Acacia saligna* (88 to 94 %) (Tozer 1998). Moreover, as *Acacia* species produce large quantities of seed every season, forming very large seed banks in the soil (Sabiiti & Wein 1987), mortality caused by fire is probably negated by seed input, and the seedbank is unlikely to be significantly depleted following a single fire. Furthermore, in the present study seeds were placed on the soil surface and were consequently afforded less protection from fire than seeds deeper in the soil.

6.5.3 Fire type

The finding at Ukulinga that back fires achieved greater maximum temperatures and fire intensities than head fires at ground level is consistent with other studies (Trollope 1974; Bailey & Anderson 1980; Trollope 1984 c). A back fire is of longer duration (Appendix 3) because the fire is moving against the wind. As the effects of an increase in soil temperature on seeds is likely to be confined to a comparatively shallow top layer of the soil (Norton & McGarity 1965; Scotter 1970; Savage 1980; Sabiiti & Wein 1987), the depth of soil heating is important, which is determined by fire temperature at the soil surface and conductivity of the soil. Back fires can heat the soil to greater depths than head fires, and influence germination of seeds deeper in the soil. Although hot back fires resulted in substantial mortality of seeds on the soil surface at Ukulinga, back fires are envisioned to exert positive effects on seeds located in the soil. To achieve temperatures sufficient for seed germination at deeper levels in the soil, the passage of a very hot fire close to the soil surface is necessary. A marked negative exponential relationship was found between soil depth and fire temperature, and consequently seeds deeper in the soil are afforded better protection from fire than seeds on or near the soil surface (Bradstock & Auld 1995). Thus, even extremely hot fires (such as the fire at Ukulinga Research Farm in 1998) can make a positive impact on seed germination, depending on the depth of seed burial.

6.5.4 Seed size

At Ukulinga seed mortality was inversely related to seed size, which supports findings that heat resistance of *Acacia* species is enhanced by larger seed size (Mucunguzi & Oryem-Origa 1996; Babalwa & Witkowski 1997). Contrary to the documented high tolerance of *A. karroo* to heating (Bond & VanWilgen 1996; Babalwa & Witkowski 1997), this species fared poorly relative to *A. sieberiana* and *A. nilotica*. This suggests that the relative success of *A. karroo* as an encroaching species must be attributed to other factors.

6.5.5 Management implications

The application of burning as a management strategy can have important consequences for woody plant recruitment, as germination of *Acacia* species was enhanced by fire, regardless of maximum temperature. It is predicted that in the presence of a large seedbank of considerable depth, germination of fire-released seeds will most likely be enhanced by all fires. Furthermore, the choice of head or back fire can further influence woody seedling dynamics, as back fires are more intense at ground level, can affect seeds buried at greater depths, and result in greater seed mortality. Therefore, the effect of a back fire and head fire on seeds deeper in the soil must be investigated to determine the overall affect of fire type on seedling recruitment. Further research must be conducted on the impact of grass species abundance on fire intensity, as certain species (such as *C. excavatus* in this experiment) burn at considerably higher temperatures than others.

CHAPTER 7

CONCLUSION

Herbivory only affected seedling dynamics after the emergence stage. The degree of seedling establishment in systems that contain small-mouthed herbivores therefore depends upon the effect of herbivory on seedling growth and survival. Furthermore, trends in seedling emergence may vary greatly in response to climatic conditions, and ultimately seedlings that manage to survive will contribute to the woody population, promoting bush encroachment. In light of the above statement, *A. karroo* should be the most successful encroaching species at Weenen and Ukulinga, whilst *A. nilotica* should be more successful than *A. tortilis* at Abu Madi, which is evident in established vegetation.

Woody establishment was influenced by animal type in both domestic and wildlife systems. Poorer performance in sheep grazed areas was attributed to herbivory, which decreased seedling growth and survival. Animal type was considered to influence seedling establishment more than graziing system. Although cattle impacted on seedlings by trampling, they did not graze on woody seedlings. In a wildlife system incorporating large numbers of small-mouthed herbivores, protection from potential herbivory resulted in significantly better seedling establishment. However, protection from potential herbivory did not result in better seedling establishment in a wildlife system lacking small-mouthed herbivores. Whilst small-mouthed herbivores utilized woody seedlings, large-mouthed herbivores did not. Consequently, an increase in woody density is more likely in the latter. Although herbivory affected seedling establishment, grass competition was found to be a more important influence in the wildlife system.

The effect of grass competition on seedling emergence depended on woody species, with *A. karroo* and *A. tortilis* illustrating relatively less emergence in the grass sward. However, overall seedling emergence was greatest for *A. karroo*, followed by *A. nilotica* and lastly *A. tortilis*. Lower grass biomass was advantageous for seedling establishment in wildlife systems, irrespective of animal species composition. This was observed over varying degrees of grass biomass reduction, as seedlings at Abu Madi experienced a total reduction and Weenen only a partial reduction in grass biomass. Below-ground competition on seedling establishment at Weenen could not be discounted. As seedlings benefitted from decreases in grass biomass, it is suggested that pre-emergence burning and high stocking pressure by cattle may promote seedling establishment, by decreasing above-ground grass biomass.

Whilst reasons for poorer seedling establishment due to grass competition were not determined in this study, above-ground competition for light influenced seedling growth. This effect was seen in greater leaf-to-height ratios of seedlings growing in areas of reduced above-ground grass biomass. Furthermore, burning and cattle grazing, by reducing above-ground grass biomass, appear to facilitate this effect. In addition to promoting the growth of seedlings, burning exerted a greater influence on seedling survival than did grass competition. However, this could not be attributed solely to a decrease in grass competition as fire influences plant dynamics in a number of ways.

The influence of treatment on seedling survival was greatest in the period after emergence, which is consistent with findings suggesting seedlings to be most vulnerable in the early stages of development. Although treatment differences were maintained, seedlings appear to acquire greater resistance to herbivory and grass competition within 6 to 7 weeks following emergence, showing noticeable improvement in survival thereafter.

The effect of fire on seedling recruitment appears to be determined by positive effects on seed germination and negative effects on potential recruitment due to seed bank mortality. Mortality was greater for seeds exposed to fire than not, regardless of fire intensity, maximum temperature and seed size. However, seed mortality in response to maximum fire temperature seems to be contingent on seed size, as mortality was inversely related to seed size, with mortality being lowest for *A. sieberiana* folllowed by *A. nilotica* and lastly *A. karroo*. Seed germination was greater than that of the controls at fire intensities below 15°C.h, and mortality was greater above this value. Whilst germination in relation to maximum temperature was too variable to tender a critical value as above, the magnitude of mortality was greatly increased at temperatures greater than 450°C. The impact on mortality and germination was likely to be influenced by fire type, as back fires had greater fire intensities and maximum temperatures than head fires at the soil surface. Although predictions based on these results suggest better recruitment for larger-seeded species, the influence of seed size on depth of burial in the soil has not been taken into account.

An important shortcoming of this study was the experimental period, which neglected dry season seedling mortality. Consequently, the interpretation of results was limited to seedling establishment over a seedlings first growing season. More intensive monitoring is also necessary, especially within the first few weeks, in order to ascertain causal factors of differences in seed mortality and growth.

Based on the current study it is hypothesized that an increase in woody plant density will take place in the absence of small-mouthed browsers and a change from continuous to

rotational grazing. This is contrary to traditional thinking, which advocates the use of rotational grazing systems and the elimination of small-mouthed herbivores to avoid veld degradation. However, whilst the latter approach may improve the grass sward, it seems to have the potential to result in bush encroachment. In order to impact on establishing woody seedlings, it is recommended that domestic and wildlife systems incorporate a mix of species, which managed correctly at reasonable stocking rates would not result in veld degradation.

As seedlings are adversely affected by grass biomass, woody seedlings may benefit from the effect of burning and cattle grazing on grass biomass. More robust conclusions would be possible if seedling growth and survival could be attributed to the effect of grazing and burning on grass biomass, an avenue for future research.

Future research on the effect of fire on seeds should focus on changes in soil temperature as a result of fire type, and subsequent effects on seed germination and mortality, subject to seed size. A modelling approach is suggested, to allow for prediction of seedling recruitment from the seed bank.

REFERENCES

Acocks JPH 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 57.1.46. Government printer, Pretoria.

Acocks JPH 1966. Non-selective grazing as a means of veld reclamation. *Proceedings of the Grassland Society of Southern Africa* 1:33-39.

Anderson KL 1965. Time of burning as it affects soil moisture in an ordinary upland bluestem prairie in the Flint Hills. *Journal of Range Management* 18:311-316.

Archer S 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545-561.

Archer S, Scifres C, Bassham CR & Maggio R 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-127.

Arnold TH & De Wet BC 1993 (eds). Plants of southern Africa: names and distributions. *Memoirs of the Botanical Survey of Southern Africa* 62: Botanical Research Institute, Pretoria.

Aucamp AJ 1976. The role of the browser in the bushveld of the Eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 11:135-138.

Auld TD 1986. Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the transition to seedlings. *Australian Journal of Ecology* 11:373-385.

Auld TD 1987. Population dynamics of the shrub *Acacia suaveolens* (Sm.) Will.: Survivorship throughout the life cycle, a synthesis. *Australian Journal of Ecology* 12:139-151.

Auld TD 1995. Seedling survival under grazing in the arid perennial *Acacia oswaldii*. *Biological Conservation* 72:27-32.

Auld TD & Bradstock RA 1996. Soil temperatures after the passage of a fire: Do they influence the germination of buried seeds? *Australian Journal of Ecology* 21:106-109.

Auld TD & O'Connell MA 1991. Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* 16:53-70.

Babalwa AM & Witkowski ETF 1997. Tolerance to soil temperatures experienced during and after the passage of fire in seeds of *Acacia karroo*, *Acacia tortilis* and *Chromolaena odorata*. *South Africa Journal of Botany* 63:421-425.

Bailey AW & Anderson ML 1980. Fire temperatures in grass, shrub and aspen forest communitiesof Central Alberta. *Journal of Range Management* 33:37-40.

Bell DT, Rokich DP, McChesney CJ & Plummer JA 1995. Effects of temperature, light and gibberellic acid on the germination off seeds of 43 species native to Western Australia. *Journal of Vegetation Science* 6:797-806.

Belsky AJ 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology* 22:271-279.

Belsky AJ 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75:922-932.

Ben-Shahar R 1996. Woodland dynamics under the influence of elephants and fire in Northern Botswana. *Vegetatio* 123:153-163.

Bergstrom R 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science* 3:315-324.

Bille JC 1985. Some aspects of bush encroachment in the African rangelands. In: *Ecology of the World's Savannas* (eds. Tothill JC & Mott JJ), Australian Academy of Science, Canberra, pp. 213-216.

Bond WJ & VanWilgen BW 1996. *Fire and plants*. Chapman & Hall, London.

Bradstock RA & Auld TD 1995. Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32:76-84.

Breebaart L 2001. Resource overlap within a guild of browsing ungulates in a South African savanna. M.Sc. Thesis, Range and Forage Resources, University of Natal.

Breebaart L, O'Connor TG, Hughes JC, Morris C & Rushworth IA 2001. The effects of topo-edaphic factors and cultivation on the woody vegetation of Weenen Nature Reserve, KwaZulu-Natal. *African Journal of Range and Forage Science,* in press.

Brooks R & Owen-Smith N 1994. Plant defences against mammalian herbivores: are juveniles more heavily defended than mature trees? *Bothalia* 24:211-215.

Brown JR & Archer S 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19-26.

Brown JR & Archer S 1990. Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos* 57:366-374.

Brown JR, Scanlan JC & McIvor JG 1998. Competition by herbs as a limiting factor in shrub invasion in grassland: a test with different growth forms. *Journal of Vegetation Science* 9:829-836.

Brown JR & Archer S 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385-2396.

Brown NAC & Booysen P 1967. Seed germination and seedling growth of two *Acacia* species under field conditions in grassveld. *South African Journal of Agricultural Science* 10:666-695.

Bush JK & VanAuken OW 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette* 151:234-239.

Bush JK & VanAuken OW 1995. Woody plant growth related to planting time and clipping of a C_4 grass. *Ecology* 76:1603-1609.

Caldwell MM, Richards JH, Manwaring JH & Eissenstat DM 1987. Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. *Nature* 327:615-616.

Cass A, Savage MJ & Wallis FM 1984. The Effect of Fire on Soil and Microclimate. In: *Ecological Effects of Fire on South African Ecosystems* (eds. Booysen P de V & Tainton NM 1984), Springer-Verlag, Berlin, pp. 311-325.

Cavanagh AK 1980. A review of some aspects of the germination of *Acacias*. *Proceedings of the Royal Society of Victoria* 91:161-180.

Chirara C, Frost PGH, & Gwarazimba VEE 1998. Grass defoliation affecting survival and growth of seedlings of *Acacia karroo*, an encroaching species in southwestern Zimbabwe. *African Journal of Range and Forage Science* 15:41-47.

Coe M & Coe C 1987. Large herbivores, acacia trees and bruchid beetles. *South African Journal of Science* 83:624-635.

Cohn EJ, VanAuken OW & Bush JK 1989. Competitive interactions between *Cynodon dactylon* and *Acacia smallii* seedlings at different nutrient levels. *The American Midland Naturalist* 121:265-272.

Cohn JS & Bradstock RA 2000. Factors affecting post-fire seedling establishment of selected mallee understorey species. *Australian Journal of Botany* 48:59-70.

Cooper SM 1982. The comparative feeding behaviour of goats and impalas. *Proceedings of the Grassland Society of Southern Africa* 17:117-121.

Cooper SM & Owen-Smith N 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 8:446-455.

Cumming DHM 1982. The influence of large herbivores on savanna structure in Africa. In: *Ecology of tropical savannas* (eds. Huntley BJ & Walker BH), Springer-Verlag, Berlin, pp. 217-245.

Danckwerts JE, Aucamp AJ & Barnard HJ 1983. Herbaceous species preference by cattle in the false thornveld of the eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 18:89-94.

Demment MW 1983. Feeding ecology and the evolution of body sizes in baboons. *African Journal of Ecology* 21:219-233.

Dent MC, Lynch SD & Sculze RE 1987. *Mapping mean annual and other rainfall statistics over Southern Africa.* WRC Report No 109/1/89.

Donaldson CH 1979. Goats and/or cattle on mopaneveld. *Proceedings of the Grassland Society of southern Africa* 14:119-123.

Du Toit PF 1967. An autecological study of the seedling of *Acacia karroo. Proceedings of the Grassland Society of Southern Africa* 2:119-126.

Du Toit PF 1972 a. Incidence and intrusion of *Acacia karroo* in the eastern Cape region: influence of Angora goat and Merino sheep grazing on *A. karroo* regrowth. 1968-1971. Final report. OK-Do 57/3. Department of Agriculture and Technical Services, South Africa.

Du Toit PF 1972 b. The goat in a bush-grass community. *Proceedings of the Grassland Society of southern Africa* 7:44-50.

Du Toit JT, Bryant JP & Frisby K 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology* 71:149-154.

Dye PJ & Spear PT 1982. The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. *Zimbabwe Journal of Agricultural Research* 20:103-117.Edwards D 1967. *A plant ecological survey of the Tugela river basin.* Phd. Thesis, University of Natal, Pietermaritzburg, 145 pp.

Edwards GR, Parsons AJ, Newman JA & Wright IA 1996. The spatial pattern of vegetation in cut and grazed grass/white clover pastures. *Grass and Forage Science* 51:219-231.

Edwards PJ 1961. Studies in veld burning and mowing in the Tall Grassveld of Natal. M.Sc. Thesis, University of Natal.

Ellison L 1960. The influence of grazing on plant succession. *Botanical Reviews* 26:1-78.

Emslie R & Adcock K 1993. *Black Rhino 2000 Final Report,* Ecoscot Consultancy Services, volume 3.

Ernst WHO 1988. Seed and seedling ecology of *Brachystegia spiciformis*, a predominant tree component in miombo woodlands in South Central Africa. *Forest Ecology and Management* 25:195-210.

Fahnestock JT & Knapp AK 1994. Plant responses to selective grazing by bison: interaction between light, herbivory and water stress. *Vegetatio* 115:123-131.

Friedel MH 1987. A preliminary investigation of woody plant increase in the western Transvaal and implications for veld assessment. *Journal of the Grassland Society of Southern Africa* 4:25-30.

Frost PGH & Robertson F 1985 The ecological effects of fire in savannas. In:. *Determinants of Tropical Savannas* (ed. Walker BH), IRL Press, Oxford, pp. 93-140.

Fuls ER 1992. Ecosystem modification created by patch-overgrazing in semi-arid grassland due to patch-selective grazing. *Journal of Arid Environments* 23:59-69.

GENSTAT (1993) *Genstat 5.3. Reference Manual.* Clarendon Press, Oxford, UK.

Gill AM 1981. Adaptive responses of Australian vascular plant species to fires. In: *Fire and the Australian biota* (ed. Gill AM), Australian Academy of Science, Canberra, pp. 243-272.

Goldberg D 1990. Components of resource competition in plant communities. In: *Perspectives on plant competition* (eds Grace JB & Tilman D), Academic Press, New York, pp.51-55.

Goodman PS 1975. *The relation between vegetation structure and its use by wild herbivores in a riverine habitat.* M.Sc. thesis, University of Zimbabwe.

Gordon IJ & Illius AW 1996. The nutritional ecology of African ruminants: a reinterpretation. *Journal of Animal Ecology* 65:18-28.

Gowda JH 1997. Physical and chemical response of juvenile *Acacia tortilis* trees to browsing. Experimental evidence. *Functional Ecology* 11:106-111.

Grossman D, Grunow JO & Theron GK 1981. The effect of fire with and without subsequent defoliation on the herbaceous layer of *Burkea africana* savanna. *Proceedings of the Grassland Society of southern Africa* 16:117-120.

Hardy MB 1995. Short-term effects of cattle-to-sheep ratio and stocking rate on patch grazing in sour grassveld. *African Journal of Range and Forage Science* 12:121-127.

Harper JL 1977. *The population biology of plants.* Academic Press, New York, New York, USA.

Harrington GN 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72(3):1138-1149.

Hatch GP 1991. Species and area-selection patterns in the Southern Tall Grassveld of Natal. M.Sc.(Agric.) Thesis, Grassland Science, University of Natal.

Hatch G, Morley T & Huse J 1988. *The vegetation types of Weenen Nature Reserve*. Natal Parks Board Publication, Pietermaritzburg.

Hatch GP & Tainton NM 1990. A preliminary investigation of area-selective grazing in the Southern Tall Grassveld of Natal. *Journal of theGrassland Society of Southern Africa* 7:238-242.

Heady HF & Child RD 1994. *Rangeland Ecology and Management.*, Westview Press, Oxford.

Higgins SI, Bond WJ & Trollope WSW 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213-229.

Hill RS 1982. Rainforest Fire in Western Tasmania. *Australian Journal of Botany* 30:583-589.

Hodgkinson KC 1991. Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology* 28:60-70.

Hodgkinson KC & Harrington GN 1985. The case for prescribed burning to control shrubs in eastern semi-arid woodlands. *Ausralian Rangeland Journal* 7:64-74.

Hodgkinson KC & Oxley RE 1990. Influence of fire and edaphic factors on germination of the arid zone shrubs *Acacia aneura*, *Cassia nemophila* and *Dodonaea viscosa*. *Australian Journal of Botany* 38:269-279.

Hoffman MT & O'Connor TG 1999. Vegetation change over 40 years in the Weenen/Muden area, KwaZulu-Natal: evidence from photo panoramas. *African Journal of Range and Forage Science* 16:71-88.

Holland EA & Detling JK 1990. Plant response to herbivory and below ground nitrogen cycling. *Ecology* 71:1040-1049.

Holmes PM 1988. Implications of alien *Acacia* seed bank viability and germination for clearing. *South African Journal of Botany* 54: 281-284.

Hughes JC 1989. *Soil Survey of the Weenen Nature Reserve*. The Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, Natal. (unpublished)

Hulbert LC 1969. Fire and litter effects in undisturbed bluestem. *Ecology* 50:874-877.

Illius AW & Gordon IJ 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56:989-999.

Jeltsch F, Milton SJ, Dean WRJ & VanRooyen N 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* 84:583-595.

Jordaan JJ 1995. Research note: The short-term effect of fire on the woody component of the Sourish Mixed Bushveld.

Knapp AK & Seastedt TR 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36:662-668.

Knoop WT & Walker BH 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73:235-253.

Kreuter UP & Tainton NM 1988. The effect of continuous and rotational grazing of sourveld on the selection of plant fractions by simmentaler heifers. *Journal of the Grassland Society of Southern Africa* 5:68-71.

Lamprey HF, Halevy G & Makacha S 1974. Interaction between *Acacia* bruchid seed beetles and large herbivores. *East African Wildlife Journal* 12:81-85.

Launchbaugh JL 1955. Vegetational changes in the San Antonio prairie associated with grazing, retirement from grazing, and abandonment from civilisation. *Ecological Monographs* 29:39-74.

Leuthold W 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. *Oecologia* 35:241-252.

Lutge BU, Hatch GP & Hardy MB 1995. The influence of urine and dung deposition on patch grazing patterns of cattle and sheep in Southern Tall Grassveld. *African Journal of Range and Forage Science* 12:104-110.

Madany MH & West NE 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64:661-667.

Martin RE, Miller RL & Cushwa CT 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56:1441-1445

Mbalo BA & Witkowski 1997. Tolerance to soil temperatures experienced during and after the passage of fire in seeds of *Acacia karroo, Acacia tortilis* and *Chromolaena odorata*: a laboratory study. *South African Journal of Botany* 63:421-425.

McDonald P, Edwards RA & Greenhalgh JFD 1992. *Animal Nutrition 4th edition*. Longman Scientific and Technical, John Wiley & Sons, New York.

McNaughton SJ, Wallace LL & Coughenour MB 1983. Plant adaptation in an ecosystem context: effects of defoiliation, nitrogen, and water on growth of an African C_4 sedge. *Ecology* 66:307-318.

Menaut JC, Gignoux J, Prado C & Clobert J 1990. Tree community dynamics in a humid savanna of the Cote-d'Ivoire: Modelling the effects of fire and competition with grass and neighbours. *Journal of Biogeography* 17:471-481.

Meney KA, Nielssen GM & Dixon KW 1994. Seed bank patterns in *Restoniaceae* and *Epacridaceae* after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* 5:5-12.

Mentis MT 1981. The animal factor. In: *Veld and pasture management in South Africa* (ed. Tainton NM), University of Natal Press, Pietermaritzburg, pp. 313-377.

Milewski AV, Young TP & Madden D 1991. Thorns as induced defences: experimental evidence. *Oecologia* 86:70-75.

Mills JN 1986. Herbivores and early postfire succession in southern California chaparral. *Ecology* 67:1637-1649.

Milton SJ 1982. Effects of shading on nursery grown *Acacia* seedlings. *South African Journal of Botany* 48:245-272.

Monleon VJ, Cromack K & Landsberg JD 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in Oregon. *Canadian Journal of Forest Research* 27:369-378.

Moreno JM & Oechel WC 1991. Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. *Oecologia* 85:429-433.

Morris CD, Derry JF & Hardy MB 1999. Effect of cattle and sheep on the structure of Highland Sourveld swards in South Africa. *Tropical Grasslands* 33:111-121

Mucunguzi P 1995. Effects of bruchid beetles on germination and establishment of *Acacia* species. *African Journal of Ecology* 33:64-70.

Mucunguzi P & Oryem-Origa H 1996. Effects of heat and fire on the germination of *Acacia sieberiana* D.C. and *Acacia gerrardii* Benth. In Uganda. *Journal of Tropical Ecology* 12:1-10.

Mwalyosi RBB 1990. The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. *African Journal of Ecology* 28:189-199.

Nolan T & Conolly J 1977. Mixed stocking by sheep and steers - a review. *Herbage Abstracts* 47:367-374.

Norton BE & McGarity JW 1965. The effect of burning of native pasture on soil temperature in Northern New South Wales. *Journal of the British Grassland Society* 20:101-105.

Noy-Meir I 1982. Stability of plant-herbivore models and possible applications to savanna. In: *Ecology of Tropical Savannas* (eds Huntley BJ & Walker BH), Springer-Verlag: Berlin, pp. 519-609.

O'Connor TG 1995. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103:214-223.

O'Connor TG 1996. Individual, population and community responses of woody plants to browsing in African savannas. *Bulletin of the Grassland Society of Southern Africa* 7:14-18.

O'Reagain PH & Mentis 1990. The effect of veld condition on the quality of diet selected by cattle grazing the Natal Sour Sandveld. *Journal of the Grassland Society of Southern Africa* 9:38-49.

O'Reagain PJ & Stuart-Hill GC 1991. The effect of plant structure on the acceptability of different grass species to cattle and sheep grazing African sour grassveld. *IVth International Rangeland Congress*, Montpellier, France, pp. 489-491.

O'Reagain PJ, Goetsch BC & Owen-Smith N 1996. Effect of species composition and sward structure on the ingestive behaviour of cattle and sheep grazing South African sourveld. *Journal of Agricultural Science* 127:271-280.

Ojima DS, Schimel DS, Parton WJ & Owensby CE 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 24:67-84.

Owen-Smith N 1985 a. The ecology of browsing by African wild ungulates. In: *Ecology of the World's Savannas* (eds JC Tothill & JJ Mott), Australian Academy of Science, Canberra, pp. 345-349.

Owen-Smith N 1985 b. Niche separation among African ungulates. In: *Species and Speciation* (ed. Vrba ES), Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria, pp. 167-171.

Owen-Smith RN 1988. *Megaherbivores: the influence of a very large body size on ecology.* Cambridge University Press, Cambridge.

Owen-Smith N 1993. Overcoming limitations on the productivity of browsing ungulates in African savanna vegetation. *Proceedings of the XVII International Grassland Congress*, pp. 2094-2095.

Owen-Smith N 1999. The animal factor in veld management. In: *Veld Management in South Africa* (ed. Tainton NM), University of Natal Press, Scottsville, pp. 117-138.

Owen-Smith N & Robbins CT 1993. Browse and browsers: interactions between woody plants and mammalian herbivores. *Tree* 8:158-160.

Pellew RA 1983 a. The giraffe and its food resource in the Serengeti, I. Composition, biomass and production of available browse. *African Journal of Ecology* 21:241-267.

Pellew RA 1983 b. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* 21:41-47.

Pieterse PJ 1986. *Aspekte van die demografie van Acacia longifolia (Andr.) Willd. In die Banhoekvallei in die Suidwes-Kaap.* Thesis M.Sc. (Agric.) Universiteit van Stellenbosch.

Pieterse PJ & Cairns ALP 1987. The effect of fire on an *Acacia longifolia* seed bank and the growth, mortality and reproduction of seedlings establishing after a fire in the South West Cape. *Applied Plant Science* 1:34-38.

Pitt MD, Newman RF, Youwe PL ,Wikeem BM & Quinton DA. Using a grazing pressure index to predict cattle damage of regenerating tree saplings. *Journal of Range Management* 51:417-422.

Portlock CC, Shea SR, Majer JD & Bell DT 1990. Stimulation of germination of *Acacia pulchella*: laboratory basis for management options. *Journal of Applied Ecology* 27:319-324.

Prins HHT & Vander Jeugd HP 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81:305-314.

Rees WA 1974. Preliminary studies into bush utilization by cattle in Zambia. *Journal of Applied Ecology* 11:207-214.

Reid RS & Ellis JE 1995. Impacts of pastoralists on woodlands in South Turkana, Kenya: Livestock-mediated tree recruitment. *Ecological Applications* 5:978-992.

Rice EL & Parenti RL 1978. Causes of decreases in productivity in undisturbed tallgrass prairie. *American Journal of Botany* 65:1091-1097.

Roques KG, O'Connor TG & Watkinson AE 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38:268-280.

Rutherford MC 1981. Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana - Ochna pulchra* savanna. *Bothalia* 13:531-552.

Sabiiti EN 1983. Ecological studies on *Macroptilium atropurpureum* Urb. In Rwenzori National Park, Uganda. I. Effects of pre-treating seeds with concentrated sulphuric acid, scarification, boiling and burning on germination. *African Journal of Ecology* 21:285-289.

Sabiiti EN & Wein RW 1987. Fire and *Acacia* seeds: a hypothesis for colonization success. *Journal of Ecology* 74:937-946.

Salihi DO & Norton BE 1987. Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. *Journal of Applied Ecology* 24:145-151.

Savage MJ 1980. The effect of fire on the grassland microclimate. *Herbage Abstracts* 50:589-603.

Savage MJ, Everson CS & Metelerkamp BR 1997. Evaporation measurement above vegetated surfaces using micrometeorological techniques. Water Research Commission Report No. 349/1/97, p248, ISBN No: 1 86845 363 4.

Savage MJ & Vermeulen K 1983. Microclimate modification of tall moist grasslands of Natal by spring burning. *Journal of Range Management* 36:172-174.

Scholes RJ & Walker BH (eds) 1993. *An African Savanna. Synthesis of the Nylsvley study.* Cambridge University Press, Cambridge.

Schultz AM, Lauenbach JL & Biswell HH 1955. Relationship between grass density and brush seedling survival. *Ecology* 36:226-238.

Scott JD 1949. A contribution to the study of the Drakensberg area. In: Story R 1952 (eds). A botanical survey of the Keiskammahoek district. *Memoirs of the Botanical Survey of South Africa* 27.

Scotter DR 1970. Soil temperatures under grass fires. *Australian Journal of Soil Research* 8:273-279.

Seif El Din A & Obeid M 1971. Ecological studies of the vegetation of Sudan. *Journal of Applied Ecology* 8:211-216.

Shea SR, McCormick J & Portlock CC 1979. The effect of fires on regeneration of leguminous species in the northern jarrah (*Eucalyptus marginata* Sm.) Forest of Western Australia. *Australian Journal of Ecology* 4:195-205.

Skarpe C 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology* 27:873-885.

Skinner JD & Smithers RHN 1990. *The mammals of the southern African subregion* (2ed.). Mammal Research Institute, University of Pretoria, Pretoria.

Smith JMB 1998. *Handbook for Agricultural Advisors in KwaZulu-Natal.* Department of Agriculture, KwaZulu-Natal.

Smith TM & Goodman PS 1986. The effect of competition on the structure and dynamics of African savannas. *African Journal of Ecology* 74:1028-1044.

Smith TM & Goodman PS 1987. Successional dynamics in an *Acacia nilotica - Euclea divinorum* savannah in southern Africa. *Journal of Ecology* 75:603-610.

Smith TM & Shackleton SE 1987. The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. *South African Journal of Botany* 54:375-379.

Stephens DW & Krebs JR 1986. Foraging theory. Princeton: Princeton University Press.

Stoltsz CW & Danckwerts JE 1990. Grass species selection patterns on rotationally-grazed Dohne Sourveld during Autumn and early winter. *Journal of the Grassland Society of Southern Africa* 7:92-96.

Story R 1952. A botanical survey of the Keiskammahoek district. *Memoirs of the Botanical Survey of South Africa* 27.

Stuart-Hill GC & Tainton NM 1989. The competitive interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. *Journal of Applied Ecology* 26:285-298.

Sweet RJ & Tacheba G 1985. Bush control with fire in semi-arid savanna in Botswana. *Proceedings of the Grassland Society of Southern Africa* 17:25-28.

Sweet RJ & Mphinyane W 1986. Preliminary observations on the ability of goats to control post-burning regrowth in *Acacia nigrescens/Combretum apiculatum* savanna in Botswana. *Journal of the Grassland Society of Southern Africa* 3:79-84.

Taylor RD & Walker BH 1978. Comparisons of vegetation use and herbivore biomass on a Rhodesian game and cattle ranch. *Journal of Applied Ecology* 15:565-581.

Tchie NA & Gakahu GC 1984. Responses of important woody species of Kenya's rangeland to a prescribed burning. *African Journal of Ecology* 27:119-128.

Teague WR 1985. Leaf growth of *Acacia karroo* trees in response to frequency and intensity of defoliation. *Ecology and Management of the World's Savannas. International Savanna Symposium 1984* (eds Tothill JC & Mott JJ), pp. 220-222.

Teague WR 1989 a. The response of *Acacia karroo* plants to defoliation of the upper or lower canopy. *Journal of the Grassland Society of Southern Africa* 6:225-229.

Teague WR 1989 b. Effect of intensity and frequency of defoliation on aerial growth and carbohydrate reserve levels in *Acacia karroo* plants. *Journal of the Grassland Society of Southern Africa* 6:132-138.

Teague WR 1989 c. Patterns of defoliation of *Acacia karroo* by goats and changes in tannin levels and *in vitro* digestibility following defoliation. *Journal of the Grassland Society of Southern Africa* 6:230-235.

Teague WR & Walker BH 1988. Effect of intensity of defoliation by goats at different phenophases on leaf and shoot growth of *Acacia karroo* Hayne. *Journal of the Grassland Society of Southern Africa* 5:197-206.

Teketay D 1996. Germination of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *Forest Ecology and Management* 80:209-223.

Ter Braak CJF & Smilauer P 1988. CANOCO Reference Manual and User's Guide to Canoco for Windows Software for Canonical Community Ordination (version4). Microcomputer Power (Ithaca, New York, USA).

Tothill JC & Mott JJ 1985. *Ecology of the World's Savannas.* Australian Academy of Science, Canberra.

Tozer MG 1998. Distribution of the soil seedbank and influence of fire on seedling emergence in *Acacia saligna* growing on the central coast of New South Wales. *Australian Journal of Botany* 46:743-755.

Trollope WSW 1974. Role of fire in preventing bush encroachment in the Eastern Cape. *Proceedings of the Grassland Society of Southern Africa* 9:67-72.

Trollope WSW 1978. Fire behaviour: a preliminary study. *Proceedings of the Grassland Society of South Africa* 13:123-128.

Trollope WSW 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 9:67-72.

Trollope WSW 1983. *Control of bush encroachment with fire in the arid savannas of south-eastern Africa.* Ph.D. thesis, University of Natal.

Trollope WSW 1984 a. Fire in savanna. In: *Ecological effects of fire* (eds Booysen P de V. & Tainton NM), pp. 149-176.

Trollope WSW 1984 b. Control of indigenous encroaching plants in the Eastern Cape. *Dohne Agric* 6:27-34.

Trollope WSW 1984 c. Fire behaviour. In: *Ecological effects of fire* (eds Booysen P de V. & Tainton NM), Springer-Verlag, Berlin, pp. 199-218.

Van Auken OW & Bush JK 1991. Influence of shade and herbaceous competition on the seedling growth of two woody species. *Madrono* 38:149-157.

Van Rooyen AF 1992. Diets of impala and nyala in two game reserves in Natal, South Africa. *South African Journal of Wildlife Research* 22:98-101.

Van Soest PJ 1982. *Nutritional Ecology of the Ruminant.* O & B Books, Corvallis, Oregon.

Van Vegten JA 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3-7.

Walker BH 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research* 6:1-31.

Walker BH 1985. Structure and function of savannas: an overview. In: *Ecology of the World's Savannas* (eds Tothill JC & Mott JJ), Australian Academy of Science, Canberra, pp. 83-91.

Walker BH, Ludwig D, Holling C & Peterman RM 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* 4:473-498.

Walker BH & Noy-Meir I 1982. Aspects of the stability and resilience of savanna ecosystems. In: *Ecology of Tropical Savannas* (eds Huntley BJ & Walker BH). Springer-Verlag, Berlin, pp 556-590.

Walter H 1971. *Ecology of Tropical and Subtropical Vegetation*, Edinburgh,Oliver & Boyd.

Wellington AB & Noble IR 1985. Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology* 73:645-656.

Wilson JB 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25:279-296.

Young TP 1987. Increased spine length in *Acacia depranolobium* - an induced response to browsing. *Oecologia* 71:436-438.

APPENDICES

Appendix 1 Stocking rates for paddocks at Ukulinga Research Farm over the (a) 1996/1997 and (b) 1997/1998 growing seasons (AUE = animal unit equivalents)

(a) 15 September 1996 to 20 March 1997

Paddock number	Stocking rate (AUE/ha)	days on	days off
1	0.938	18	168
2	0.831	23	163
3	0.651	23	163
4	0.692	18	168
5	0.168	62	126
6	0.359	40	146
7	0.335	32	156
8	0.170	62	126

(b) 21 September 1997 to 3 December 1997

Paddock number	Stocking rate (AUE/ha)	days on	days off
1	1.357	21	52
2	1.663	63	10
3	1.303	21	52
4	1.001	63	10
5	1.397	21	52
6	1.077	63	10
7	1.006	21	52
8	1.413	63	10

4 December 1997 to 24 March 1998

| Paddock number	Stocking rate (AUE/ha)	days on	days off
1	0.9048	31	72
2	1.6630	94	10
3	1.3030	31	72
4	0.8346	94	10
5	1.3970	31	72
6	0.8976	94	10
7	0.8384	31	72
8	1.4138*	94	10

* This changed to 0.7069 AU/ha after the 20th December due to stock theft

Appendix 2 Grass biomass accumulation (tons/ha)

| Camp	Treatment	1997		1998	
		dry weight	moisture content (%)	dry weight	moisture content (%)
1	sheep rotational	3.040	38.63	1.479	17.60
2	cattle conrtinuous	3.372	34.68	1.054	19.19
3	cattle rotational	2.406	32.25	0.863	17.64
4	sheep continuous	3.038	38.49	2.419	22.46
5	cattle rotational	2.726	30.12	0.969	18.10
6	sheep continuous	2.903	28.44	1.860	19.60
7	sheep rotational	2.905	30.92	1.806	20.21
8	cattle continouos	3.994	42.67	1.924	24.38

Appendix 3 Changes in temperature (°C) over time exhibited at ground level for each microsite at (a) six fires in 1997 and (b) four fires in 1998

(a) 1997
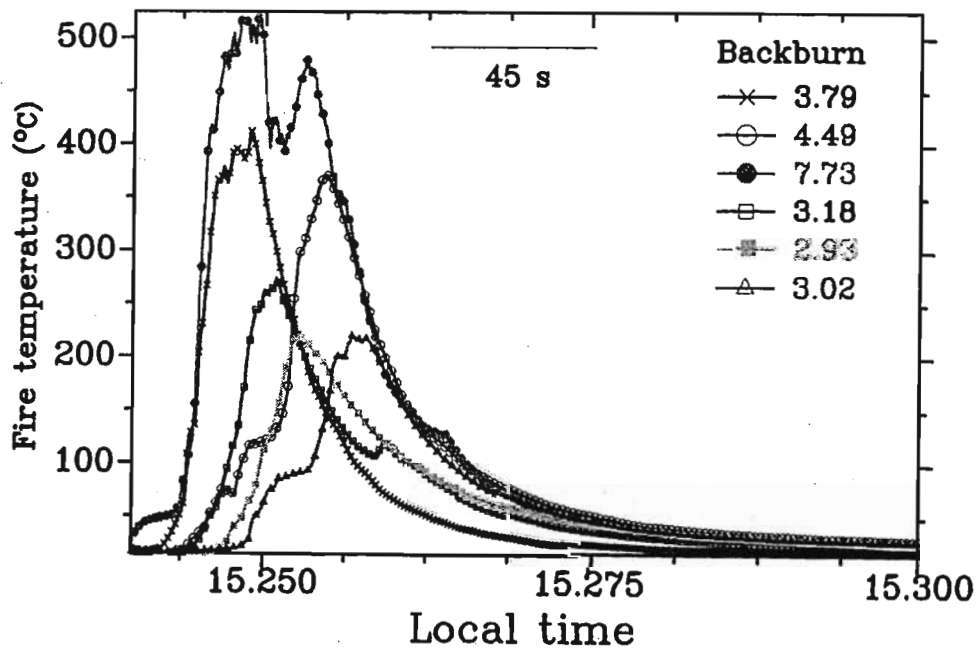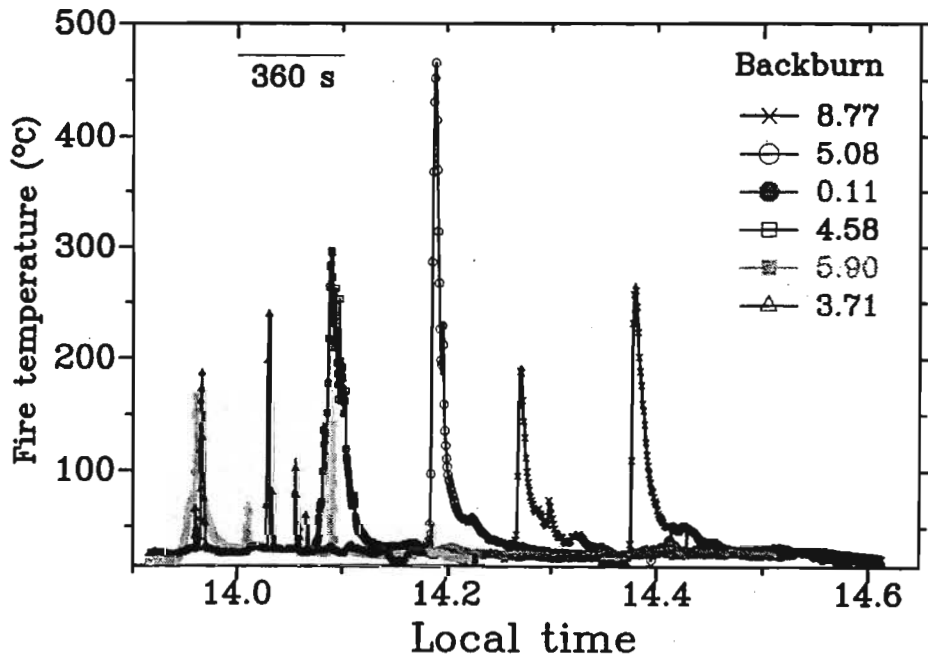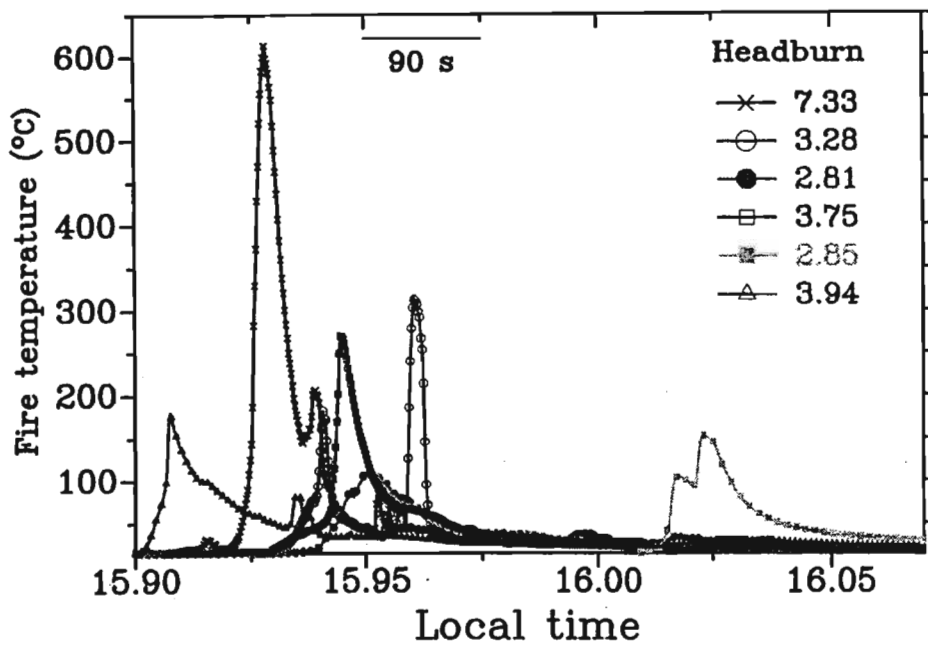
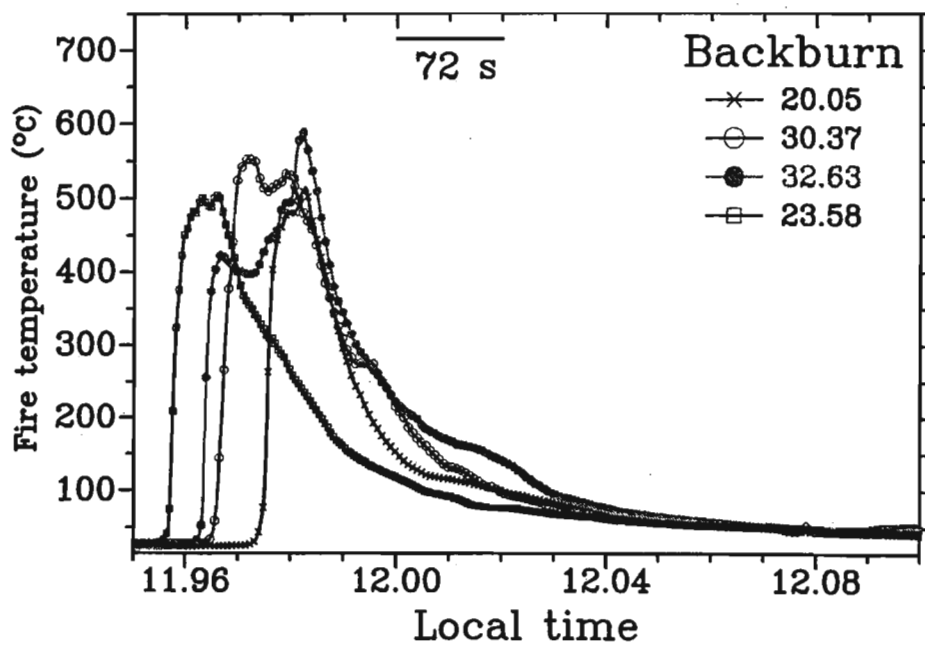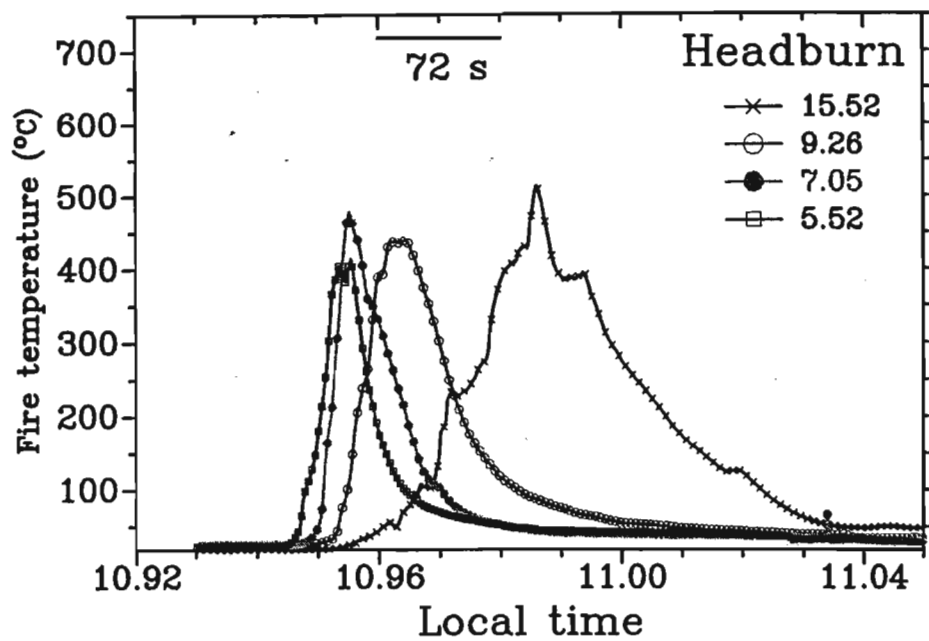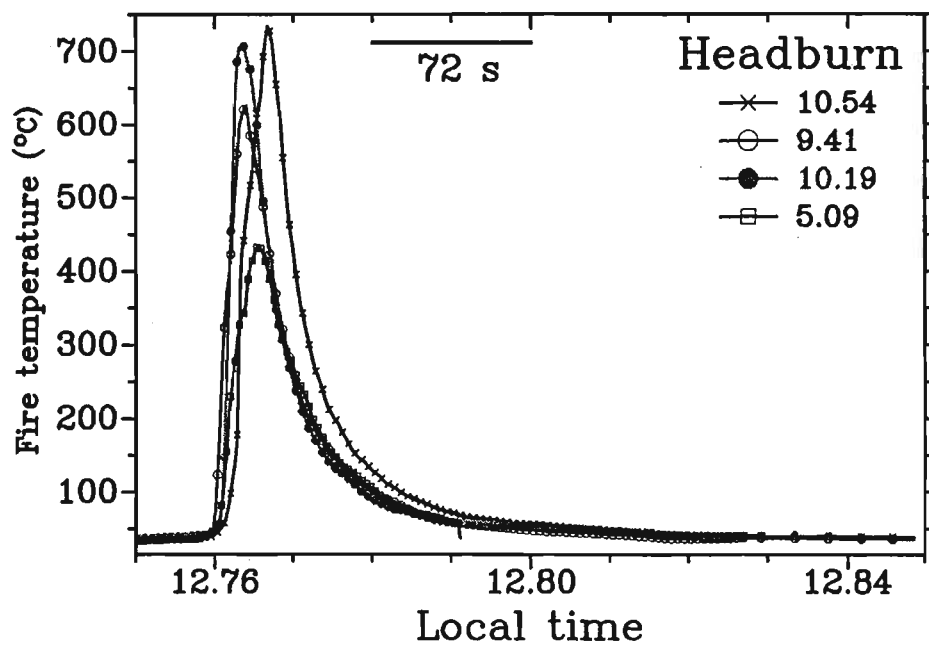(b) 1998
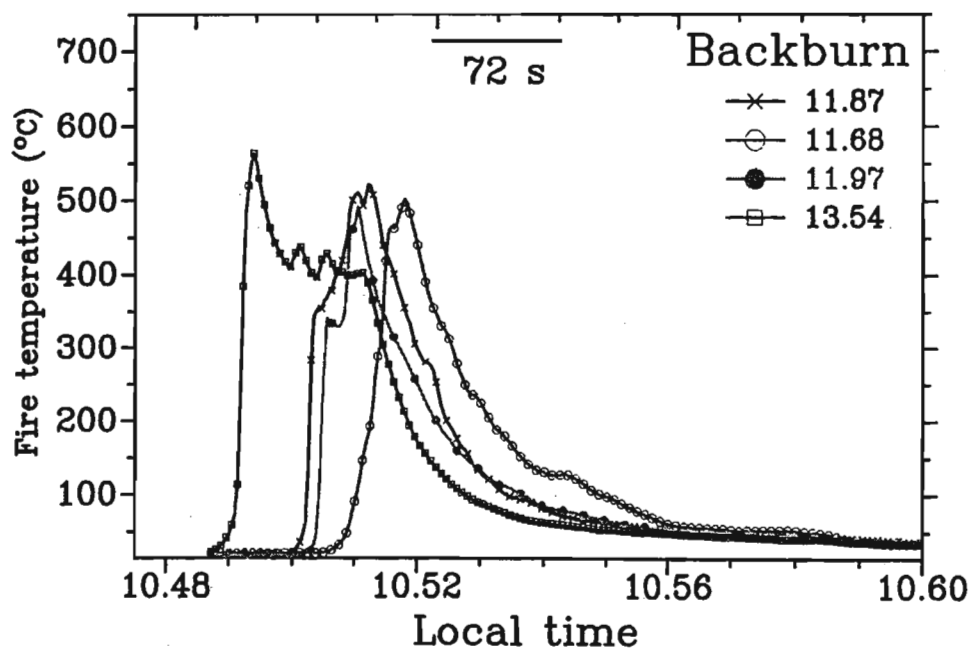
Appendix 4 Confidence limits (95%) of fire intensity ($^{\circ}$C.h) and maximum temperature ($^{\circ}$C) of head and back fires in (i) 1997 and (ii) 1998.

(a)

Fire type		fire intensity ($^{\circ}$C.h)	maximum temperature ($^{\circ}$C)
back 1			
mean		5.68	289.20
standard deviation		1.73	95.93
95% confidence limits	upper	7.98	385.13
	lower	4.17	193.27
back 2			
mean		4.18	339.33
standard deviation		1.68	111.52
95% confidence limits	upper	5.52	428.56
	lower	2.84	250.10
head 1			
mean		3.17	210.00
standard deviation		0.68	78.81
95% confidence limits	upper	3.77	279.08
	lower	2.51	140.92

(b)

back 1			
mean		12.65	524.25
standard deviation		0.74	29.61
95% confidence limits	upper	13.24	547.94
	lower	12.06	500.56
back 2			
mean		26.66	541.75
standard deviation		5.06	37.01
95% confidence limits	upper	30.71	571.36
	lower	22.61	512.14
head 1			
mean		9.33	462.00
standard deviation		3.81	31.99
95% confidence limits	upper	12.38	487.60
	lower	6.28	436.40
head 2			
mean		8800	627.50
standard deviation		2.18	112.72
95% confidence limits	upper	10.55	717.69
	lower	7.05	537.31

Appendix 5 Meteorological conditions during the fires of (a) 29 June 1997 and (b) 28 August 1998

(a)

Time	Ambient temperature (°C)	Relative humidity (%)	Wind speed (m/s)	Total radiation (MJ/m^2)
1000	18.15	65.12	0.85	3.40
1015	18.22	-	-	-
1030	17.84	-	-	-
1045	17.76	-	-	-
1100	16.95	73.84	1.15	3.10
1115	16.33	-	-	-
1130	16.02	-	-	-
1145	15.67	-	-	-
1200	15.22	88.26	3.55	2.50
1215	15.01	-	-	-
1230	14.63	-	-	-
1245	13.9	-	-	-
1300	13.65	91.20	3.60	2.40

(b)

Time	Ambient temperature (°C)	Relative humidity (%)	Wind speed (m/s)	Solar irradiance (W.m^{-2})
1000	20.20	32.61	0.95	517.5
1015	20.45	31.88	2.45	520.20
1030	20.92	37.41	2.45	536.50
1045	21.62	34.09	3.95	567.50
1100	22.03	31.77	3.20	562.50
1115	22.42	28.46	3.20	571.20
1130	22.87	29.39	3.20	571.10
1145	23.12	29.36	3.20	580.00
1200	23.69	25.98	3.20	605.00
1215	24.26	23.76	5.45	600.00
1230	24.75	22.66	4.70	585.00
1245	25.30	22.29	3.95	581.10
1300	25.20	22.69	3.95	556.50
1315	25.16	23.83	3.20	572.5

Appendix 6 Fuel load and moisture content of the grass swards prior to burning in 1997 and 1998

	1997	1998
Fuel load (kg/ha)	2451	2822
Moisture content (%)	34.5	19.9