

Tree Invasion In a Semi-arid Savanna In Zimbabwe

Seedling
Recruitment
of
Acacia karroo

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Tree Invasion In a Semi-arid Savanna In Zimbabwe

*Seedling Recruitment of *Acacia karroo**

Halfdroge savannes in Zimbabwe groeien dicht met bomen het succes van
kiemplanten van *Acacia karroo*

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad
van doctor aan de Universiteit Utrecht
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Chipangura Chirara

geboren op 1 december 1968 te Charter
Zimbabwe

Promotor: Prof. dr. M. J. A. Werger
Faculteit Biologie, Universiteit Utrecht

To my wife Grace and our twin sons
Craig and Carel

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General Introduction

Savannas are broadly defined as tropical or near-tropical seasonal ecosystems that are characterised by a continuous herbaceous layer dominated by grasses and sedges, which is occasionally interrupted by trees and shrubs (Bourliere and Hadley 1970, Werger 1983, Johnson and Tohill 1985, Frost *et al.* 1986, Scholes and Walker 1993). The typical physiognomy of the savanna is clearly distinct from that of grassland and forest, but there is only a gradual change in structure, ecology and floristic composition from barely wooded grassland, through savanna to woodland (Werger 1983). Savannas are geographically extensive (Scholes and Archer 1997) and occur in nearly all the continents. Tropical savannas cover nearly a third of the world's land surface and occur in Africa, Australia, South America, India and South-East Asia (Werger 1983, Werner 1991).

Savanna land use

Savannas are important to the socio-economic lives of the people living in tropical regions (Tohill and Mott 1985). The co-occurrence and balanced distribution of trees and grasses in savanna lands provide a natural resource base from which the majority of the people of these regions derive their livelihood. In Africa, 40% of the land surface is savanna and is inhabited by large and fast-growing human and livestock populations. Though people have lived in African savannas for more than a million years, these areas have not been used intensively until recently (Solbrig and Young 1993). In the past 6000 years, increasing human densities have resulted in increased use of these ecosystems.

Land use practices in savannas include livestock grazing, wildlife management, crop production, and wood harvesting. In savannas, there are contrasting levels of land use practice vis-à-vis technology and scale of crop and livestock production. One system is high-input commercial agricultural production. Management in this type of production involves the manipulation of water and nutrients, two principal limiting resources in these lands (Cole 1985, Medina 1986). Inputs such as fertilizers, stock feed, pesticides and machinery are used. Irrigation is also practised and this reduces the risk of crop failure. Users are able to grow crops that would otherwise not thrive in low rainfall areas. In addition, crops can be grown during the dry season. In arid and semi-arid savannas,

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ranching or large-scale livestock production is the most frequent type of land utilisation. The management objective of commercial agricultural production is market-oriented and at times seeks to achieve short-term maximisation of profits. In such cases, overuse of resources may lead to soil degradation and grassland invasion by unpalatable species. Maintenance of a sustainable stocking rate is one of the management challenges facing land users (Ralphs *et al.* 1990).

The other mode of savanna land use is extensive livestock grazing and subsistence crop production. In the savannas of southern Africa for example, this form of land use has been practiced mainly by indigenous communities whose land was expropriated by white settlers (Murphree and Cumming 1993) and they were moved into established “communal lands” where resource use and management is governed by common-property regimes. Lack of inputs and fertile agricultural land means that crop production in these areas is low. In most cases, no irrigation is practiced; crop production is mainly for subsistence and depends on the amount and distribution of rainfall. Even in low rainfall areas, some form of crop production is still practised though with high rates of crop failure due to drought and erratic rainfall. Cattle rearing is more successful than crop production in the drought-prone areas except in very dry years when cattle also die. The natural vegetation is generally the only source of food for livestock (Kelly and Walker 1976). Because the land base is restricted, degradation arising from overgrazing and soil erosion are some of the environmental problems faced as each member of the community tries to get the maximum out of the resource in a typical Hardin’s “commons” scenario (Hardin 1968).

Bush encroachment

One problem that emanates from savanna land use and management is that of bush encroachment. Bush encroachment is the phenomenon whereby trees and shrubs invade into open grassland or thicken up in already wooded areas (Trollope 1980). This woody-plant encroachment has occurred in many parts of the world including North America (Archer 1989), Australia (Walker and Gillison 1982) and Africa (van Vegten 1983, O’Connor 1995).

Invasion of grasslands by trees and shrubs is generally thought to have resulted from overgrazing by livestock (Walter 1954, Werger 1977a, 1983, Walker and Noy-Meir 1982, van Vegten 1983, Stuart-Hill and Tainton 1989). Overgrazing reduces grass biomass and vigour and thus its capacity to exploit moisture from the upper layers of the soil (Knoop and Walker 1985). This ultimately reduces the competitiveness of the grass against establishing tree seedlings. In addition overgrazing reduces grass fuel that is needed to support fires that destroy juvenile trees and shrubs and prevents them from growing to a taller, fire-resistant stage (Trollope 1980). Besides fire and grass competition, factors that

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could have helped prevent bush encroachment before the advent of commercial livestock production include browsing, plant diseases and insects.

In semi-arid savannas, the invasion of grassland by woody plants is a sign of ranch deterioration and reduces grazing capacity (Jeltsch *et al.* 1997). Increased tree density results in decline in the productivity of grasses (Du Toit 1972, Dye 1983, Dye and Spear 1982). Bush encroachment may result in intensification in grazing pressure because farmers do not often destock in response to decreases in grass production caused by increased tree density (Scholes and Archer 1997). Research at various sites in Zimbabwe has shown that grass productivity increases by between 160 and 400% when trees are removed (Robinson and Robertshaw 1975, Barnes 1979). Increases in grass yield in response to woody plant removal have been reported elsewhere (Tiedemann and Klemmedson 1977, Harrington and Johns 1990). Partial clearing of trees may also be beneficial in terms of grass productivity. For example, grass yield has been found to be higher under the canopy of isolated trees than in open areas because of a stable microenvironment and greater soil fertility under trees (Kennard and Walker 1973, Belsky *et al.* 1989, Stuart-Hill and Tainton 1989).

Though tree removal has been shown to be beneficial in terms of grass yield, farmers might not see the short-term economic benefits of investing in bush clearing. Tree clearing methods include ring barking, stumping and use of chemical arboricides. Chemical means may be the appropriate method for large-scale eradication of trees but it is expensive. Alternative means of controlling bush like the combined use of browsers and fire might be used, but this is only possible in areas where there is still enough grass fuel to support reasonably intense fires. In the past, researchers had to deal with the problem of bush encroachment when large tracks of savanna land already had mature trees and consequently research on bush encroachment has focused on the grass-adult tree dynamics. Much effort has been invested in the eradication of trees from encroached grasslands but much less has been done to prevent recruitment through seedlings. It is important to prevent bush encroachment at its inception phase – the seedling stage.

Determinants concerning factors involved in the dynamics of savannas

The co-existence of trees and grasses is a characteristic feature of all savannas. A complex set of factors, referred to as determinants, influences the balance between trees and grasses in savanna ecosystems. The principal determinants of savanna structure and functioning are soil moisture, soil nutrients, herbivory and fire (Walter 1971, Huntley 1982, Bourliere and Hadley 1983, Werger 1978, 1983, Sarmiento 1984, Tothill and Mott 1985, Walker 1987, Skarpe 1992, Frost 1996). Soil moisture and soil nutrients are the key environmental variables as they regulate the productivity and relative abundance of savanna vegetation (Walter 1971, Knoop and Walker 1985, Burke *et al.* 1990). Understanding the effects of

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these and other determinants on tree-grass balance in savannas will help researchers find ways of combating bush encroachment.

Soil moisture

Generally, primary production in semi-arid savanna ecosystems is highly variable due to the unpredictable rainfall pattern. Absolute yearly rainfall in savannas varies between 300 and 1800 mm (Young and Solbrig 1993). These savannas are water-limited for at least part of the year as the climate is characterised by the alternation of a dry and a rainy period. The amount and distribution of rainfall, infiltration and evapotranspiration, determine the soil moisture regime of a particular region (Frost *et al.* 1986).

The coexistence of trees and grasses in savanna ecosystems has been attributed to the spatial division of soil water resources between shallow-rooted perennial grasses and deep-rooted trees. Walter (1954, 1971) proposed an equilibrium model for coexistence in savannas. The model argues that water is the limiting factor in semi-arid savanna ecosystems. According to Walter's hypothesis, grasses are more efficient than trees in extracting water from the upper layers of the soil as their roots are mainly located there. Trees, which have most of their roots situated in the subsoil, have almost exclusive access to moisture that gets through to the deeper horizons and at the same time they access water in the topsoil. Although there is partial overlapping in the water resources used by trees and grasses (Belsky 1994), each vegetation component dominates in a different layer. Based on root distribution and soil water data from field studies, Knoop and Walker (1985) showed that grasses are superior competitors in the topsoil, and trees in the subsoil. Grasses may therefore outcompete trees and restrict their growth and abundance (Walker and Noy-Meir 1982). When grasses are removed by overgrazing, more water is made available for trees and shrubs, leading to increases in woody vegetation in savannas (Walker *et al.* 1981, Knoop and Walker 1985, Stuart-Hill and Tainton 1989, Skarpe 1990).

In any environment with a given climate and soil, Walter's two-layer hypothesis predicts that there should be a characteristic tree-grass ratio (Scholes and Archer 1997). Permeable soils like sands under wet climates favour trees while soil with high water-holding capacity and arid conditions are disadvantageous to trees.

Upon germination, tree seedlings share the same resource base as established grasses. These seedlings compete with the grasses for soil moisture in the topsoil. Grazing reduces grass vigour and thus their competitiveness against tree seedlings resulting in bush encroachment.

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Herbivory

Savanna is home to a wide range of animals that utilise both woody and herbaceous vegetation. African savannas are said to have evolved in the presence of a multi-species herbivore population that included both grazers and browsers. People who inhabited these savannas were mainly pastoralists and hunter-gatherers. Extensive herding of ruminants that included cattle, sheep and goats was first practised in Africa about 6000 years ago (Smith 1992). The output of this type of extensive livestock production is low but has proven to be ecologically sustainable (Solbrig 1993). The introduction of intensive commercial cattle production by European settlers in the eighteenth and nineteenth centuries saw the fencing off of large tracts of land and at times browsers like goats and other large herbivores were eliminated. Thus, domestic livestock in higher densities subsequently replaced wild herbivores and the highly mobile nomadic livestock that earlier on constituted the major grazing and browsing fauna of these savannas.

The increase in the population of domestic livestock has led to changes in vegetation structure and land degradation. Cleghorn (1966) reported that in the 1960s, 49% of the available grazing land in the communal areas of Zimbabwe was either bare or severely overgrazed because of high stocking rates of domestic livestock. High stocking rates lead to a reduced herbaceous ground cover, a depletion of perennial grasses and an increase in annuals and unpalatable grasses (Cumming 1982). In some areas, this decline in herbaceous cover when coupled by a lack of fires results in bush encroachment (Werger 1977b, 1978; Huntley 1982).

Though livestock is the most important consumer group in the savanna (Singh *et al.* 1985), and has attracted notable attention from researchers (Kothmann and Smith 1983, Ralphs *et al.* 1990, De Leeuw and Tohill 1993, Ellis *et al.* 1993), little has been done on small herbivores which exert considerable control over the structure and function of these ecosystems. Insect grazers for example, are important in the establishment of plant populations in savannas as they feed on seedlings (Whelan and Main 1979).

Fire

Grass fires are a characteristic of tropical savannas (Frost and Robertson 1987, Van Wilgen and Scholes 1997). They have been a feature of African savannas since time immemorial (Scott 1970) and have been one of the factors attributed to the genesis of savannas and the maintenance of the balance between trees and grasses in these ecosystems (Tainton 1981, Werger 1983, Singh *et al.* 1985, Menaut *et al.* 1985). Both man and natural causes such as lightning can be the source of ignition of savannas fires. Historically both African pastoralists and hunter-gatherers set fires especially during the dry season. This helped maintain grass cover in savannas and prevented succession from developing into thickets which might be undesirable for savanna use. Trees are favoured by the absence of fire to

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which they are sensitive during the early stages of establishment (Stocks *et al.* 1997, Van de Vijver 1999). Thus fire has been used, though inadvertently, in the control of bush encroachment in these ecosystems (Donaldson 1969, Trollope 1974) since savanna trees only recruit into the adult population once they escape the zone of influence of grass fires (Higgins *et al.* 2000). In moist savannas, fire can be used to control bush encroachment but in arid savannas it has the role of maintaining trees and shrubs at an available height and in acceptable state to browsers (Trollope 1980). This is so because in moist savannas rainfall is high enough to enable grass fuel to accumulate to support frequent enough fires to burn down tree seedlings and coppice growth.

The occurrence of fire depends on several factors that include enough fuel to support the fire, the right climatic conditions, and a source of ignition. Aboveground primary productivity, which provides fuel for fires, is largely determined by the amount of rainfall a site receives and other savanna determinants. Generally spoken, fire, once started, cannot be carried (maintained over extensive areas) in climates with less than 300 mm annual rainfall, where the annual grass production falls below 1 ton per ha per year (Werger 1983).

Grazing reduces the standing crop of grasses and thus fire intensity (Goldstein and Sarmiento 1987). This reduces their effectiveness in controlling the establishment of woody vegetation. Modern range managers and researchers have realised the importance of fire in savanna management as it can readily be manipulated. Researchers in fire ecology have shown that fire is important and usually beneficial in maintaining the diversity, structure and functioning of savannas ecosystems (Frost 1984, 1985, Van de Vijver 1999). The effectiveness of fire in savanna range management depends on other interacting factors like rainfall, herbivory and soil nutrient status.

Soil nutrients

The nutrient status of the soil, together with soil moisture availability influences the general physiognomy and primary productivity of tropical savannas. These factors also interact with herbivory, fire and land use management practices. Soils of low nutrient status select for species of low nutritional requirements or for those plants that are efficient in acquiring soil nutrient resources (Medina 1986). Plants that manage to grow on nutrient-poor soils are generally less palatable and of lower nutritional value to herbivores than those from nutrient-rich soils. Therefore, the nutrient status of the soil has some effect on the carrying capacity of the savanna (Scholes and Walker 1993).

In moist savannas, soil moisture is not limiting during the growth season and so may not directly explain the vegetation structure in these regions. Moist savannas are limited more by soil nutrients than they are by soil moisture. In such situations, grasses can access and deplete nutrients that are mineralised in the topsoil more than trees because they are shallow-rooted and fast-growing (Frost *et al.* 1986). Thus they have prior access to soil

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nutrients and this may limit nutrient availability to trees and affect the tree-grass balance in these savanna ecosystems. The availability of nutrients to either vegetation component also depends on the soil type. Soil that is readily leached may be advantageous for trees. Soil leaching drains nutrients to deeper zones where they are accessed more by trees than by grasses.

Soil nutrients interact with other savanna determinants to influence the tree-grass ratios in savannas. Protection of savannas from fire, for example, increases the organic content of the upper soil layers and this results in higher availability of nitrogen and other nutrients (Bilbao and Medina 1991). Herbivores and soil moisture are also important in the nutrient dynamics of savannas as they influence nutrient cycling.

Bush encroachment and research priorities in Zimbabwe

Research on bush encroachment in Zimbabwe started in the 1940s (Staples 1945, West 1947). The researchers realised the impact that bushes had on livestock production in the country. West (1947) said the problem was more prevalent in the arid parts of the country and stressed that “there can be no future in the cattle industry in these parts unless the invading thorn can be controlled”. The invading thorn trees were mainly the *Acacias* and they are still encroaching into grasslands in the semi-arid parts of the country.

Several researchers have studied bush encroachment in southern African ecosystems. Most of the investigations were initiated when encroachment had already taken place and therefore focused on restoring the situation and increasing grass productivity in these ecosystems. Investigators have thus concentrated on the interaction between adult trees and grass, mainly based on Walter’s two-layer hypothesis.

Few researchers have done work on tree seedlings and their interaction with grasses. Work on seedlings of invasive species includes that of Brown and Booysen (1967) and O’Connor (1995). Understanding the factors influencing seedling recruitment by invasive species and their general ecology might provide information on ways to controlling their expansion. In recent years in Zimbabwe, it has been difficult to justify and get support for research that generally seeks to improve current knowledge without direct benefit to the communal farmer. Seedling recruitment for example, though it might result in encroachment within a few years, might not be seen as an area that urgently needs to be researched. In 1993 the Department of Plant Ecology of Utrecht University started a joint programme with the University of Zimbabwe on tree-grass interactions. The work reported in this thesis was supported by this programme and allowed this researcher to work on tree seedling-grass interactions.

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Study area

Zimbabwe lies entirely within the tropics. The country is subdivided into five agro-ecological regions based on climate (Figure 1). Land use practice in these regions depends on the amount of rainfall.

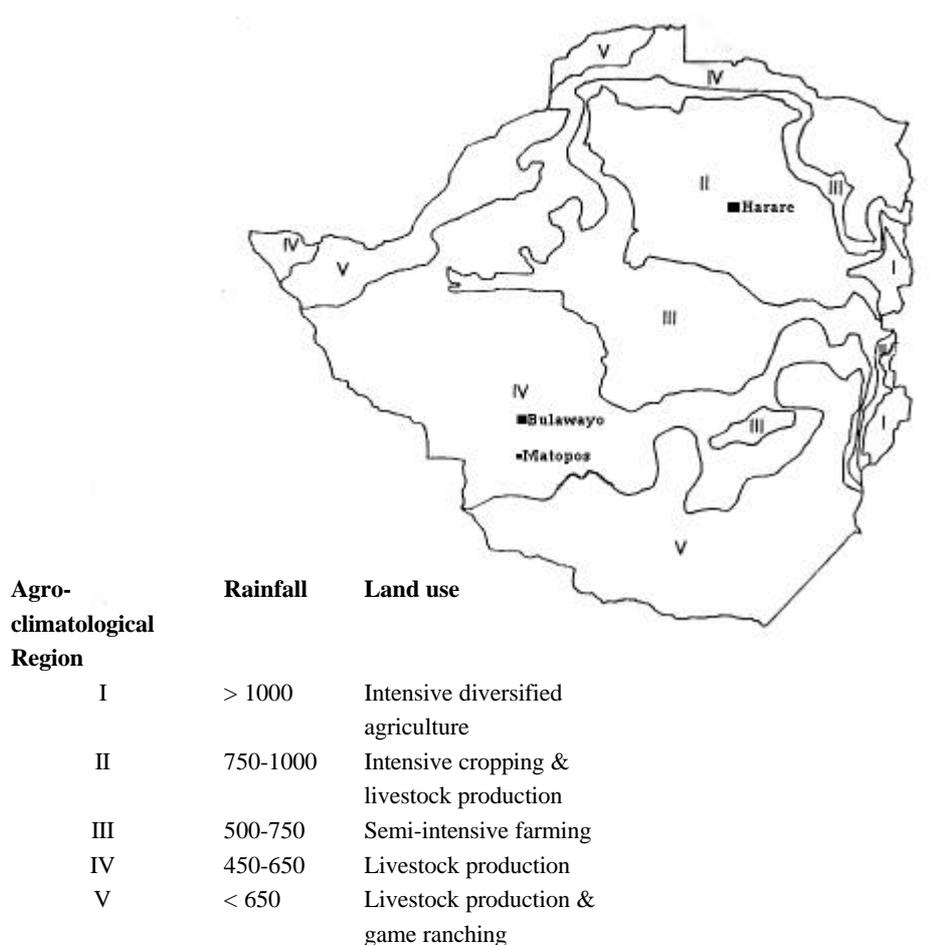


Figure 1. The agro-climatological regions of Zimbabwe and land use practices best suited for the regions. Rainfall is in mm per year.

Field studies were carried out at Matopos Research Station (20°23'S, 28°28'E). Matopos lies 30 km south of Bulawayo, within Natural Farming Region IV. The average annual rainfall for Matopos is 600mm though it is highly variable and ranges between 250 – 1400mm. Most rain falls between the months of October and April. Because of the often low and erratic rainfall, this region is generally unsuitable for dryland crop production but

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suitable for livestock production. The area is underlain by quartz-meta gabbro parent material giving rise to siallitic, medium textured red clay soils (Dye 1983).

The vegetation is *Acacia*-savanna. The dominant grass species in the area are *Cymbopogon plurinodis*, *Heteropogon contortus*, *Hyparrhenia filipendula* and *Themeda triandra*. *Setaria incrassata* dominates in the wet and fertile low-lying areas. The dominant woody species is *Acacia karroo* followed by *A. nilotica*.

Study species

Acacia karroo Hayne belongs to the family Leguminosae, subfamily Mimosoideae. This species is widespread in southern Africa and occurs in Zimbabwe, Botswana, Swaziland, Lesotho, Namibia, South Africa, Mozambique, Zambia, and further north. *Acacia karroo* is a pioneer species and generally invades under disturbed conditions. It grows in a range of soils from sands to heavy clays. In Zimbabwe, it occurs on heavy-textured alluvial soils and is common on red clays along watercourses. In high rainfall areas, it occurs on clayey soils and is an indicator of fertile soils (Timberlake *et al.* 1993). *Acacia karroo* is also found on sands in South Africa and other parts of the sub-region (Venter 1971).

Acacia karroo produces pods that are dehiscent on the parent tree. Dehiscence of the pods is not explosive so seed dispersal is thought to be mainly through ingestion by herbivores. The seeds of *A. karroo* are water impermeable and can remain damp for 29 months without germinating or rotting but it takes three or four days to germinate when the seed coat is penetrated (Barnes *et al.* 1996). Seed dormancy of *A. karroo* can be broken artificially by boiling in water, hot wire abrasion or any technique that scarifies the seed coat. Under field conditions, it is thought that the dormancy is broken by passage of the seeds through the digestive tract of browsers or by the mechanical and/or chemical erosion in moist soil.

Acacia karroo nodulates more than other common southern Africa *Acacias* and its growth is often associated with symbiotic associations with *Rhizobium* species (Barnes *et al.* 1996). The species fixes nitrogen and is therefore important in the nutrient dynamics of southern African savannas. Seedlings of *A. karroo* are sensitive to desiccation. The species produces a deep taproot.

Foliage, flowers and green pods of *A. karroo* are important browse for both livestock and browsers. The species can be used in traditional medicine to treat several ailments (Gelfand *et al.* 1993). The species also has several other uses in the agrochemical, mining and glue industries.

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Aim and outline of this thesis

This study seeks to investigate factors influencing the recruitment of seedlings of *A. karroo*, an important invasive species in the semi-arid savannas of Zimbabwe. This study first goes into the field situation to investigate *A. karroo* seedling growth and establishment under natural conditions. Here the important factors in seedling recruitment are identified and they are further investigated under controlled conditions.

Chapter 2 deals with the effects of grass defoliation intensity on the germination and establishment of *A. karroo* seedlings in areas with different grazing histories. Seedling survival and grass productivity are monitored for one dry and one wet season under field conditions.

Chapter 3 investigates the effects of competition between *A. karroo* seedlings and a perennial grass species *Setaria incrassata* under controlled conditions. This chapter also investigates the relationship between grass biomass and water utilization, and the subsequent effect this has on tree seedling growth and survival.

Chapter 4 follows on from the results of Chapter 3. This section deals with the question that has been asked by researchers for a long time: Is competition between tree seedlings and grasses belowground or aboveground? To answer this question *A. karroo* seedlings are grown in four different light conditions under wet and dry conditions.

Chapter 5 develops the idea of Chapter 4 a step further. The study in this Chapter simulates the changes in environmental conditions experienced by seedlings during the first season of growth. Acclimation of *A. karroo* seedlings to changes in light and soil moisture environment are investigated by growing the seedlings in one set of light and moisture conditions and shifting them to different conditions midway through the period of the study.

The seedlings of this species suffer herbivory from grazers when they are eaten together with grasses, and from invertebrate herbivores like termites. **Chapter 6** deals with defoliation of *A. karroo* seedlings under different light conditions.

Chapter 7 summarises the different studies on *A. karroo* seedlings and interprets the results in the context of bush encroachment in southern African savannas.

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2

Grass defoliation affects survival and growth of seedlings of *Acacia karroo*, an encroaching species in southwestern Zimbabwe

C. Chirara, P.G.H. Frost and V.E.E. Gwarazimba

Abstract

Two experiments were conducted, one in the field and the other in the greenhouse, to investigate the effects of the intensity and frequency of grass defoliation on the survival and growth of *Acacia karroo* seedlings. In the greenhouse, seedlings growing with heavily clipped grasses had higher biomass production than those competing with moderately clipped grasses. Root/shoot ratios of *A. karroo* were higher in treatments with unclipped grasses. There was a negative relationship between grass root production and *A. karroo* biomass production. The field experiment was carried out in two paddocks, one previously heavily grazed and the other lightly grazed. Grazing in both paddocks was simulated by artificial defoliation. Generally, more *A. karroo* seedlings emerged under lightly defoliated treatments. Clipping frequency had a strong effect ($p = 0.066$) on the survival of emerged seedlings during the wet season. There were no differences in survival rate at the end of the dry season. Though grass defoliation was shown to enhance seedling growth under controlled conditions, no evidence was found to suggest that seedling establishment during the first year is influenced by the intensity of grass defoliation.

Keywords: Bush encroachment, grazing, seedling establishment

Introduction

The natural savanna vegetation of Africa evolved in the presence of a multi-species herbivore population with a wide range of diet preferences (Kelly and Walker 1976). These animals used both the woody and herbaceous vegetation, and, together with periodic fires, helped maintain grassland or open woodland (Frost and Robertson 1987). Bush encroachment, the thickening-up of trees and shrubs to form dense thickets, is on the

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increase in southern African ecosystems, particularly in heavily grazed areas (van Vegten 1983). The increase of woody vegetation in semi-arid ecosystems is largely attributed to reduced grass competitiveness because of over-utilisation by grazers (Skarpe 1990).

In Zimbabwe, the problem of shrub invasion has been long recognised (Kennan *et al* 1955, Plowes 1956, West 1947, 1958). It is generally accepted that bush encroachment is a result of the reduction in competition between grasses and woody plants as a result of overgrazing. Under both commercial and subsistence cattle production large numbers of grazers have been introduced and browsers have generally been excluded. Grasslands have been overutilised when high stocking rates have been maintained for long periods inside paddocks or through restricting herds to localised areas year round by herding. The resulting sustained grazing pressure, especially on the more palatable perennials, has reduced their regrowth capacity and vigour, thereby hastening the establishment and growth of woody plants (Kennan 1966). Grass fuel loads have been reduced and, in extreme situations, fire has been rendered ineffective as a tool for suppressing the growth of woody plants.

To be able to combat the problem of bush encroachment, researchers need to understand the mechanisms of the processes involved. Research to date has been focused mainly on eradicating established woody vegetation and increasing grass production (Dye and Spear 1982). Studies on the effect of grazing and other disturbance factors on seedling recruitment of the invasive tree species in southern Africa are increasing (O'Connor 1995).

Seedling establishment is probably the critical life history stage for population persistence and expansion (Goldberg 1990). Seedlings establishing in a community of already established plants are likely to face competition from such plants. Excessive defoliation is presumed to reduce the competitiveness of the grasses against woody plant seedlings, mainly through lower carbon assimilation and root growth (Clement *et al.* 1978, Chapin and Slack 1979). In perennial grasses, excessive defoliation reduces their vigour because continual depletion of the shoots means storage products are continually withdrawn from the roots and translocation of photosynthate to the root often decreases. This reduces storage reserves necessary for regrowth during the following growing season. Furthermore, limited root growth arising from inadequate supply of carbon assimilates reduces access to water and nutrients. Intense grass defoliation can result in increased availability of soil water (McNaughton *et al.* 1983), and this creates conditions conducive for woody seedling establishment. In moisture-limited environments with high nutrient levels, bush encroachment may therefore be a function of the moisture status of the soil and this can be influenced by fire and herbivory.

The objective of this study was to investigate the effect of the frequency and intensity of grass defoliation on the establishment, growth and survival of seedlings of a woody plant species, *Acacia karroo*, in a semi-arid ecosystem in southwestern Zimbabwe. The

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following hypothesis was tested in the field and under controlled conditions in the greenhouse:

Intense and frequent defoliation of grasses results in a reduced root system as resources are channelled to shoot regeneration. Resource uptake by grasses, presumably soil moisture, is diminished and more water is made available for establishing woody seedlings. Seedlings therefore survive and grow better when competing with intensely clipped grasses.

Materials and Methods

Study site

The study was conducted at Mahiye, a section of Matopos research Station (20°23'S, 28°28'E), situated 30 km southwest of Bulawayo, in southwestern Zimbabwe. Matopos lies in area where rainfall is both limited and highly variable (200 to 1400 mm per annum, average 600 mm), mostly falling from October to April. October is the hottest month (mean maximum 29.4°C). Frost occurs during the dry season (May - September). Elevation is approximately 1340 m. The soils are dark reddish brown clay loams derived from epidiorite. The area is dominated by *Acacia* species, mainly *A. karroo*, *A. nilotica*, *A. gerrardi*, *A. rehmanniana* and *A. nigrescens*. Common grass species include *Heteropogon contortus*, *Cymbopogon plurinodis*, *Themeda triandra* and *Hyparrhenia* species. *Setaria incrassata* also occurs, especially on wetter areas. A detailed description of the site can be found in Dye (1983).

Effect of defoliation of grass (*Setaria incrassata*) on *Acacia karroo* seedling growth under controlled conditions

Pots, 30 cm in diameter and 50 cm deep, were filled with soil from the study site. *Setaria incrassata* was grown in the pots and allowed to establish. Five pre-germinated *A. karroo* seedlings were introduced and later reduced to three after establishment. Grass was clipped at 5 cm and 11 cm at one-, two-, and four-weekly intervals in a factorial design. There were two controls; pots with no grass and with unclipped grass. Each treatment was replicated five times. The plants were watered to about 80% of field capacity once every five days. The clipped grass biomass was dried at 80°C for 48 hours and weighed. The experiment ran for ten weeks before the grass and the seedlings were harvested. At harvest the grass and seedlings in each pot were carefully separated. *Acacia karroo* seedlings were separated into root and shoot (stem and leaves). The root and stem lengths of the seedlings were measured. The different plant parts were dried at 80°C and weighed. The grass was separated into root and shoot and their dry masses determined.

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Effect of grass clipping intensity on *Acacia karroo* seedling survival under natural conditions

The experiment was carried out in two paddocks with different grazing histories. One paddock, hereafter called the heavily grazed paddock, had been heavily grazed for ten years in an earlier experiment. The stocking rate in this paddock had been 2.5 hectares per livestock unit (a livestock unit being defined as an animal with an average mass of 450 kg). The other paddock (henceforth called the lightly grazed paddock) had been moderately grazed with a stocking rate of 4 hectares per livestock unit. There was more grass basal cover in the lightly grazed paddock. The grazing experiment stopped a year before the present study was started. In each of the two paddocks, seven 4m x 4 m plots were fenced off. Inside each plot, six 1m x 1 m subplots were marked. The treatments applied to these plots are described below.

Clipping treatments and measurements

Grass in the 1m x 1 m subplots was clipped at 5 cm and 11 cm every week and every four weeks. Twenty-five pre-germinated *A. karroo* seedlings were introduced into each 1 m² plot in November 1993 but they did not survive because of the combined effects of drought and termite activity in the study area. Clipping treatments were however continued until the end of the growing season. In each case, the dry mass of the clipped grass was determined. In the 1994/95 growing season new seeds were introduced and clipping treatments were continued as in the previous season. *Acacia karroo* is a hard-seeded species, so seeds were manually scarified to enhance germination. Fifty *A. karroo* seeds were planted at least 10 cm apart in a grid in each of the subplots (1 m²). The number of the seedlings that emerged in each subplot within two weeks of planting was recorded and their positions noted. Monitoring for any new germinants continued beyond this period but no further seedlings emerged. Seedling survival was monitored during the growing season and at the start of the next rain season. During a three-week dry spell after 77 mm of rainfall, measurements were taken in selected plots to determine the rate of soil moisture decrease in the top 15 cm of the different treatments. Soil moisture was measured using a Time Domain Reflectometry trace (TDR) (Dalton *et al.* 1984).

Data analysis

The greenhouse data were subjected to two-way analysis of variance (ANOVA). Field data were analysed using split-plot ANOVA with paddocks as between-subject factors and clipping frequency and clipping height as within-subject factors. All analyses were done using SPSS (SPSS/PC+, 1988). Specific stem length (SSL) and specific root length (SRL) were calculated as:

$$\text{SSL} = \text{stem length/stem mass, and SRL} = \text{root length/root mass}$$

Results

Effect of *Setaria incrassata* clipping intensity on *Acacia karroo* seedling growth in the greenhouse

Biomass production in *A. karroo* seedlings increased with increasing clipping intensity (Table 1). Root dry mass of *S. incrassata* was highest in unclipped and moderately clipped treatments (Table 2). There was a negative relationship between *A. karroo* dry mass and *S. incrassata* root biomass (Figure 1). The absolute root length of seedlings was higher in treatments without grass and where the grass was intensely clipped, but the specific root length was higher in the unclipped and moderately clipped treatments (Figures 2a and 2b). The absolute stem length and specific stem length followed the same pattern as absolute and specific root lengths, respectively (Figures 3a and 3b). F-values from analyses of these results show that both clipping height and clipping frequency had significant effects on almost all of the growth variables of the woody seedlings (Table 1). Seedlings growing in competition with unclipped grass swards had the highest root/shoot ratio while those competing with intensely clipped grass had the least (Table 1). No seedling mortality was observed in any of the treatments.

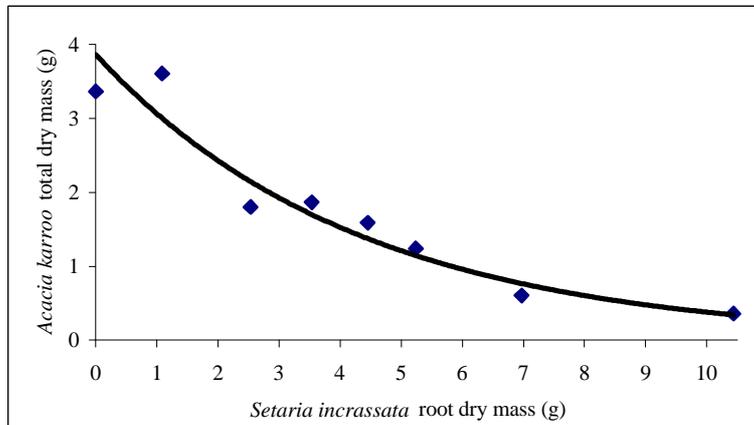


Figure 1. The relationship between *Acacia karroo* and *Setaria incrassata* root biomass production

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Table 1. Means and F-values from a two-way ANOVA for the effects of grass clipping frequency, height and frequency x height on several *Acacia karroo* variables. Standard error values are presented in parentheses. ^{NS} = P>0.05; * = 0.01<P<0.05; ** = 0.001<P<0.01; *** = P<0.001

Treatment		Length (mm)		Dry mass (g)					Root:shootRatio (g/g)
Clip. height (cm)	Freq. (wk)	Root	Shoot	Leaves	Stem	Shoot	Root	Total	
5	1	444.40 (26.195)	350.90 (13.837)	1.94 (0.168)	0.81 (0.101)	2.75 (0.267)	0.85 (0.138)	3.61 (0.356)	0.31 (0.043)
	2	317.60 (4.220)	277.27 (17.248)	1.06 (0.137)	0.36 (0.054)	1.42 (0.190)	0.44 (0.068)	1.87 (0.249)	0.32 (0.034)
	4	318.73 (39.647)	200.33 (16.714)	0.64 (0.136)	0.25 (0.050)	0.89 (0.185)	0.34 (0.071)	1.24 (0.241)	0.40 (0.051)
11	1	352.80 (18.853)	257.67 (33.464)	0.95 (0.148)	0.41 (0.103)	1.36 (0.251)	0.44 (0.093)	1.80 (0.343)	0.32 (0.014)
	2	334.53 (11.725)	255.53 (45.138)	0.90 (0.281)	0.33 (0.122)	1.23 (0.402)	0.36 (0.940)	1.59 (0.493)	0.31 (0.020)
	4	243.16 (8.387)	164.33 (13.710)	0.30 (0.058)	0.12 (0.026)	0.42 (0.083)	0.18 (0.032)	0.61 (0.105)	0.49 (0.119)
No clipping		252.47 (26.192)	102.70 (5.285)	0.17 (0.027)	0.06 (0.010)	0.23 (0.035)	0.13 (0.019)	0.36 (0.054)	0.55 (0.021)
No grass		422.73 (30.316)	338.47 (15.61)	1.75 (0.126)	0.77 (0.050)	2.52 (0.171)	0.85 (0.096)	3.37 (0.166)	0.35 (0.049)
F-values									
Frequency		14.89***	11.36***	16.75***	13.04***	15.71***	9.59**	15.40***	3.49*
Height		7.95**	5.54*	13.21**	7.59*	11.41**	9.03**	11.91**	0.43 ^{NS}
Freq. x Height		3.36*	1.05 ^{NS}	3.37 ^{NS}	2.64 ^{NS}	3.18 ^{NS}	1.88 ^{NS}	3.11 ^{NS}	0.38 ^{NS}

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Table 2. Mean biomass of *S. incrassata* at harvest

Treatment		Mass (g)		
Clip. height (cm)	Freq. (wk)	Root	Shoot	Total
5	1	1.08	1.01	2.09
	2	3.54	3.11	6.65
	4	5.24	8.14	13.38
11	1	2.54	2.71	5.24
	2	4.45	4.94	9.39
	4	6.97	10.60	17.57
No clipping		10.44	23.41	33.84

Emergence and survival of *Acacia karroo* seedlings in the field

The proportion of seedlings that emerged during the first two weeks and survived until the end of the growing and dry seasons is shown in Table 3. Generally, in both paddocks, more seedlings emerged in the unclipped or moderately clipped treatments than in the heavily clipped treatments.

At the end of the growing season, plots in the heavily grazed paddock had a higher seedling survival rate than those in the lightly grazed paddock. Seedling survival in this (heavily-grazed) paddock up to the end of the rainy season did not show any distinct pattern. In the lightly grazed paddock, more *A. karroo* seedlings survived in the treatments where the grass was clipped more frequently. Though not significant, clipping frequency tended to have an effect on seedling survival up to the end of the growing season (Table 4, $p=0.066$).

Seedling survival at the end of the dry season had a different pattern. Neither clipping frequency nor clipping height had a significant effect on the survival of the seedlings. The effect of frequency was however different in the two paddocks (Table 4, $p<0.05$). In the lightly grazed paddock, more seedlings survived in the more frequently clipped treatments and none in the treatments clipped four-weekly. In the heavily grazed paddock, more seedlings survived in the less frequently clipped treatments.

The amount of clipped grass over the two wet seasons was higher in the lightly grazed than in the heavily grazed paddock (Table 5). Perennials dominated the lightly grazed paddock. In this paddock there was less grass clipped in the second wet season compared to the first. There was greater reduction in the more intensely clipped (5 cm) treatments. In the heavily grazed paddock dominated by annuals, there was a general increase in the dry mass of clipped grass in the second season. There was generally more rainfall in the second wet season than in the first (558 mm compared to 406 mm).

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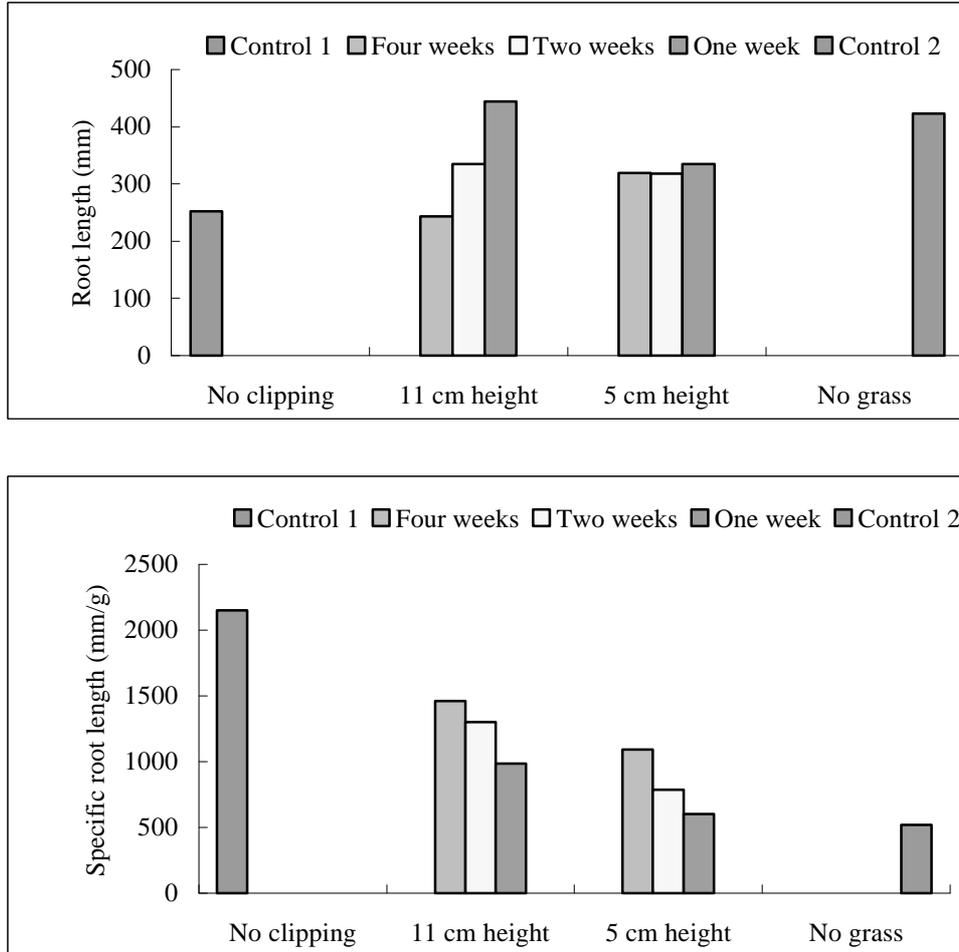


Figure 2. Root extension of *Acacia karroo* seedlings competing with grass clipped at different regimes indicating (a) absolute root length and (b) specific root length.

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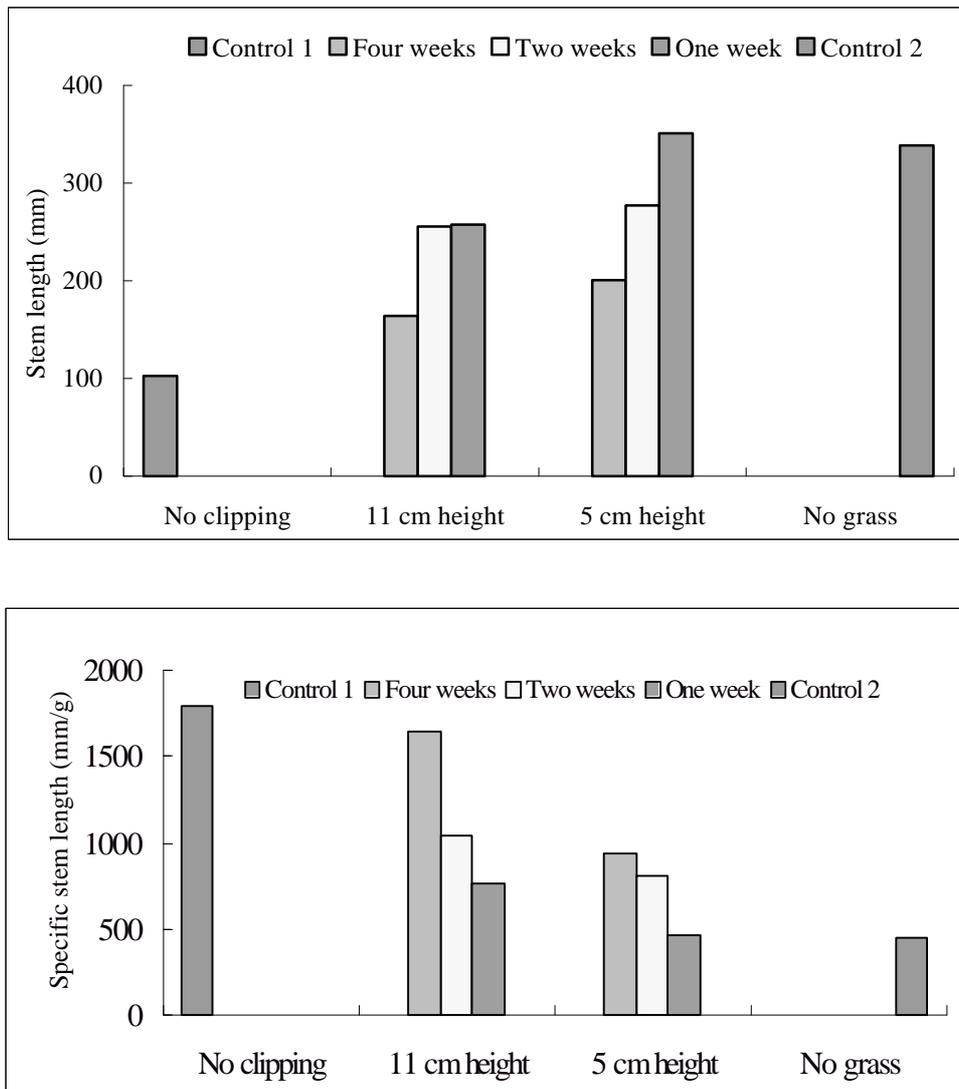


Figure 3. Stem extension of *Acacia karroo* seedlings competing with grass clipped at different regimes indicating (a) absolute stem length, and (b) specific stem length.

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Table 3. *Acacia karroo* seedling emergence and survival in the two paddocks. Standard errors are presented in parentheses (the standard errors for the dry season measurements were very high because of low survival rates)

Treatment	Seedling emerg. (%)		Seedling survival (%)			
			Wet season		Dry season	
	Lightly-grazed	Heavily-grazed	Lightly-grazed	Heavily-grazed	Lightly-grazed	Heavily-grazed
No grass	18.3 (3.2)	12.3 (2.9)	28.3 (7.8)	53.3 (8.7)	5.6	2.5
1 wk x 5 cm	15.7 (5.0)	14.6 (2.6)	38.4 (8.5)	22.8(10.3)	3.2	1.1
1 wk x 11 cm	10.9 (2.2)	17.1 (1.9)	21.0 (6.1)	33.8 (9.0)	2.8	1.0
4 wk x 5 cm	18.0 (3.6)	10.0 (1.7)	11.4 (5.1)	16.0 (6.4)	0.0	5.2
4 wk x 11 cm	21.4 (5.2)	19.4 (3.7)	11.9 (4.7)	41.5(14.0)	0.0	4.9
No clip	21.7 (3.7)	30.0 (4.5)	22.0 (9.7)	36.7 (8.6)	3.0	6.0

Table 4. Split-plot ANOVA of seedling survival in the field, with paddock type as the between-subjects factor, and clipping height and clipping frequency as within-subjects factors

Source of variation	Wet season		Dry season	
	F _{1,10}	P	F _{1,10}	P
<i>Between paddocks</i>	0.85	0.379	0.49	0.499
<i>Within paddocks</i>				
Frequency	4.28	0.066	0.07	0.800
Paddock x Frequency	4.61	0.057	6.27	0.031
Height	1.21	0.297	0.00	0.962
Paddock x Height	2.70	0.131	0.01	0.912
Frequency x Height	1.06	0.328	0.01	0.933
Paddock x Freq. x Height	0.02	0.892	0.00	0.984

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Table 5. Clipped grass dry mass (gm^{-2}) in the two paddocks over two growing seasons

Clipping treatment	Lightly-grazed paddock				Heavily-grazed paddock			
	1993/4	1994/5	% change	Total	1993/4	1994/5	% change	Total
1 wk x 5 cm	267.03	110.67	-58.6	377.70	106.59	108.60	+1.9	215.19
1 wk x 11 cm	269.93	143.15	-47.0	413.08	119.45	167.00	+40.2	286.94
4 wk x 5 cm	340.82	130.38	-61.7	471.20	182.04	135.97	-25.3	318.01
4 wk x 11 cm	251.85	165.11	-34.4	416.96	179.10	205.29	+14.6	384.39
Total	1129.63	549.31		1678.94	587.18	617.35		1204.53

During the three-week dry spell, there were no differences in soil moisture content between the two paddocks. The unclipped and moderately clipped treatments recorded slightly higher initial levels. Soil moisture level in all treatments was about 49% of field capacity by the end of this period.

Discussion

Growth of competing *Acacia karroo* seedlings in the greenhouse

Intense clipping of grasses resulted in a decrease in grass root and total biomass production. This finding is in agreement with studies on the effects of defoliation of other grass species (Chapin and Slack 1979, McNaughton and Chapin 1985). The growth of *A. karroo* seedlings was negatively related to grass root biomass, possibly because of reduced resource availability when grass growth was vigorous. Because all plants were watered at the same time interval, seedlings competing with heavily defoliated grass could have experienced a moister environment because of the low rate of moisture depletion by the grasses. Soil moisture in pots with unclipped grass was likely to fluctuate more markedly because of high rates of water depletion. The soil used in this experiment has been

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described as fertile red clays (Dye 1983) and thus soil moisture rather than soil nutrients is likely to be the main limiting resource for seedling growth. It is possible, however, that nutrient addition due to root mortality and decay could also have enhanced seedling growth under heavy clipping (1 wk x 5 cm) compared to the bare (no grass) stands.

To survive, seedlings in arid environments need to put down a deep root system in order to be able to extract moisture from the dry season water table. Although stressed *A. karroo* seedlings have shorter roots because of limited resources, they morphologically respond to stress by having high specific root lengths, implying a more diversified root system. The ratio of root-to-shoot biomass increases when nutrient or water availability is low and it decreases under low light levels (Chapin 1980). The observed increase in root-to-shoot ratio with decreasing clipping intensity could therefore be a response to moisture stress. This ratio is also influenced by the developmental stage of the plant. In another study, no correlation was found between root/shoot ratio and biomass production of pure stands of differently-aged *A. karroo* seedlings supplied with adequate moisture (Chirara, unpublished data). Shading has been shown to be a major factor limiting *Acacia* seedling growth (Smith and Shackleton 1988). The high specific stem lengths of seedlings competing with unclipped or moderately clipped grass suggest a response to shade.

Survival of *Acacia karroo* seedlings competing with defoliated grass in the field

Acacia karroo seedling survival in the field was not different in the two paddocks, though the lightly grazed paddock had higher basal cover. This does not support the hypothesis that competition for resources is lower under a low grass biomass. The grass defoliation regime did not affect seedling survival patterns in the heavily grazed paddock.

In the lightly grazed paddock, there was higher seedling survival in the intensely clipped than the moderately clipped treatments. In the growing season only grass clipping frequency had a significant effect on seedling survival ($p < 0.1$). Less frequent defoliation allows the grass to invest in roots as there is less stress on the shoot. Moreover, grasses that are moderately defoliated initially have higher total leaf area and the total carbon assimilation is higher. When the defoliation frequency is increased, more assimilate is allocated to shoot regeneration and less to root growth. Resource uptake by grasses, most likely soil moisture, decreases and *A. karroo* seedlings have a better chance of survival. Grass defoliation, besides enhancing soil moisture availability by reducing the transpiring leaf area, also increases light availability (Fahnestock and Knapp 1994).

The effect of shade on *A. karroo* seedlings however needs further investigation. Prolonged shading decreases seedling root/shoot ratio (Withers 1979). The change in dry matter allocation patterns may determine subsequent seedling survival as they will not have roots long enough to reach the dry season water table. Shade may influence seedling survival in two ways; first by reducing evaporative moisture loss from the soil, and second by

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changing resource allocation patterns of competing seedlings which subsequently determines survival during the dry season. *Acacia karroo* seedlings have been reported to survive better under shade, principally because of an improved soil moisture environment (O'Connor 1995).

In addition to moisture stress and shade, the success of establishment of competing *Acacia* seedlings may be influenced by the time of seedling emergence. Acacias have hard seed coats that allow the seeds to germinate at different times during the growing season. Seedlings emerging early in the growing season may be under less stress than those emerging later in the season. At the onset of the wet season, there is less competition as perennials regenerate and seeds of annuals germinate, but in the middle and towards the end of the season grasses are fully established. These seedlings are however under risk because of the unreliability of the early rains. Likewise, seedlings emerging late may be under greater risk of insufficient growth being achieved before the start of the next dry season. The influence of time of seed germination and emergence on seedling survival therefore needs further investigation.

Higher soil moisture was observed under unclipped grass swards after a rainfall event but this decreased to the same level as under heavily clipped treatments by the end of three weeks. Thus, while undefoliated grass swards may provide a conducive initial moisture environment for seedling establishment, in the absence of further moisture input, the pattern may change as the two growth forms compete for moisture. During long intra-seasonal droughts and the dry season, soil moisture may be low under undefoliated swards.

The results of this study did not support the hypothesis that intense grass defoliation would enhance dry season seedling survival. There were no differences between the different paddocks and among the different treatments. *Acacia karroo* seedling establishment may therefore, during the first year of establishment, not be influenced by the grass defoliation regime. O'Connor (1995) found similar results and suggested that heavy grass defoliation may promote growth of already established seedlings rather than initial establishment. Only under controlled conditions and during the wet season were differences due to defoliation noticed.

In conclusion, heavy grass defoliation was shown to enhance seedling growth under controlled conditions. It is most likely that grass defoliation reduces soil water uptake and increases the amount of moisture available for woody seedling growth. Shade may also be important in determining woody seedling survival. The interaction between aboveground and belowground competition and the effect of this on woody seedling survival needs to be studied further. There was no evidence to suggest that seedling establishment during the first year is influenced by the grass defoliation regime.

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Acknowledgements

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3

Grass defoliation and *Acacia karroo* seedlings: the role of herbaceous competition with encroaching woody plants

C. Chirara and W. Dijkman

Abstract

The effects of defoliation and drought on grass production and on growth and survival of the invasive woody plant species *Acacia karroo* Hayne were investigated in a greenhouse experiment in grass-*Acacia* seedling mixtures. We tested the hypothesis that heavy and repeated clipping of grasses reduces both their above- and below-ground biomass and results in diminished soil water use. This would enhance *A. karroo* seedling performance. In one experiment, seedlings of *A. karroo* were planted in pots with established tussocks of *Setaria incrassata* and were either adequately watered or subjected to periodic droughts. The grass was clipped to different heights (clipped to 5cm, clipped to 11 cm and no clipping). Heavy grass defoliation resulted in reduced biomass production in both moisture environments. *Acacia karroo* plants showed low biomass production, low relative growth rate, and higher root weight ratios at low soil moisture availability. Unclipped grass significantly reduced *A. karroo* biomass production, even under wet conditions, where standing crop reached 1026 g.m⁻². In another experiment, *A. karroo* seedlings growing with established grasses clipped to different heights were subjected to 35 days of drought during which soil moisture change and seedling survival were monitored. Pots with heavily clipped grasses always had higher moisture than unclipped or lightly clipped treatments. There was a positive correlation between *A. karroo* seedling survival and soil moisture content. Heavy grass defoliation enhances tree seedling survival as it reduces grass biomass production and thus increases soil moisture availability. We conclude that intense grass defoliation is an important factor determining competition between tree seedlings and grasses in semi-arid savannas.

Keywords: *Acacia karroo*, bush encroachment, grass defoliation, seedling survival

Introduction

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The semi-arid savannas of Africa support a large proportion of the continent's livestock populations, mainly cattle, goats and sheep. Intensive use of these savannas by herbivores has caused degradation of the herbaceous component and a progressive increase in the density of woody plants (bush encroachment). Increased abundance of woody species in general is thought to be a result of overgrazing by an ever-increasing number of domestic herbivores (Walter 1939, 1954, 1971; Barnes 1979, Werger 1983). However, biological mechanisms that regulate the balance between woody plants and herbaceous vegetation are poorly understood (Frost *et al.* 1986, Scholes & Archer 1997).

Many models used to analyse the dynamics of savanna structure are based on Walter's (1971) two-layer hypothesis in which grasses are superior competitors in the topsoil and trees have exclusive access to subsoil moisture (Walker *et al.* 1981, Walker & Noy-Meir 1982, Sala *et al.* 1989). The two-layer model describes the general pattern of competition between grasses and established trees. Thus, field studies on competition for soil moisture between tree species and grasses in the arid and semi-arid ecosystems of Africa have mainly focused on the interaction between the herbaceous layer and adult woody vegetation (Kelly & Walker 1976, Knoop & Walker 1985, Smith and Goodman 1986, Stuart-Hill & Tainton 1989, Skarpe 1990). However, during their early developmental stages, woody seedlings share the same resource base with already established grasses and may therefore experience more competitive stress than adult trees. In fact, competition with grasses seems paramount at this stage. The competition may lead to soil moisture stress and may result in high mortality among tree seedlings.

High grazing intensities reduce the density, spread and depth of penetration of grass roots (Schuster 1964, Pandey & Singh 1992), and thus affect the uptake of soil moisture. In this improved soil moisture environment, emerging woody seedlings would have a better chance of survival. In a greenhouse experiment, Brown, Scanlan & McIvor (1998) found no effect of grass defoliation on seedling emergence, survival and biomass accumulation of *Acacia nilotica*, but in field studies, mortality of *A. karroo* seedlings competing with grasses has been observed to be higher during the dry season than the wet season (Chirara *et al.* 1999, O'Connor 1995). In these studies however, no evidence was found to suggest that *Acacia* seedling establishment during dry the season was influenced by the grass defoliation regime.

Thus, there are contrasting reports on the effect of grass canopy structure on mortality of *Acacia* seedlings in mixed stands, and the role of soil moisture stress has not been quantified. In this study, we investigate grass biomass production under different clipping regimes and the effect thereof on *Acacia karroo* seedling growth and survival, as influenced by resulting soil water availability. We test the hypothesis that heavy and

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repeated clipping reduces both the above- and below-ground biomass production of grasses, resulting in diminished water uptake. This enhances the survival and growth of *A. karroo* seedlings.

Material and Methods

The experiment was carried out in the greenhouse at Matopos Research Station. Tussocks of the grass species *Setaria incrassata* (hereafter called *Setaria*) were transplanted from the field and grown in 150 pots (30 cm diameter and 50 cm deep) containing soil from a site dominated by *A. karroo* at Mahiye, Matopos Research Station (20°23'S, 28°28'E), in southwestern Zimbabwe. This area is underlain by basement schists giving rise to deep reddish-brown clay soil of moderate nutrient status. A detailed description of the site can be found in Dye (1983).

Experiment 1: *Setaria* defoliation and the effects on competing *A. karroo* seedlings

Five scarified *A. karroo* seeds were planted in each of 90 pots with tussocks of *Setaria*. Another set of 30 pots had *A. karroo* seeds only. Treatments were started one week after seedling emergence. Grass in each of 30 pots was clipped to either 5 cm, 11 cm, or not clipped at all. Grass in the 11-cm (moderately clipped) treatment was allowed to grow to about 17 cm, and then cut back to 11 cm. Each time the 11-cm grass was cut, that in the heavily clipped treatment was reduced to 5 cm. The clipped grass was dried at 80°C for 48 hours and weighed. The pots were subjected to minimum soil moisture levels of either 70% of field capacity (which we will refer to as wet) or 20% of field capacity (dry). For each soil moisture treatment, the plants were watered to about 95% of field capacity and then allowed to decrease to the respective minimum levels, after which they were re-watered. Soil moisture was measured using a Time Domain Reflectometry trace (TDR) (Dalton *et al.* 1984), up to a depth of 20 cm. We therefore had four levels of grass treatment (clipping to 5 cm, clipping to 11 cm, no clipping, and no grass) and two moisture levels. Each treatment was replicated 15 times. A subsample of five pots in each treatment was sampled at each of three harvesting times. The plants were harvested after three, six and nine weeks of treatment, i.e. when the seedlings were four, seven and 10 weeks old, respectively. At each harvest the roots of *Setaria* and *A. karroo* seedlings were carefully separated. Stem and root lengths of the seedlings were measured. The number of leaves on each stem was counted. Each seedling was separated into leaves, stem and root and they were dried at 80°C for 48 hours and weighed. Grass plants in each pot were separated into root and shoot, dried at 80°C for 48 hours and weighed. Grass biomass was expressed as gm⁻² of pot area.

Experiment 2: Survival of *A. karroo* seedlings subjected to drought and grass

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competition

Fifteen scarified *A. karroo* seeds were sown in each of 20 pots with existing *Setaria* tussocks and allowed to germinate. The seedlings were reduced to ten per pot two weeks after germination. All pots were watered to 90% of field capacity at the beginning of the experiment and no more thereafter. Grass was clipped to 5 cm and 11 cm as in Experiment 1. The clipped grass was dried at 80°C for 48 hours and weighed. There were two controls, one without grass and the other with unclipped grass. Each treatment was replicated five times so that the total number of pots was 20. Seedling survival and soil moisture change were monitored in each pot every five days for a total of 35 days. Soil moisture was measured using the TDR.

Analysis

The data from Experiment 1 were subjected to two-way analysis of variance (ANOVA). The data on seedling survival and soil moisture measurements for Experiment 2 were subjected to repeated measures ANOVA with grass height as the within-subject factor and time as the between subjects factor since the seedlings in this experiment were watered once and no more thereafter. All analyses were done using SPSS (SPSS/PC+ 1988). Relative growth rate (RGR) for *Acacia* seedlings was calculated per treatment for Experiment 1 using the formula (Hunt 1978):

$$\text{RGR} = [\text{Ln}(W_2) - \text{Ln}(W_1)] / (t_2 - t_1),$$

where W_1 and W_2 are seedling dry masses at the first and last harvests respectively, and $(t_2 - t_1)$ is the time between the harvests in weeks.

Differences in relative growth rates were tested using ANOVA on ln-transformed plant mass data (Poorter & Lewis 1986). Specific stem length (SSL) and specific root length (SRL) were calculated as:

$$\text{SSL} = \text{stem length/stem mass, and SRL} = \text{root length/root mass.}$$

Results

Effects of defoliation on *Setaria* biomass production

The highest grass biomass was produced in treatments where there was no clipping and the least in heavily clipped treatments (Table 1). Soil moisture and clipping height had significant effects on total dry mass production of *Setaria* ($p < 0.05$). The amount of grass regrowth decreased with each successive clipping to 5 cm. For the 11-cm and no clipping treatments, grass production was higher under a wet than in a dry environment ($p < 0.05$).

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Table 1. Means, F-values and significance levels for two-way ANOVA examining the effects of clipping height, moisture and moisture x height on several variables of eleven-week old *A. karroo* seedlings and *Setaria* biomass production. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's new multiple range test. ^{NS} = p>0.05; * = 0.01<p<0.05; ** = 0.001<p<0.01; *** = p<0.001

Treatment		Length (mm)		Total dry weight (g)	RGR	Ratios	
Clip. height (cm)	Moisture	Root	Shoot			RMR	SMR
No grass	Dry	446.4 ^{bc} (25.4)	115.7 ^{ab} (12.6)	0.63 ^a (0.09)	0.25	0.33 ^b (0.01)	0.18 ^a (0.01)
	Wet	538.4 ^{cd} (46.6)	369.5 ^c (36.4)	2.76 ^b (0.45)	0.41	0.20 ^a (0.01)	0.25 ^c (0.01)
5 cm	Dry	405.9 ^b (21.2)	131.3 ^{ab} (23.0)	0.61 ^a (0.15)	0.28	0.29 ^b (0.00)	0.19 ^a (0.01)
	Wet	653.4 ^d (21.1)	391.3 ^c (25.8)	3.50 ^b (0.47)	0.46	0.21 ^a (0.00)	0.24 ^{bc} (0.01)
11 cm	Dry	376.9 ^b (39.5)	99.1 ^{ab} (20.4)	0.41 ^a (0.13)	0.26	0.32 ^b (0.03)	0.17 ^a (0.01)
	Wet	594.7 ^d (59.3)	340.2 ^c (33.1)	2.61 ^b (0.64)	0.41	0.23 ^a (0.02)	0.22 ^{abc} (0.01)
No clipping	Dry	244.1 ^a (44.1)	59.7 ^a (9.8)	0.11 ^a (0.02)	0.05	0.30 ^b (0.02)	0.22 ^{abc} (0.04)
	Wet	365.1 ^b (36.0)	138.7 ^b (20.6)	0.58 ^a (0.12)	0.25	0.29 ^b (0.01)	0.19 ^{ab} (0.01)
F-values							
Moisture		38.25* **	147.64 ***	64.68***		44.85***	10.81**
Clipping height		13.54* **	18.11* **	9.65***		2.00 ^{NS}	0.64 ^{NS}
Moisture x Clipping height		1.86 ^{NS}	6.38**	4.61**		4.24*	3.32*

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(continued)

Table 1. Means, F-values and significance levels for two-way ANOVA examining the effects of clipping height, moisture and moisture x height on several variables of eleven-week old *A. karroo* seedlings and *Setaria* biomass production. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's new multiple range test. ^{NS} = $p > 0.05$; * = $0.01 < p < 0.05$; ** = $0.001 < p < 0.01$; *** = $p < 0.001$

Treatment		Ratios		Setaria dry mass production (gm ⁻²)			
Clip. height (cm)	Moisture	LMR	Root/shoot	Total clipped	Harvested		Total production
					Root	Shoot	
No grass	Dry	0.49 ^a (0.01)	0.50 ^b (0.02)	0.000	0.0	0.000	0.000
	Wet	0.55 ^b (0.01)	0.26 ^a (0.01)	0.000	0.0	0.000	0.000
5 cm	Dry	0.52 ^{ab} (0.01)	0.42 ^b (0.03)	122.1 ^a (11.5)	63.2 ^a (4.0)	38.3 ^a (7.4)	223.6 ^a (10.4)
	Wet	0.55 ^b (0.01)	0.27 ^a (0.02)	126.1 ^a (11.5)	55.0 ^a (9.6)	53.1 ^a (13.4)	234.1 ^a (22.7)
11 cm	Dry	0.51 ^{ab} (0.02)	0.48 ^b (0.05)	90.5 ^a (14.5)	42.6 ^a (5.7)	83.9 ^a (1.9)	217.1 ^a (12.1)
	Wet	0.55 ^b (0.01)	0.30 ^a (0.03)	245.7 ^b (48.3)	256.9 ^b (75.9)	265.4 ^b (60.2)	768.0 ^b (142.4)
No clipping	Dry	0.49 ^a (0.03)	0.43 ^b (0.05)	0.0	413.7 ^c (54.8)	612.9 ^c (120.3)	1026.6 ^b (167.1)
	Wet	0.52 ^{ab} (0.01)	0.40 ^b (0.03)	0.0	426.7 ^c (68.1)	1029.2 ^d (113.7)	1456.0 ^c (166.2)
F-values							
Moisture		12.31* *	40.03***	NS	*	*	*
Clipping height		1.56 ^{NS}	1.65 ^{NS}	*	*	*	*
Moisture x Clipping height		0.28 ^{NS}	3.56*	*	*	*	*

Grass in the unclipped treatments overtopped the seedlings and grew to heights of at least

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60 cm. By the end of the experiment *Setaria* roots had grown to the bottom of the pots.

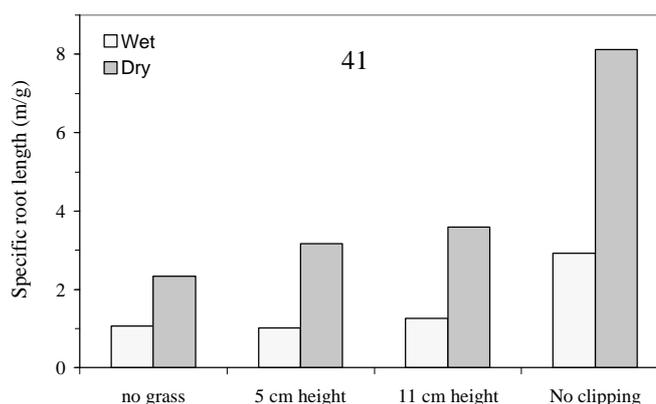
***Acacia karroo* growth and dry matter allocation**

Generally, the total *A. karroo* seedling dry weight was higher in wet than in dry conditions, except in the unclipped treatment where there were no differences between the two moisture levels (Table 1). High grass production in the absence of defoliation greatly reduced seedling biomass production, even under wet conditions. Both grass clipping height and moisture level significantly affected RGR (Table 2).

Acacia karroo seedlings growing in dry conditions had higher root/shoot ratios than plants with high soil moisture in all but the treatment where *Setaria* was not clipped (Table 1). Here the root/shoot ratio in both moisture levels was similar to the root/shoot ratios in the other dry treatments. Seedlings under water stress also had higher root mass ratios (RMR) than those growing in continuously moist soil, except at no clipping where there were no differences between moisture treatments. The RMR, leaf mass ratio (LMR) and stem mass ratio (SMR) were influenced only by soil moisture. Seedlings in high moisture environment had longer roots and shoots than those under water stress (Table 1). Both the *Setaria* clipping height and soil moisture had significant effects on *A. karroo* root and stem lengths. Under wet conditions, seedlings growing with unclipped grass had the shortest roots. The specific root length and specific stem length were greatest in the unclipped treatment under moisture stress (Figures 1a and 1b).

Table 2. ANOVA (with repeated measures) using data on total *A. karroo* seedling dry weight (ln-transformed) to test the effects of *Setaria* clipping height, moisture and time on RGR (after Poorter & Lewis, 1986).

Source of variation	SS	df	P
Height	1.75	3	0.00
Moisture	3.55	1	0.00
Time	6.76	1	0.00
Height x Moisture	0.37	3	0.01
Height x Time	1.21	3	0.00
Moisture x Time	2.27	1	0.00
Height x moisture x Time	0.27	3	0.03



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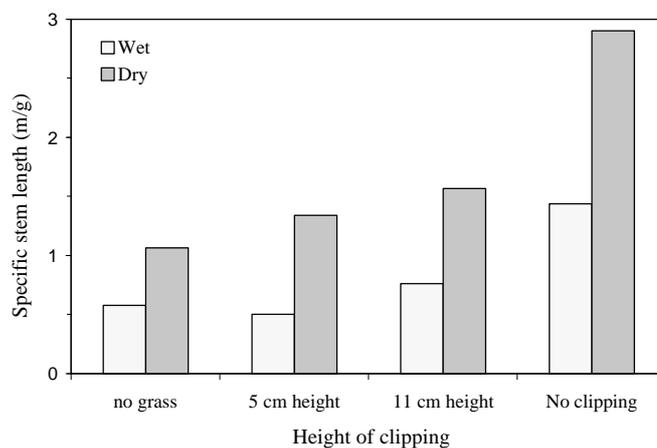


Figure 1. The effect of *Setaria* defoliation regime and soil moisture status on (a) specific root length and (b) specific stem length of *A. karroo* seedlings

Survival of *Acacia karroo* seedlings under drought conditions

Soil moisture and *A. karroo* seedling survival decreased with time (Figure 2). *Setaria* clipping height and time had significant effects on both soil moisture reduction and seedling survival ($p < 0.05$). Unclipped or moderately clipped (to 11 cm) grasses utilised more moisture, resulting in a sharp decline in soil moisture content with time (Figure 2a). By day 30 most of the grass swards in all treatments had died back and decrease in soil moisture thereafter was mainly a function of evaporation and utilisation by surviving *A.*

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karroo seedlings. Survival of the *Acacia* seedlings was highest in pots without grass and in the 5-cm clipping treatment (Figure 2b). There were no differences in seedling survival between the 5-cm and no-grass treatments, though by the end of the experiment there was a significant difference in soil moisture ($p < 0.05$). The corresponding moisture levels in these two treatments were relatively high throughout the period of the experiment ($> 22\%$ by day 35). The highest seedling mortality occurred in the treatment with unclipped grass, in which soil moisture had decreased to less than 10% of field capacity by the end of the experiment.

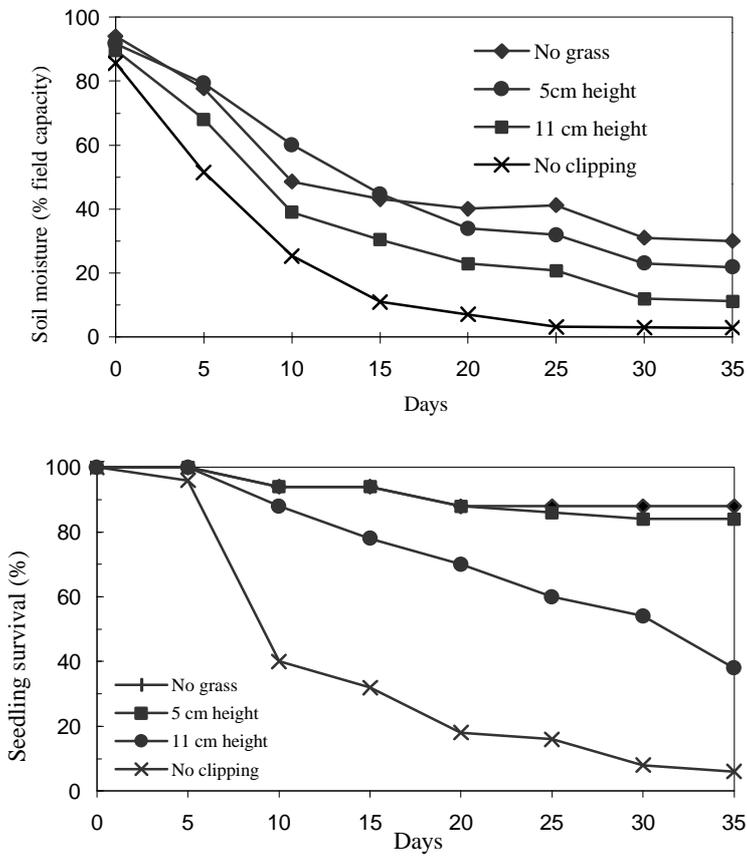


Figure 2. The effects of prolonged drought and grass clipping on (a) soil moisture and (b) *A. karroo* seedling survival

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Discussion

Grassland invasion by woody plants in the semi-arid savannas of southern Africa has for a long time been thought to be a result of overgrazing by herbivores (West 1947, 1958; Brown & Booysen 1967, Kennan 1969, Robinson and Robertshaw 1975, Van Vegten 1983). Over-utilisation of the herbaceous layer may result in, first, reduced production and change in species composition from perennial to annual grasses (O'Connor 1991, Fensham & Skull 1999). This reduces the effectiveness of fire which is an important determinant of these savannas (Scott 1970, Frost *et al.* 1986). Secondly, grass vigour is reduced and this is thought to decrease the sward's competitiveness against establishing woody plants. The role of grass competition in reducing encroachment of woody plants has come under increased investigation in recent years in southern Africa (O'Connor 1995, Chirara *et al.* 1999) and Australia (Brown *et al.* 1998). These studies however give contrasting reports on the effects of grass competition on seedling recruitment by two important encroaching *Acacias*, *A. karroo* and *A. nilotica*.

In the present study grass defoliation and soil moisture interacted to determine grass productivity. Intense defoliation of *Setaria* resulted in reduced total biomass production. This agrees with similar studies on other grass species (Schuster 1964, Pandey & Singh 1992). Soil moisture did not determine grass production under severe clipping but did so under light clipping. Under a light clipping regime, grass under wet conditions produced almost four times the dry mass of that growing in a moisture-limited environment. This study showed that heavy defoliation lowers both above and below-ground grass productivity. In the absence of, or under light clipping, productivity also depends on soil moisture conditions.

The high biomass production of *A. karroo* under clipped and no-grass situations supports the notion that growth of competing woody plant seedlings is enhanced by intense grass defoliation most likely because more resources are made available to the seedlings. Competition from *Setaria* in the absence of defoliation resulted in reduced biomass accumulation of the woody seedlings, even under continuously wet conditions. This suggests that a large *Setaria* biomass limits growth by reducing the amount of light available since the grass overtopped the tree seedlings.

However, the low biomass of competing *A. karroo* seedlings and the relatively high root/shoot ratio displayed when they are grown with unclipped grass suggest that there is also belowground competition. Water-limited plants allocate more dry matter to roots (Kramer & Kozlowski 1979). This increases the seedling's capacity to absorb soil resources. Water stress often reduces shoot growth more than it reduces photosynthesis and thus proportionally more photosynthate is allocated to root growth resulting in an increase

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in root to shoot ratio (Brouwer 1962, Kozlowski *et al.* 1991). When light is limiting the reverse occurs: leaf growth is promoted relative to root growth (Hirose 1987).

The root-to-shoot ratios observed in this experiment showed that *A. karroo* responded to water stress by changing their resource allocation patterns. The grass-clipping regime had no effect on the root/shoot ratio. This maybe because firstly, the light levels in these treatments were high enough for this species to grow without significantly altering resource allocation patterns. Secondly, plants may first have invested in the root before developing the shoot. The root to shoot ratio may thus also depend on the ontogenetic stage of the plant. There was a weak correlation between total dry weight and root/shoot ratio ($r^2 = 0.105$) for differently aged *A. karroo* seedlings growing in wet conditions without grass competition. Therefore, the observed trends in the root-to-shoot ratio were due to the treatments rather than to differences in the developmental stage of plants.

An important characteristic of root systems of semi-arid plants that influences their survival is the ability of the root to extend rapidly enough to keep in contact with a receding soil moisture zone. Seedlings competing with moderately clipped grasses under low moisture or unclipped grass had the lowest relative growth rates and shortest absolute root lengths. Such seedlings however responded to moisture limitation by having high specific root lengths.

When subjected to a long drought period, soil moisture decreased more rapidly under unclipped and moderately clipped grass swards than under heavily clipped grasses. This study showed a close correlation between soil moisture decrease caused by a low-intensity *Setaria* clipping regime or no clipping, and *A. karroo* seedling mortality. This result supports the hypothesis that intense grass defoliation reduces the ability of grasses to deplete soil water resources. Thus heavy grass defoliation can promote range expansion of woody plants by creating a conducive soil moisture environment for colonising seedlings.

The semi-arid savannas of southern Africa have a single rainy season lasting from November to April followed by a prolonged winter drought (Walker 1987). Thus, there is generally high moisture availability during the rainy season. During the non-rainy season, soil moisture level decreases, the water table drops and light availability improves as perennials die back. The response of seedlings to soil moisture status during the rainy season is important in determining subsequent survival. Seedlings under shade, for example, might channel resources to the shoot at the expense of root extension. Seedlings of other *Acacia* species have been shown to respond to a decrease in light by having a low root biomass production (Milton 1982, Smith & Shackleton 1988, Loth 1999). Such seedlings might then not survive the dry season as they would not have an adequately developed root system.

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In conclusion, herbaceous vegetation reduces the survival and growth of seedlings of the encroaching *A. karroo*. Intense grass defoliation was shown to enhance *A. karroo* seedling survival because of reduced soil moisture uptake. Heavy clipping reduced grass biomass and soil moisture uptake and thus making more water available for woody seedling growth and survival. Drought and grazing may interact to determine woody seedling dynamics in semi-arid ecosystems. From the results of this experiment, we have evidence to support the hypothesis that grass competition can limit the growth of seedlings of *A. karroo*. We therefore suggest that among other factors, there is a need to control the grazing intensity in savannas as grasses have a role to play in the establishment and hence encroachment of woody species.

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4

The effect of below and aboveground resource limitation on the growth and dry mass partitioning of seedlings of *Acacia karroo*

C. Chirara

Abstract

The response of seedlings of *Acacia karroo* Hayne to four levels of irradiance (4%, 19%, 38% and 100% of full light) under dry and wet conditions was investigated in a factorial experiment in the greenhouse. There was a significant decrease in total dry mass and root length under deep shade at both moisture conditions. Low light levels resulted in increased height growth under dry conditions. With decreasing irradiance, when subjected to water stress, the root/shoot ratio declined whereas both leaf area ratio and specific leaf area increased. Under wet conditions, the root/shoot ratio was low at the 4% irradiance level and constant in the other treatments.

Keywords: Aboveground competition, belowground competition, biomass allocation, drought, shade

Introduction

The woody species *Acacia karroo* is an important invader of grassland in southern Africa's semi-arid savannas (Friedel 1987, O'Connor 1995). Increased density of this species and other invading woody plants has resulted in reduced grass quantity and quality and hence animal productivity (Stuart-Hill and Tainton 1989). The seedling recruitment stage is important in the range expansion of such encroaching trees.

Seedlings of woody plants compete with grasses for resources such as soil moisture and light (Harrington 1991). Defoliation alters both the above- and belowground biomass production of grasses (Schuster 1964, Pandey and Singh 1992), and thus their ability to compete with tree seedlings. Reduced biomass of grass results in increased availability of

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soil moisture (Chirara *et al.* 1999) and may be expected to improve the light environment of competing tree seedlings.

The level of irradiance is one of the important factors that influence plant growth and survival. Milton (1982) showed that some invasive Australian *Acacia* species have reduced growth under low irradiance and suggests deep shade as a means controlling their regeneration. Studies on other African *Acacia* species have shown that they fail to establish under the canopy of established trees (Smith and Goodman 1986). *Acacia tortilis* seedlings respond to low irradiance by significantly reducing their biomass production and root/shoot ratios (Smith and Shackleton 1988). Previous experiments have also shown that tall and dense grass swards reduce the growth of *A. karroo* seedlings even under a moist environment of moderate nutrient status (Chirara and Dijkman in prep.). This suggests an effect of shade from the grass. *Acacia karroo* is thought to be heliophytic and to require high irradiance for optimal growth. However, no studies have been done to ascertain this. In field studies, survival of *A. karroo* seedlings has been shown to be enhanced by shade, apparently through amelioration of soil moisture (O'Connor 1995).

The distribution of dry matter between the plant's root and shoot systems is influenced largely by external factors such as moisture regime and light. Plants growing in zones of low moisture availability allocate more dry matter to the root. Such water-limited plants may also have high root length per unit mass (specific root length). This increases the capacity of a seedling to absorb soil water. Shade promotes resource allocation to leaves, resulting in a decrease in root/shoot ratio. Shaded plants have a high specific stem length and produce long internodes. Elongation of internodes is a mechanism of plants of foraging for light as they position their leaves in the upper layers where irradiance is higher (Grime *et al.* 1986, Slade and Hutchings 1987). Thus when subjected to resource limitation, plants may change their dry matter allocation and morphology so as to facilitate the acquisition of the most limiting resource (Brouwer 1962).

Table 1. Mean irradiance levels at ground level (% of full light) at Matopos under clipped and unclipped grass on a sunny day during the 1996/97 growing season. Standard error values are in parentheses.

Plot	Clipped to 5 cm height	No clipping
1	91.5 (1.56)	6.9 (0.64)
2	96.3 (1.09)	5.6 (1.29)
3	85.2 (9.23)	6.4 (0.39)

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The southern African semi-arid savannas in which *A. karroo* is encroaching are characterised by low rainfall during the growing season (November – March), which is often interrupted by long intra-seasonal drought spells. This is followed by an even longer dry season (April – October). In the absence of intense grass defoliation, the establishing tree seedlings are subjected to relatively intense shade of about 6% of full light (Table 1) and generally high soil moisture. At the onset of the dry season the water table gradually recedes to deeper layers. Survival of the seedlings therefore depends on, firstly, their ability to obtain moisture from deeper layers. This is influenced by biomass partitioning and root extension during the growing season. Secondly, survival depends on the capability of the seedlings to thrive under the shade of the grasses during the growing season.

The present study investigates the response of *A. karroo* seedlings to limitation in both light and soil moisture. The study tests the hypothesis that *A. karroo* seedlings under shade have reduced growth and allocate more resources to shoot development than to the root because they need to outgrow the grasses to access light. This allocation to the shoot is reduced when the seedlings are under moisture stress which increases sink strength of the roots.

Materials and Methods

The experiment was carried out at the University of Zimbabwe, Harare. Four enclosures were erected in the greenhouse. These were left uncovered, covered with one, two and four layers of black shade cloth to give 100%, 38%, 19% and 4% of full light respectively. Soil was collected from a site dominated by mature *A. karroo* trees at Matopos Research Station in southwestern Zimbabwe (20°23'S, 28°28'E). The soils are dark reddish brown clay loams derived from epidiorite (Nyamapfene 1991). A description of the site can be found in Dye (1983). The soil was sieved to remove large particles and stones and transferred to 63 pots 30 cm in diameter and 50 cm deep.

Ten scarified *A. karroo* seeds were planted in each pot. One week after emergence, the seedlings in each pot were reduced to three by selecting seedlings of the same height and uprooting the rest. Seven pots were randomly selected and the seedlings harvested. The seedlings were oven dried and their mass determined. For the remainder, seedlings in fourteen pots were transferred to each of the four different light environments. The seedlings in each light environment were subjected to two minimum moisture levels of 20% and 80% of field capacity (F.C.), to give seven replicates per treatment. The plants were initially watered to about 95% F.C. and then allowed to drop to their respective minimum moisture levels, after which they were re-watered. Soil moisture was monitored gravimetrically. The plants were harvested after twelve weeks of treatment. At harvest, the plastic pots were cut out and the seedlings were carefully removed from their containers

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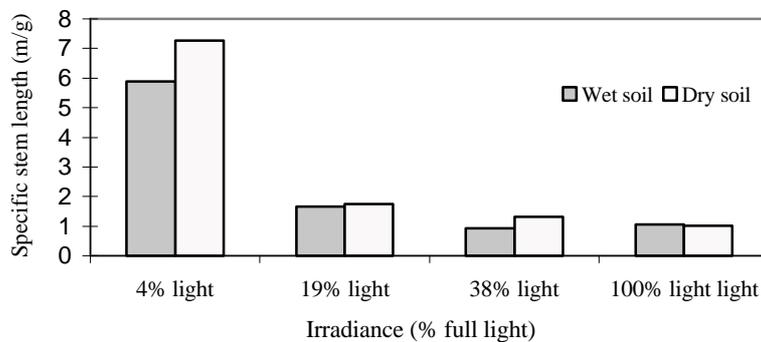
by slowly flushing the soil from around the roots. The lengths of the taproots and stems, and the first four stem internodes, were measured. The plants were separated into root, stem and leaves, oven-dried at 80°C for 48 hours and had their dry mass determined. Leaf area was determined for a randomly selected subsample of (three seedlings) each treatment by scanning photocopies of fresh leaves, which were then dried and weighed separately.

Calculations and data treatment

Leaf area ratio (LAR) was determined by dividing the leaf area (cm²) by the total seedling biomass (g). Specific leaf area (SLA) was calculated by dividing the leaf area by the leaf mass. Leaf, stem, and root mass ratios (LMR, SMR and RMR, respectively) were calculated by dividing the biomass of these parts by the total seedling biomass. The LMR, SMR and RMR were arcsine-transformed and the root/shoot ratio ln-transformed before analysis. Analysis of variance (ANOVA) was used to determine differences between seedling variables of the different treatments, using the procedures of SPSS (SPSS/PC+ 1988).

Results

Both irradiance and soil moisture level significantly affected seedling dry mass production ($p < 0.001$). The interaction between these two factors was significant ($p < 0.05$). The lowest biomass was in seedlings that grew in deep shade (4% of light) under the two moisture environments. When subjected to the same amount of light, *A. karroo* seedlings in wet conditions produced more dry mass than those in dry conditions, except under deep shade where the differences between moisture treatments was not significant (Table 2). Under dry conditions, plants receiving 19% of full light and above produced the same amount of total dry mass ($p > 0.05$). No mortalities were recorded for any treatments.



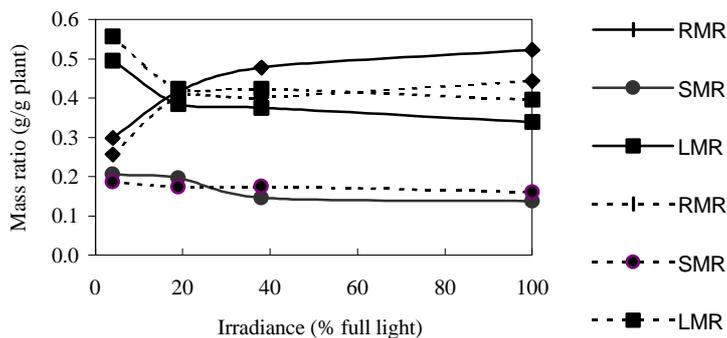
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Figure 1. The specific stem lengths of seedlings growing under different light and moisture regimes.

Acacia karroo seedlings growing in 4% light had the shortest roots under the two moisture environments. The plants grew tap roots that did not extend beyond 30 cm. Seedlings stem lengths responded differently under the two moisture levels. In dry conditions, the shortest stems were in seedlings growing in full light. Seedlings in the other light levels were not significantly different from each other ($P>0.05$). Under wet conditions, stems were longest in treatments receiving 38% of light. Seedlings growing in deep shade had high specific stem lengths, moreso under dry conditions (Figure 1). At each moisture condition, internodal length decreased with increasing irradiance. Only irradiance had a significant effect on internodal length ($p<0.001$).

Under each moisture environment, LAR was highest at 4% of full sunlight and decreased with increasing irradiance. Both light and moisture had significant effects on the LAR and their interaction was significant ($p<0.05$). The SLA was significantly influenced only by irradiance ($p<0.001$) and was highest under deep shade and lowest under full sunlight for both moisture treatments.

Under wet soil conditions, seedlings that received 4% irradiance produced the lowest root/shoot ratio. The other irradiance treatments at this moisture level had higher root/shoot ratios and there were no differences among them ($p>0.05$). In drier soil, seedling root to shoot ratios increased with increasing irradiance (Table 2). Figure 2 shows *A. karroo* seedling dry matter allocation to the root, stem and leaves over a range of light conditions. The LMR was highest under deep shade for both moisture treatments. The lowest RMR was in shaded seedlings and this increased with increases in the level of irradiance.



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Figure 2. Changes in root, stem and leaf mass ratios of *A. karroo* seedlings over a range of irradiance levels under dry () and wet (·····) conditions

Table 2. Dry mass production, biomass partitioning and leaf characteristics of *Acacia karroo* seedlings subjected to two moisture levels and four light regimes. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's new multiple range test. ^{NS} = p>0.05; * = 0.01<p<0.05; ** = 0.001<p<0.01; *** = p<0.001

Moisture condition	Irradiance (% full light)	Root length (mm)	Stem length (mm)	Internode length (mm)	No of leaves	Root mass (g)	Stem mass (g)
Dry	4	284.0 ^a (26.0)	124.6 ^b (8.7)	13.1 ^d (0.9)	8.6 ^a (0.5)	0.027 ^a (0.004)	0.018 ^a (0.002)
	19	385.5 ^b (8.0)	119.6 ^b (9.3)	11.2 ^c (0.7)	10.6 ^{ab} (0.6)	0.153 ^{ab} (0.016)	0.069 ^{ab} (0.006)
	38	407.6 ^b (12.5)	124.1 ^b (7.7)	7.8 ^b (0.2)	13.5 ^c (0.8)	0.315 ^c (0.028)	0.096 ^b (0.008)
	100	445.7 ^{bc} (15.8)	68.8 ^a (9.5)	5.1 ^a (0.2)	10.7 ^{ab} (0.8)	0.271 ^{bc} (0.037)	0.096 ^{ab} (0.014)
Wet	4	268.5 ^a (17.8)	146.7 ^{bc} (12.5)	13.3 ^d (0.7)	11.4 ^{bc} (0.7)	0.033 ^a (0.003)	0.026 ^a (0.003)
	19	490.7 ^{cd} (26.3)	190.7 ^{de} (19.4)	10.9 ^c (1.1)	16.2 ^d (0.5)	0.287 ^{bc} (0.039)	0.130 ^b (0.025)
	38	494.4 ^{cd} (30.7)	222.9 ^e (13.4)	9.0 ^b (0.4)	18.9 ^e (0.8)	0.554 ^d (0.029)	0.244 ^c (0.021)
	100	519.5 ^d (32.3)	171.5 ^{cd} (17.8)	5.8 ^a (0.3)	19.2 ^e (1.6)	0.60 ^d (0.124)	0.214 ^c (0.047)
F-Values							
Irradiance		33.00***	6.39**	53.60***	19.56***	30.13***	18.54***
Moisture level		15.13***	64.77***	1.08 ^{NS}	83.41***	25.00***	35.09***
Irradiance x moisture level		2.78 ^{NS}	4.11*	0.48 ^{NS}	3.83*	3.86*	5.01*

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In this study *A. karroo* seedling growth was assumed to be governed by irradiance and soil moisture availability. These factors interacted to determine biomass production. At low irradiance levels the rate of photosynthesis increases linearly in proportion to light intensity (Hall and Rao 1987). Accordingly, *A. karroo* seedlings growing in wet conditions under low irradiance levels (4% and 19%) produced low biomass compared to those receiving higher amounts of irradiance. Irradiance levels of 38% of full light and above did not result

Table 2. Dry mass production, biomass partitioning and leaf characteristics of *Acacia karroo* seedlings subjected to two moisture levels and four light regimes. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's new multiple range test. ^{NS} = $p > 0.05$; * = $0.01 < p < 0.05$; ** = $0.001 < p < 0.01$; *** = $p < 0.001$

Moisture condition	Irradiance (% full light)	Leaf mass (g)	Total dry mass (g)	LAR (cm ² g ⁻¹)	SLA (cm ² g ⁻¹)	R/S Ratio (g/g)
Dry	4	0.044 ^a (0.005)	0.089 ^a (0.010)	237.6 ^c (4.0)	480.2 ^c (38.2)	0.430 ^a (0.036)
	19	0.141 ^{abc} (0.013)	0.364 ^{ab} (0.026)	117.13 ^b (0.3)	308.4 ^b (0.4)	0.730 ^b (0.063)
	38	0.249 ^{cd} (0.025)	0.659 ^{bc} (0.056)	94.3 ^b (2.1)	237.5 ^{ab} (2.8)	0.927 ^{cd} (0.058)
	100	0.173 ^{bc} (0.021)	0.516 ^{bc} (0.070)	46.5 ^a (3.2)	156.3 ^a (16.9)	1.115 ^d (0.085)
Wet	4	0.076 ^{ab} (0.007)	0.135 ^a (0.011)	287.0 ^d (5.71)	560.6 ^c (38.3)	0.358 ^a (0.056)
	19	0.297 ^d (0.037)	0.714 ^c (0.099)	93.4 ^b (0.7)	226.8 ^{ab} (6.0)	0.676 ^b (0.029)
	38	0.592 ^e (0.046)	1.391 ^d (0.065)	111.3 ^b (18.4)	246.6 ^{ab} (35.5)	0.687 ^b (0.070)
	100	0.502 ^e (0.086)	1.317 ^d (0.241)	56.7 ^a (10.1)	186.0 ^a (0.0)	0.811 ^{bc} (0.066)
F-Values						
Irradiance		31.66***	31.81***	297.12** *	63.54***	31.76***
Moisture level		60.02***	42.18***	5.74*	0.22 ^{NS}	15.47**
Irradiance x moisture level		7.16*	5.52*	7.73**	2.96 ^{NS}	2.10 ^{NS}

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in significant increases in seedling biomass because at these levels light was no longer limiting growth. However, under dry conditions biomass production was limited more by water than light and the seedlings responded less to increases in irradiance than those in wet soil.

Shade influences plant morphology. Under dry conditions seedlings subjected to deep shade had the lowest dry mass but they had longer stems and internodes than those in full light. Therefore, despite their low biomass due to light and moisture limitations, they etiolated in order to grow out of the shade and access more light. Shoot etiolation in response to shading has been reported to be characteristic of sun-adapted plants (Grime 1966). Similar responses to shade have been observed in *A. tortilis* (Smith and Shackleton 1988), some Australian *Acacias* (Milton 1982) and other shade avoiding woody species (Withers 1979). This rapid elongation in shade may help the tree seedlings escape grassy layers, but if the grasses are dense and tall the seedlings in the end fail to outgrow the shade and may eventually die. In this study, seedlings under deep shade (4% light) were bending over by the time of harvest, because of a relatively large leaf mass being supported by a thin and long stem, and probably would soon have collapsed onto the soil if they had been given more time to grow. In the wetter environment stems were always longer. Longer stems in the field situation will enable the seedlings to display their leaves in a better-lit environment, and this will re-enforce their biomass accumulation.

Root length was lowest under deep shade at both moisture levels. By the end of the experiment roots of seedlings growing under 4% of light were less than 30 cm deep under both wet and dry soil. This was attributed to the relatively lower allocation of biomass to the root as the continuously shaded seedlings directed resources to leaf and stem growth. Poor root development due to shading has been reported for other *Acacia* species (Milton 1982, Loth 1999). Under field conditions having short roots lowers the seedlings' chances of survival during dry periods.

Generally, a plant's production rate increases with the amount of leaf area. When subjected to both deep shade and low soil moisture, *A. karroo* seedlings invested dry matter into leaf and stem growth at the expense of the root. The results suggest that 4% irradiance has a more negative effect on growth than 20% F.C. soil moisture. The LAR, SMR and RMR indicate how a plant invests biomass in photosynthetic area, woody shoot growth and moisture acquisition, respectively (McKee 1995). Under dry conditions, the tendency is for plants to invest in roots but this study shows that when light is limiting biomass partitioning to roots would only increase with an increase in irradiance.

Acacia karroo seedlings growing in shade invested more photosynthate in leaf area and thus had high LARs. Such high LARs have also been reported for *A. tortilis* seedlings growing under low photon flux densities (Smith and Shackleton 1988). *Acacia karroo* seedlings growing in a low irradiance environment also had a high SLA, indicating that

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they maximised potential capture of light. High LARs and SLAs are usually interpreted as adaptations allowing seedlings to outgrow grasses and emerge from the shady stratum via increased light harvesting resulting in more height growth (Loach 1970). This plasticity in leaf morphology in response to shade has been reported for temperate shrub seedlings (Grubb *et al.* 1996) and other tropical tree seedling species (Fetcher *et al.* 1983, Oberbauer and Strain 1985, McKee 1995). The plasticity displayed by *A. karroo* seedlings can however constitute a short-term risk for their survival. Should drought occur, as is often the case during and between seasons, they risk desiccation: Shaded seedlings that have high specific leaf area would lose water rapidly under dry situations. In addition, root-to-shoot ratios were lowest in seedlings with the highest SLA and this aggravates water loss as there is reduced soil moisture uptake (Loach 1970).

The results of this experiment have important implications for grassland invasion by *Acacias* in the arid and semi-arid savannas of Africa. The major mode of encroachment of *Acacias* onto grasslands is by recruitment through seed in areas with already established (mostly perennial) grasses (Brown and Booysen 1967, Du Toit 1967). Newly germinated seedlings share the same resource base with grasses and thus the two growth forms inevitably compete for light and soil water. Deep shade resulting from a dense grass sward would reduce seedling growth and root extension and thus lowers *A. karroo* seedling survival in semi-arid grasslands particularly during the dry season. In the field situation, opening up of the grass matrix by grazing increases light availability to establishing seedlings and thus enhances their survival chances.

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Response of seedlings of *Acacia karroo* to changes in light and soil moisture environment

Chipangura Chirara

Abstract

Tree seedlings growing in savanna regions are exposed to high soil moisture during the rainy season and drought during the dry season. Grasses overtop and shade establishing seedlings during the rainy season and die-off in the dry season. Thus, seedlings are exposed to shade and high moisture availability in summer and low moisture and high irradiance in the non-rainy season. To survive, tree seedlings need to acclimate to changing light and moisture conditions. An experiment was carried out in the greenhouse to investigate the response of seedlings of *Acacia karroo* Hayne to changes in both the moisture and irradiance environment. Seedlings were first grown in clayey soil in shade and wet conditions and then transferred to light and dry, light and wet, and shade and dry conditions. In all treatments, the root lengths of the seedlings grew to at least 56 cm within eight weeks of emergence. After 13 weeks seedlings in light had longer roots than those in shade. Roots of transferred plants grew to the same length as those plants that grew in the transferred environment throughout. Shaded seedlings allocated more biomass to the leaves than to roots. The *A. karroo* seedlings adjusted their leaf characteristics and resource allocation patterns to suit their new environments. When the plants were transferred from shaded and wet conditions to higher irradiance conditions the leaf area ratio (LAR) decreased significantly to values of those seedlings that grew in these conditions for the whole period of the study. The results of this experiment suggest that tree seedlings can survive and grow in areas that already have grass and adapt well to the drastic seasonal changes occurring in established grasslands.

Keywords: Acclimation, irradiance, resource allocation

Introduction

Tropical savannas are characterized by distinct wet and dry seasons that are coupled with high temperatures (Werger 1983, Goldstein and Sarmiento 1986). Rainfall in these areas is highly variable between and within seasons. Herbaceous biomass production is mainly dependent upon the amount of rainfall (Danckwerts and Stuart-Hill 1988). Because of the relatively high amount of grass biomass in these regions, they have for a long time been utilised for livestock production. Over the years, increases in cattle production have resulted in increased density of woody plants (bush encroachment) in savannas. In southern African savannas, *Acacia karroo* is one of the dominant tree species occurring on heavy or fine-textured soils. While it is generally accepted that the major cause for the success of establishment of this and other savanna woody invader species is the reduction of herbaceous competition by overgrazing (Walter 1939, 1954, 1971; Walker *et al.* 1981, O'Connor 1995, Brown *et al.* 1998), the mechanisms involved are not fully understood.

To survive, arid and semi-arid savanna plants have to be adapted to highly temporally variable environmental conditions (Loth 1999). Success of establishment of tree seedlings depends, among other factors, on precipitation, the amount of vegetation already present, herbivory and the availability of nutrients. Germination of non-scarified *Acacia* seeds at any one time can be as low as 3% (Miller 1994). This is a survival strategy as seedlings emerge at different times during the growing season and can, as a result, exploit windows of favourable conditions. Survival of establishing woody plants may depend on the time of seed germination and the time that they need to reach the wet soil zone. Germination of seeds late in the rainy season means the seedlings have to put down deep roots within a short time to keep track of a receding water table. At the onset of the dry season, the soil begins to dry out from the surface downwards and therefore plants whose roots are restricted to the upper layers may not survive. The deeper soil layers retain water for a long time as they are isolated by the topsoil.

Away from the canopy shade of established trees, tree seedlings are shaded during the wet season by perennial grasses, annuals and moribund material. In order to gain access to sunlight, newly germinated *A. karroo* seedlings need to elongate their stems sufficiently to overtop the grasses. To do this, the plants might allocate more resources to shoot extension at the expense of the root, resulting in them having short roots. At the onset of the dry season, such seedlings have relatively short roots that do not reach the water table and may as a result fail to survive the dry season. In addition, at the end of the wet season, perennials die back leaving the soil surface exposed to sunlight and the upper soil layers dry faster. Seedlings whose roots are in the upper soil strata die after the end of the rainy season because they cannot access water from deeper layers. Moreover, biomass partitioning and characteristics developed under shaded and moist conditions may affect the subsequent survival of the seedlings when the moisture and irradiance environment

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change. If the seedlings respond to long periods of shading by increasing the surface area of the leaves, exposure to sunlight may result in mortality because of increased water loss due to high evapo-transpiration. In earlier experiments with seedlings of *A. karroo* in the field, high mortalities were observed at the onset of, and during the dry season (O'Connor 1995, Chirara *et al.* 1999).

Grazing and trampling creates light gaps within the grass matrix by reducing the height of the grasses. Thus, previously shaded seedlings can be exposed to more sunlight at different times of the season. For successful establishment, woody seedlings should have the potential to adapt to varying light and moisture conditions. This study was undertaken to investigate the response of *A. karroo* seedlings to changes in both irradiance and soil moisture conditions in the greenhouse. The hypothesis tested was that seedlings of *A. karroo* adapt to changes in light and moisture conditions by adjusting their leaf characteristics and biomass allocation patterns, in order to enhance acquisition of these resources. Moreover, I also hypothesize that biomass production of seedlings growing in shaded and wet conditions tend to decrease when the seedlings are transferred to dry conditions but increase when irradiance increases.

Materials and Methods

The experiment was carried out at the University of Zimbabwe, at Harare. A 15 x 3 m² enclosure was erected in the greenhouse. It was constructed on a bench that was 1 m above the ground and the enclosure rose a further 1.5 m above the benches. This enclosure was covered with three layers of black shade cloth at the top as well as on all four sides, leaving the bottom uncovered to allow free circulation of air. The shade cloth allowed about 8% of light inside the greenhouse to pass through. One hundred and ten PVC pots, 14 cm in diameter and 100 cm deep, were filled with clayey soil (59.6% clay, 22.6% silt and 17.8% sand) from around Harare. This soil was inoculated with small amounts of soil from underneath mature *A. karroo* trees at Matopos Research Station (20°23 S, 28 °28 E), an area where this species occurs naturally. This was done because *Acacias* form symbiotic associations with *Rhizobium* species (Tolsma *et al.* 1987).

Five scarified *A. karroo* seeds were planted in each of the pots at the beginning of the experiment. Seedlings emerged within a week of planting and were reduced to one per pot by choosing seedlings of the same height and uprooting the rest. Two weeks after emergence, a sub-sample of these seedlings was harvested. The remainder were allowed to continue growing in light or transferred to shade. The plants within each of the two irradiance environments were subjected to two moisture regimes - dry or wet. Plants were initially watered to field capacity and then allowed to drop either to 70% (wet) or 20% (dry) of field capacity, after which they were re-watered. Soil moisture was monitored gravimetrically. Thus, there were seedlings that grew under each of these conditions - light

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and wet (LW), light and dry (LD), shaded and wet (SW) and shaded and dry (SD). When the seedlings were eight weeks old (i.e., after six weeks of treatment), a sub-sample of ten plants from each of the four environments was harvested. Another set of ten plants (hereafter called controls) was allowed to continue growing for a further five weeks in each of these conditions. In addition, groups of ten plants were transferred from the SW environment to each of SD, LW and LD conditions, and were allowed to grow for five weeks in these new conditions. These plants will be referred to as transferred plants. All plants were relocated regularly within each treatment to avoid the effects of location within the greenhouse. All plants were harvested when they were thirteen weeks old (i.e. after a total of 11 weeks of treatment). Figure 1 below shows the design of the experiment.

Harvesting and measurements

At each harvesting period the PVC pipes were cut out and the plants extracted by carefully flushing the soil with a jet of water. The plants were separated into root, stem and leaves. The lengths of roots and stems were determined. Leaf area was determined by making photocopies of leaves and then measuring area using a scanner. The individual plant parts were oven-dried at 80°C for 48 hours and then weighed.

The following parameters were derived from the primary dry mass data: Root/shoot ratio (R/S, root dry mass/stem + leaf dry mass), leaf area ratio (LAR, leaf area/total plant dry mass), specific leaf area (SLA, leaf area/leaf dry mass). Stem, leaf and root mass ratios (RMR, SMR and LMR respectively) were derived by dividing the dry mass of these parts by the total plant mass.

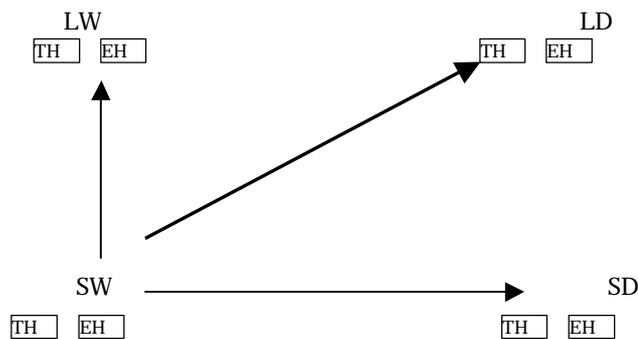


Figure 1 showing the design of the experiment. TH = harvest at transfer and EH = harvest at the end of the experiment.

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Analyses

The data were analysed using three-way analysis of variance (ANOVA) to test the effects of irradiance, water and age. Comparisons between transplanted plants and controls were done using one-way ANOVA contrasts. All analyses were done using the procedures of SPSS (SPSS/PC+ 1988). Relative growth rate (RGR) was calculated as (Evans 1972):

$$\text{RGR} = (\ln M(t_2) - \ln M(t_1)) / (t_2 - t_1)$$

where M is total plant dry mass (g) and t is time in weeks. Differences in RGRs were tested using ANOVA on ln-transformed plant mass data (Poorter and Lewis 1986). Root/shoot ratios were ln-transformed and RMR, LMR and SMR were arcsine-transformed before analyses.

Results

Seedlings put down deep roots of more than 56 cm within eight weeks of emergence, irrespective of their light and soil moisture conditions (Table 1). There were no differences between treatments ($p > 0.05$) at this age. After 13 weeks, the longest roots were in the light treatments and the shortest in SD treatment. The root length was influenced by irradiance and the age of the plants. For transferred plants, the roots developed to the same length as that of plants that grew in these conditions continuously (Table 3).

The seedlings' absolute stem length was significantly influenced by soil moisture but the specific stem length was affected by irradiance only. After eight weeks of growth, SW plants had significantly longer stems than those in other control treatments. However, at the end of 13 weeks, seedlings in LW condition had by far the longest stems, which explains the significant I x A interaction (Table 1). After 13 weeks, transferred plants had the same stem length as eight-week-old seedlings in SW conditions (Table 3). Seedlings transferred to LW (SW-LW) had shorter stems than those that were in LW all the time. Seedlings growing in shade had higher specific stem lengths and therefore thinner stems compared to those in light at both ages. When transferred to high irradiance conditions, the seedlings decreased their specific stem length (Tables 2 and 3). For controls, plants growing in full sunlight had shorter internodes than those growing in shade. The internodal length was affected only by irradiance.

Generally, *A. karroo* seedlings in light were heavier than those in shade (Table 1). Both irradiance and soil moisture significantly influenced seedling biomass production ($p < 0.001$). Seedlings transferred to LW and LD produced less biomass than those that grew in these conditions throughout (Table 3). The root/shoot ratio was influenced by both irradiance and soil moisture availability (Table 2, $p < 0.05$). The lowest root/shoot ratio was in eight-week-old plants in the SW environment ($p < 0.05$). All other treatments had higher root/shoot ratios and by the end of the thirteenth week, those in the SD and LD

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Table 1. Mean values (with s.e.) for primary data for *A. karroo* seedlings subjected to different light and soil moisture treatments. For details on treatments see text. Means in the same column with different superscript letters were different by Duncan's new multiple range test. Also shown are F-values for three-way ANOVA for control treatments. ^{NS} = $p > 0.05$; * = $0.01 < p < 0.05$; ** = $0.001 < p < 0.01$; *** = $p < 0.001$

Treatment	Length (mm)		
	Root	Stem	Internodes
Harvest at 8 weeks			
LW	690.4 ^{ab} (60.7)	61.0 ^{ab} (4.5)	5.9 ^a (0.4)
LD	626.8 ^{ab} (87.6)	53.8 ^a (5.7)	5.7 ^a (0.4)
SW	561.1 ^a (64.7)	116.1 ^{cd} (4.7)	11.4 ^c (0.9)
SD	589.1 ^{ab} (62.9)	85.8 ^{abc} (8.7)	8.9 ^b (0.8)
Harvest at 13 weeks			
Controls			
LW	918.1 ^c (41.7)	204.8 ^c (15.9)	6.6 ^a (0.5)
LD	938.9 ^c (41.4)	112.5 ^{cd} (11.1)	7.6 ^{ab} (0.6)
SW	774.8 ^{bc} (66.1)	136.6 ^d (24.7)	12.3 ^c (0.9)
SD	598.4 ^{ab} (61.9)	97.3 ^{bc} (15.0)	12.7 ^c (1.3)
Transfers			
SW-LW	816.6 (43.8)	122.4 (8.1)	12.1 (1.2)
SW-LD	921.8 (45.8)	120.2 (15.0)	12.0 (1.0)
SW-SD	771.8 (52.5)	131.4 (12.4)	12.0 (0.8)
F-values			
Irradiance (I)	14.78***	0.01 ^{NS}	75.73***
Moisture (M)	1.56 ^{NS}	22.01***	0.29 ^{NS}
Age (A)	17.11***	42.27***	10.02**
I x M	0.51 ^{NS}	0.68 ^{NS}	1.52 ^{NS}
I x A	3.84 ^{NS}	4.57*	0.83 ^{NS}
M x A	0.72 ^{NS}	6.82*	3.12 ^{NS}
I x M x A	3.23 ^{NS}	4.45*	0.51 ^{NS}

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Table 1. Mean values (with s.e.) for primary data for *A. karroo* seedlings subjected to different light and soil moisture treatments. For details on treatments see text. Means in the same column with different superscript letters were different by Duncan's new multiple range test. Also shown are F-values for three-way ANOVA for control treatments. ^{NS} = $p > 0.05$; * = $0.01 < p < 0.05$; ** = $0.001 < p < 0.01$; *** = $p < 0.001$

Treatment	Mass (g)				Number of leaves
	Root	Stem	Leaf	Total	
Harvest at 8 weeks					
LW	0.103 ^{ab} (0.011)	0.032 ^a (0.005)	0.118 ^a (0.011)	0.253 ^a (0.024)	9.4 ^{bc} (0.3)
LD	0.095 ^{ab} (0.010)	0.038 ^a (0.007)	0.108 ^a (0.016)	0.241 ^a (0.027)	7.8 ^{ab} (0.7)
SW	0.037 ^a (0.004)	0.031 ^a (0.003)	0.089 ^a (0.008)	0.157 ^a (0.013)	6.8 ^a (0.6)
SD	0.053 ^{ab} (0.008)	0.026 ^a (0.003)	0.079 ^a (0.010)	0.158 ^a (0.019)	6.1 ^a (0.5)
Harvest at 13 weeks					
Controls					
LW	0.509 ^d (0.058)	0.269 ^c (0.038)	0.614 ^c (0.065)	1.391 ^c (0.159)	18.1 ^e (1.0)
LD	0.347 ^c (0.047)	0.117 ^b (0.022)	0.255 ^b (0.032)	0.719 ^b (0.092)	12.6 ^d (1.0)
SW	0.115 ^{ab} (0.020)	0.056 ^a (0.010)	0.146 ^a (0.032)	0.318 ^a (0.063)	10.9 ^{cd} (1.1)
SD	0.133 ^b (0.020)	0.028 ^a (0.004)	0.099 ^a (0.017)	0.259 ^a (0.036)	8.4 ^{ab} (0.9)
Transfers					
SW-LW	0.208 (0.025)	0.090 (0.015)	0.184 (0.031)	0.481 (0.069)	10.3 (1.3)
SW-LD	0.168 (0.029)	0.070 (0.017)	0.120 (0.033)	0.358 (0.072)	10.2 (1.4)
SW-SD	0.154 (0.029)	0.056 (0.009)	0.161 (0.019)	0.371 (0.054)	10.2 (0.5)
F-values					
Irradiance (I)	72.41***	45.83***	68.07***	72.20***	47.22***
Moisture (M)	2.61 ^{NS}	14.82***	26.52***	13.49**	20.59***
Age (A)	93.80***	53.97**	75.72***	86.60***	74.56***
I x M	5.85*	5.74*	14.15***	9.64**	2.76 ^{NS}
I x A	35.24***	38.46***	46.74***	45.06***	9.99**
M x A	3.28 ^{NS}	15.24***	21.87***	12.78**	0.16 ^{NS}
I x M x A	3.38 ^{NS}	8.34**	14.19***	8.87**	0.97 ^{NS}

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Table 2. Mean values (with s.e.) for variables of *A. karroo* seedlings in control and transfer treatments. For details on treatments see text. The F-values shown are for three-way ANOVA for control treatments. Means in the same column with different superscript letters were different by Duncan's new multiple range test. ^{NS} = p>0.05; * = 0.01<p<0.05; ** = 0.001<p<0.01; *** = p<0.001

Treatment	RGR (gg ⁻¹ week ⁻¹)	R/S ratio (gg ⁻¹)	SLA (cm ² g ⁻¹)	LAR (cm ² g ⁻¹)	Specific stem length (m/g)
Harvest at 8 weeks					
LW	0.033 ^a	0.69 ^c (0.04)	116.9 ^a (19.8)	56.1 ^a (9.7)	2.29 ^b (0.31)
LD	0.032 ^a	0.73 ^c (0.14)	95.7 ^a (13.1)	44.8 ^a (3.5)	1.71 ^{ab} (0.37)
SW	0.020 ^a	0.31 ^a (0.03)	332.9 ^{de} (37.6)	181.7 ^b (17.8)	4.01 ^d (0.37)
SD	0.020 ^a	0.50 ^b (0.04)	280.0 ^{cd} (27.9)	142.3 ^b (19.7)	3.62 ^{cd} (0.50)
Harvest at 13 weeks					
Controls					
LW	0.077 ^c	0.58 ^{bc} (0.03)	164.9 ^{ab} (3.2)	71.9 ^a (0.7)	0.84 ^a (0.1)
LD	0.047 ^b	0.96 ^d (0.06)	217.3 ^{bc} (4.7)	79.3 ^a (0.8)	1.12 ^a (0.11)
SW	0.023 ^a	0.61 ^{bc} (0.07)	323.7 ^{de} (36.7)	155.2 ^b (18.9)	2.81 ^{bc} (0.33)
SD	0.019 ^a	1.12 ^d (0.14)	376.3 ^e (12.5)	145.0 ^b (31.9)	3.84 ^{cd} (0.55)
Transfers					
SW-LW	0.033	0.81 (0.06)	242.3 (9.7)	82.0 (3.8)	1.64 (0.29)
SW-LD	0.025	1.03 (0.21)	279.1 (75.1)	78.0 (3.1)	2.10 (0.46)
SW-SD	0.026	0.70 (0.05)	333.4 (38.6)	148.3 (21.6)	2.56 (0.19)
F-values					
Irradiance (I)	87.84***	8.24**	108.93***	56.17***	63.58***
Moisture (M)	11.49**	34.24***	0.20 ^{NS}	1.16 ^{NS}	0.11 ^{NS}
Age (A)	107.98***	32.34***	13.93**	0.28 ^{NS}	8.44**
I x M	7.07**	2.56 ^{NS}	0.21 ^{NS}	0.84 ^{NS}	0.81 ^{NS}
I x A	44.69***	19.39***	1.43 ^{NS}	2.23 ^{NS}	1.07 ^{NS}
M x A	10.51**	10.12**	6.79*	0.93 ^{NS}	4.78*
I x M x A	6.23*	0.517 ^{NS}	0.21 ^{NS}	0.05 ^{NS}	0.29 ^{NS}

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Table 3. Results of One-way ANOVA contrasts showing the effects on several *A. karroo* variables of a transfer to other environments compared to those in SW conditions at eight weeks (SW_8) and other controls at 13 weeks. The α -value was adjusted for the number of comparisons using the Dunn-Sidak method ($\alpha = 0.0085$). ns = $p > 0.0085$, * = $p < 0.0085$

Seedling variable	Contrast					
	SW_8 vs SW-SD	SW_8 vs SW-LW	SW_8 vs SW-LD	LW vs SW-LW	LD vs SW-LD	SD vs SW-SD
Root length	*	*	*	ns	ns	ns
Stem length	ns	ns	ns	*	ns	ns
Specific stem length	*	*	*	ns	ns	ns
Number of leaves	ns	ns	ns	*	ns	ns
Internodal length	ns	ns	ns	*	*	ns
Root mass	*	*	*	*	*	ns
Stem mass	ns	*	ns	*	ns	ns
Leaf mass	*	ns	ns	*	ns	ns
Total mass	*	*	ns	*	*	ns
Root/shoot ratio	*	*	*	*	ns	ns
RMR	*	*	*	*	ns	ns
SMR	*	ns	ns	ns	ns	ns
LMR	*	*	*	*	ns	ns
LAR	ns	ns	ns	ns	ns	ns
SLA	ns	ns	ns	ns	ns	ns

environments had the highest. Transferred plants had a higher root/shoot ratio than plants in SW at eight weeks. Figure 2 shows the allocation of dry matter to the roots and leaves during the 11 weeks of treatment. Plants in light (LD and LW) increased dry matter allocation to the roots and decreased that to the leaves. Seedlings in shade allocated more dry matter to the leaves than those in light during the first eight weeks of growth (six weeks of treatment). Transferred plants increased allocation to the root, more so when transferred to light conditions. There were significant differences in LMR and RMR between seedlings transferred to LW and the controls (seedlings that grew in LW conditions throughout).

Both the SLA and the LAR were significantly affected by irradiance only (Table 2). In control treatments at both ages, shaded seedlings had higher SLA and LAR than those growing in full light. No significant amount of leaves was lost in any treatment. *Acacia karroo* seedlings transferred from SW to the three different situations had the same SLAs and LARs as those that grew in these conditions throughout the period of the study (Table 3).

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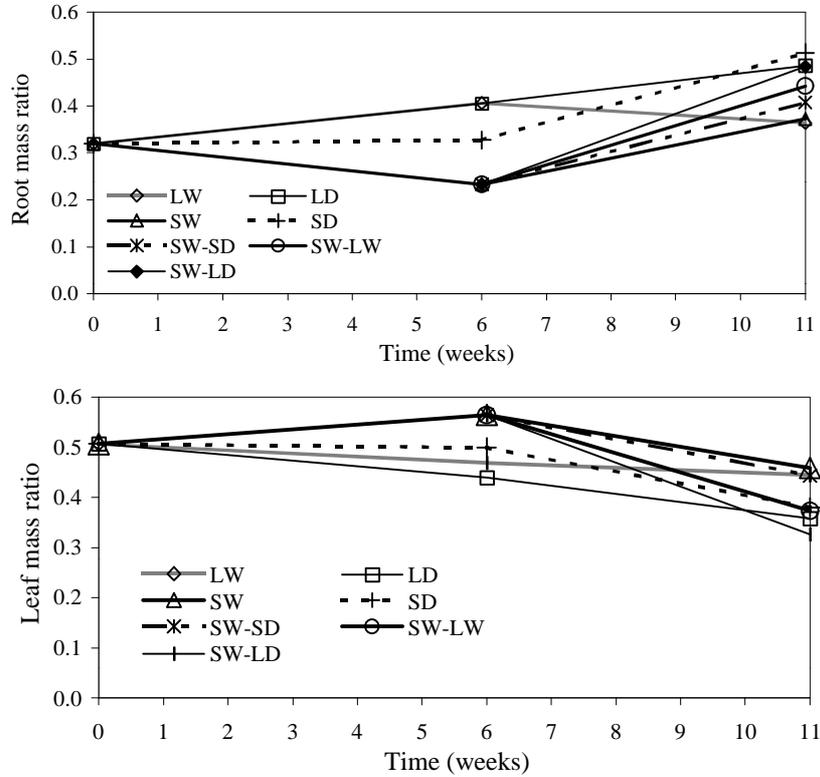


Figure 2. The effects of irradiance and soil moisture on RMR and LMR over 11 weeks of treatment.

Discussion

This study assumed that growth and survival of *A. karroo* seedlings is determined by the availability of soil moisture and irradiance, and the results of this experiment will be discussed in the context of these limiting resources. Indeed, earlier studies revealed that the water status of the soil has a profound effect on the development, morphology and growth of roots (Gregory 1987), and seedlings growing in dry soil were expected to have shorter roots as they encounter more mechanical impedance than those in wetter soil (Russell 1972). In my previous studies with less friable soil, *A. karroo* seedlings in drier soil produced also shorter roots (Chirara, in press). In the present study, however, this trend was not evident during the first eight weeks of establishment maybe because the soil used in the study was relatively friable and it formed large aggregates that left adequate micropores through which roots were able to grow.

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The plants rapidly put down a deep tap-root system with very few side roots. At the end of the experiment, plants in shade had shorter roots. There were no differences in root elongation between transferred seedlings and those that grew throughout in the environment to which the other seedlings were transferred. In the natural semi-arid savanna environment, competition for water is most intense in the topsoil that is also exploited by graminoid species which have an extensive root system (Medina and Silva 1991). Having deep roots soon after establishment is therefore a survival strategy for *Acacias*. From these results, we can conclude that seedlings of *A. karroo* are capable of accessing deeper layers during the first few weeks of establishment irrespective of their light and moisture environment. This is a useful adaptive feature for plants growing in the semi-arid tropical regions where rainfall is erratic and the topsoil dries out quickly.

Under field conditions, rapid shoot etiolation allows the plant to grow out of the shade and position its emerging leaves beyond the overtopping foliage of the herbaceous layer. Shoot etiolation of woody plants in response to shade has been reported in other studies (Oberbauer and Strain 1985, Dale and Causton 1992a). Though at eight weeks *A. karroo* seedlings in shade were taller, by the end of the study those in light had doubled in length. Seedlings under shade had longer internodes, and thin and weak stems (specific stem length > 3.60 m/g), but they increased their mechanical strength when irradiance conditions improved (upon transfer). Therefore, seedlings of this species adapt rapidly to change in irradiance conditions.

Seedlings growing in full light had larger biomass and greater RGR than those in shade. It is also important to note that for seedlings in LW conditions, RGR was higher over the 13 weeks than over eight weeks. This is an adaptation to the semi-arid conditions in which this species occurs. The plant first invests disproportionately into a long taproot and only maximises growth after accessing moisture from deep layers. Shade reduces biomass production of *A. karroo* seedlings (Chirara et al. 1999) and therefore seedlings initially grown in shade had less biomass if transferred to light when compared to those grown in light throughout. Seedlings transferred from SW to SD produced the same biomass as those that stayed in the SD environment for the whole period. The reason for this could be that shade helps conserve soil moisture underneath it and so changes in soil moisture are less drastic. Thus in the natural environment shade from grasses can enhance the survival and growth of establishing woody seedlings within their vicinity. Such ameliorating effect of shade from herbaceous vegetation has been reported before for *A. karroo* seedlings (O'Connor 1995). In the case where soil moisture decreases without further short-term recharge, as is the case at the onset of the dry season, established seedlings and late germinants have high chances of survival when shaded. Shade from grasses or moribund material allows for a gradual recession of the moisture zone to deeper layers and seedlings have access to soil moisture for longer periods. Thus, shaded seedlings have more time to reach the dry season water table and survive.

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During the first eight weeks of growth, seedlings in shade had lower root/shoot ratios indicating a proportionally higher investment of dry matter in the shoot. Under field conditions, this may allow the woody plant seedling to get above the shade of grassy layers and moribund material from the previous seasons. At 13 weeks, seedlings in dry conditions had higher root/shoot ratios. This effect of a water deficit on the preferential development of the root over the shoot is expected and is an adaptive mechanism that enables the plants to explore a greater and more lasting soil volume for water (Turner and Begg 1981). Transferring from SW to the three different conditions resulted in increases in root/shoot ratio because of two reasons. Firstly, those seedlings that were transferred to light could now allocate more biomass to the roots as irradiance was no longer limiting. Secondly, plants transferred to SD, like those shifted to LD, needed to invest more in root growth so as to improve their acquisition of soil moisture.

Plants in high irradiance treatments had lower LAR than those in shade. Shaded seedlings increased their SLA in order to increase interception of available light. When the seedlings were transferred from SW to high irradiance conditions, the plants adjusted their LAR and SLA to levels of the plants that grew in these conditions throughout. The LAR can change because of changes in either of its components, namely the SLA and the LMR (Popma and Bongers 1988; Dale and Causton 1992a). In this case, SLA was partly based on leaves produced in the previous environment. As mentioned earlier, biomass allocation to leaves and hence LMR was less under higher irradiance as light was no longer limiting and the seedlings shifted resources to the roots and the mechanical strength of the stems. Therefore, LAR declined in response to higher irradiance because of allocation of a greater proportion of biomass into non-leafy material (roots and stems) (Oberbauer and Strain 1985). Thus, when exposed to more light, the plants adjusted their LAR through changes in their SLA and LMR so as to maximise growth in the new environment.

In this study, no seedling mortality occurred when the *A. karroo* plants were transferred from SW to LD though biomass of these plants was less than those that were in LD for the entire duration of the experiment. The shift from SW to LD was expected to be the most 'stressful' transfer for two reasons. Firstly, soil moisture decreased and secondly, the seedlings already had larger and thinner leaves developed to maximise light capture in the previous environment. Because of their large surface area, such leaves would lose a lot of water through evapo-transpiration. Seedlings transferred to LD grew well in this environment because they already had long roots that developed during the first weeks of transfer that extended to over 90 cm by the end of the 13 weeks. It would therefore take long for the soil to dry out to such depth. What is more, the *A. karroo* seedlings adjusted their leaf characteristics since they developed more leaves in the new environment and through changes in resource allocation patterns.

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The results of this experiment are important for bush encroachment. *Acacia karroo* seedlings can acclimate to changing irradiance and soil moisture environments by developing deep roots even when shaded. The seedlings' ability to extend their roots seems to be limited by soil strength rather than by irradiance and soil moisture availability. They can therefore access water from deeper layers during the dry season. Moreover, since the seedling roots can grow to depths of close to 1 m within 13 weeks, it means in relatively porous soil they can exploit soil moisture from levels where grass roots are less dense. Though savanna grasses have been reported to grow roots to depth of up to 1 m (Scholes and Walker 1993), their density decreases with depth (Mordelet *et al.*1997). In addition, defoliation has been reported to reduce root biomass production of the grasses, so *A. karroo* seedlings have higher chances of survival under grazed situations. The plants are relatively plastic as they adjust their biomass allocation patterns to acclimate to new moisture and irradiance conditions.

Acacia karroo seedlings are subjected to grass shade and wet conditions during the rainy season and dry and higher irradiance conditions during the non-rainy season as grasses dieback. Grazing during both seasons can increase the amount of light reaching the seedlings. This study has shown that seedlings of this species can adapt to decreases in soil moisture and irradiance changes that accompany grass growth or dieback. Thus, *A. karroo* seedlings have the potential to encroach onto and thrive in areas with already established grasses.

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6

Effects of defoliation and changes in irradiance on the growth of *Acacia karroo* plants

Chipangura Chirara

Abstract

Herbivory is one of the major factors determining savanna structure and function. Studies in these systems have been restricted to large herbivores and trees, yet the mechanisms affecting tree-grass balance in savannas may operate at the seedling stage. In this study, the effects of the interactions between defoliation and irradiance on the regeneration and growth of seedlings of *Acacia karroo* Hayne were investigated in a greenhouse experiment. The seedlings were grown in shade or light for four weeks, after which some were transferred to the other light regime. The leaves of the plants were left unclipped or clipped by 50% or 90% at the time of transfer and the plants were allowed to grow for a further four weeks. Defoliation had no effect on root elongation of *A. karroo* seedlings but resulted in a decrease in stem length under shaded conditions. Seedling defoliation had a negative effect on growth except when seedlings were grown continuously in full light. Root/shoot ratios only recovered from defoliation if the seedlings were growing in full light after defoliation. Under shaded conditions, LAR decreased with increasing defoliation intensity. No mortalities were recorded in any treatment. *Acacia karroo* seedlings can recover well from a single defoliation treatment, although growth was significantly retarded under shaded conditions.

Keywords: Herbivory, root elongation, root/shoot ratio

Introduction

The balance between trees and grasses in savannas is influenced by a complex combination of factors that include herbivory, soil texture and nutrients, fire and water (Skarpe 1992, Scholes and Walker 1993, Higgins *et al.* 2000). While herbivory is regarded as one of the important factors governing the genesis and maintenance of savannas (Walter 1971,

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Werger 1977, McNaughton, 1979a, McPherson 1993), many studies done in these systems have been restricted to large herbivores and trees (Lay 1965, Cumming 1982, Teague and Walker 1988, Teague 1989, Huntly 1991, Prins and van der Jeugd 1993). Yet, the mechanisms affecting the balance between grasses and trees may well operate mainly at the seedling stage. Browsers and large grazing herbivores trample seedlings or eat them along with grass (Borchert *et al.* 1989). Seedlings and juvenile trees are also susceptible to herbivory by insects such as harvester termites, leaf-cutting ants and grasshoppers (Frost *et al.* 1986, Anderson and Lonsdale 1991). Small herbivores can select individual tree seedlings and pick specific plant parts (Davidson 1993). Chirara *et al.* (1999) reported that the combined effects of drought and harvester termites resulted in very low survival of planted *A. karroo* seedlings in the field.

During the growing season, the seedlings are quickly overtopped by the fast growing herbaceous vegetation (Bush and Van Auken 1990). If defoliated by insects, shading by grasses is expected to reduce the growth of the seedlings since the plants have to regenerate in low irradiance conditions using a reduced photosynthetic apparatus. In semi-arid savannas, rainfall is erratic and limits woody seedling survival and growth. Understanding the interactions between leaf loss due to herbivory, shading by grasses and soil moisture availability is therefore essential in the understanding of tree seedling dynamics in savannas.

This study investigated the response of *A. karroo* seedlings to defoliation and their acclimation to new irradiance conditions. We tested the hypothesis that when defoliated, *A. karroo* seedlings that remain in shade will show reduced recovery because of the reduced leaf area and low light availability. The seedlings that are exposed to higher irradiance should regenerate better and produce more biomass than those that remain in shade or are introduced to shade soon after defoliation.

Materials and Methods

The experiment was carried out in the greenhouse at the University of Zimbabwe, Harare. A 15 x 3 m² enclosure was erected and covered with three layers of black shade cloth. These allowed about 8% of full sunlight to pass through. Ninety-six PVC pots that were 14 cm in diameter and 1 m deep were filled with clayey soil (59.6% clay, 22.6% silt and 17.8% sand) from around Harare. This soil was inoculated with small amounts of soil from underneath mature *A. karroo* trees at Matopos Research Station (20°23'S, 28°28'E) where this species occurs naturally.

Three manually scarified *A. karroo* seeds were planted in each of the pots and allowed to germinate. The number of seedlings was reduced to one per pot after germination by selecting seedlings of similar height and number of leaves. One week after germination,

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seedlings in twelve pots were randomly selected and harvested. Their height, root length and number of leaves were recorded. The seedlings were then divided in root, stem and leaves and dried at 80°C for 48 hours and their dry masses determined. For the remainder, half were transferred to the shade environment in the enclosure and the other half was allowed to continue growing in full sunlight. The seedlings grew in these conditions for four weeks. At the end of this period, six seedlings from the shade environment and six from light were harvested and the dry biomass of the different parts determined. For the remainder of the seedlings, one half of those in light were transferred to shade and half of the seedlings in shade were transferred to light. Seedlings that grew in shade throughout will be referred to as SS and those in light as LL. Plants transferred from shade to light and light to shade will be referred to as SL and LS, respectively. At the time of transfer, equal numbers of seedlings in each environment had their leaves clipped by 90%, 50% or left unclipped. The plants were watered in such a way that soil moisture fluctuated between 50% and 100 % of field capacity. The clipped leaf biomass was dried at 80°C for 48 hours and weighed.

The *A. karroo* seedlings grew for another four weeks after defoliation. At the end of this period, plants in all treatments were harvested by carefully cutting out the PVC pipes. The seedlings were extracted by flushing the soil with a jet of water. The stem and taproot lengths were determined and the number of leaves counted. The plants were then separated into root, stem and leaves. For random subsample of the seedlings, leaf area was determined by making photocopies of fresh leaves and scanning them. The roots, stems and leaves were dried at 80°C for 48 hours and weighed.

Analysis

The data collected at the beginning of the experiment was analysed using one-way analysis of variance (ANOVA). Differences between treatments were analysed by Duncan's new multiple range test or, where there were only two comparisons to be made, using two-sample t-test. Three-way ANOVA was used to distinguish the effects of the present environment, the previous environment and the defoliation regime, where the location of the plants before the final harvest was defined as the present environment and the environment in which the plants were growing before transfer to their final location was defined as the previous environment. The root/shoot ratio (R/S), specific leaf area (SLA), leaf area ratio (LAR), root mass ratio (RMR), leaf mass ratio (LMR) and stem mass ratio (SMR) were calculated from the primary biomass data. All analyses were done using SPSS (Norušis 1993). RMR, LMR and SMR were arcsine-transformed before analysis. All biomass data were ln-transformed prior to analysis.

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Results

The characteristics of *A. karroo* seedlings at the beginning of the experiment and at the time of defoliation are shown in Table 1. At five weeks, shaded seedlings had shorter roots, longer stems and internodes, and lower biomass than those in light ($P < 0.05$). Shaded seedlings also had higher LAR and SLA and lower root/shoot ratios.

The defoliation regime did not significantly affect seedling root length ($p > 0.05$). The root length was significantly influenced by both the previous and the present irradiance conditions. *Acacia karroo* seedlings produced roots of at least 39 cm within the first nine weeks of growth (Table 2). The longest roots were in LL seedlings clipped to 90%. On average, seedlings initially in light had longer roots than those in shade. High irradiance conditions later in the development of the plants also enhanced length growth of the tap roots.

Table 1. *Acacia karroo* seedling characteristics at the beginning of the experiment (one week) and at the time of defoliation (five weeks). Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's New Multiple Range Test ($\alpha = 0.05$)

Age (weeks)	Irradiance conditions	Length (mm)			Number of leaves	Total mass (g)	R/s Ratio (g/g)
		Root	Shoot	Internodes			
1	Light	102.5 ^a (4.0)	11.7 ^a (0.7)		2.3 ^a (0.2)	0.022 ^a (0.002)	0.40 ^a (0.03)
5	Shade	216.7 ^b (28.5)	87.5 ^b (12.2)	10.8 ^a (0.7)	5.1 ^b (0.2)	0.025 ^a (0.002)	0.35 ^a (0.04)
5	Light	411.7 ^c (50.5)	62.0 ^b (10.5)	5.0 ^b (0.6)	6.7 ^c (0.2)	0.110 ^b (0.011)	1.10 ^b (0.12)

(continued)

Age (weeks)	Irradiance conditions	RMR	LMR	SMR	LAR	SLA
1	Light	0.29 ^a (0.02)	0.47 ^a (0.03)	0.24 ^a (0.02)		
5	Shade	0.26 ^a (0.02)	0.46 ^a (0.03)	0.28 ^a (0.03)	221.0 ^a (18.1)	494.0 ^a (62.0)
5	Light	0.51 ^b (0.03)	0.26 ^b (0.02)	0.23 ^a (0.03)	66.3 ^b (4.1)	249.2 ^b (21.7)

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Stem length was significantly influenced only by the initial irradiance conditions ($p < 0.01$) but there was a significant interaction between the present irradiance condition and the defoliation regime. Plants growing continuously in shade had the longest stems and only in this treatment, defoliation resulted in reduced stem length. The internodal length of the seedlings was influenced only by previous irradiance conditions. Seedlings that grew initially in shade had longer internodes than those in light ($P < 0.001$).

The defoliation regime, and the previous and present irradiance treatments affected the leaf mass at the end of the study. Defoliation generally resulted in reduced leaf mass, but in seedlings growing in full light throughout, the leaf mass was the same for all defoliation treatments. All the three main factors affected total seedling dry mass. Interactions between the previous and present environments, and between either and defoliation were all significant ($p < 0.05$). Total seedling dry mass was highest in LL plants and lowest in SS plants (Figure 1). Only in LL conditions, defoliation did not affect total biomass.

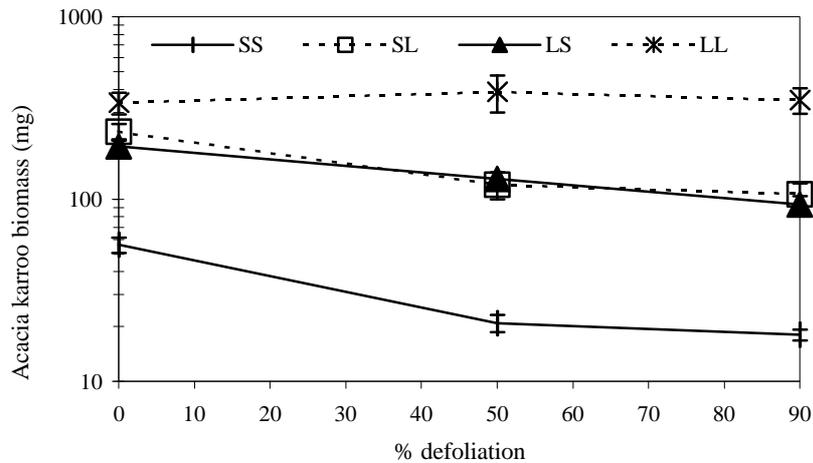


Figure 1. Biomass of *A. karroo* seedlings subjected to different defoliation treatments. Bars indicate standard errors

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Table 2. Primary data showing size characteristics of (nine-week old) *A. karroo* seedlings at the time of defoliation and four weeks after a single defoliation treatment. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's New Multiple Range Test. ^{NS} = p>0.05; * = p<0.05; ** = p<0.01; *** = p<0.001

Irradiance environment		Clip. level	Length (mm)			Number of leaves	Dry mass (g)	
Prev.	Pres.		Root	Stem	Internodes		Leaf	Root
Shade	Shade	0%	411.8 ^a (13.4)	102.2 ^c (11.47)	14.0 ^c (0.9)	7.8 ^a (0.4)	0.032 ^d (0.003)	0.014 ^b (0.003)
		50%	403.8 ^a (8.0)	59.3 ^{ab} (5.9)	11.3 ^b (0.4)	6.1 ^a (0.3)	0.008 ^a (0.002)	0.010 ^a (0.010)
		90%	391.0 ^a (5.7)	58.0 ^{ab} (8.1)	11.0 ^b (1.1)	6.3 ^a (0.3)	0.005 ^a (0.001)	0.008 ^a (0.001)
Shade	Light	0%	532.3 ^{bcd} (27.5)	72.0 ^{ab} (3.8)	11.2 ^b (0.5)	8.5 ^a (0.6)	0.092 ^{ef} (0.010)	0.104 ^{ef} (0.011)
		50%	515.2 ^{bc} (27.8)	67.5 ^{ab} (10.0)	11.4 ^b (0.4)	8.5 ^a (0.7)	0.046 ^{cd} (0.010)	0.054 ^{cd} (0.008)
		90%	527.0 ^{bcd} (54.2)	81.8 ^{bc} (3.9)	13.2 ^{bc} (0.4)	7.2 ^a (0.2)	0.040 ^{cd} (0.007)	0.047 ^c (0.005)
Light	Shade	0%	472.2 ^{ab} (30.9)	55.5 ^a (10.1)	5.3 ^a (0.3)	8.3 ^a (0.6)	0.064 ^{de} (0.004)	0.98 ^e (0.011)
		50%	526.7 ^{bcd} (39.7)	54.0 ^a (8.2)	6.0 ^a (0.7)	8.5 ^a (0.8)	0.037 ^{cd} (0.004)	0.073 ^{de} (0.006)
		90%	471.0 ^{ab} (26.2)	51.5 ^a (3.2)	5.7 ^a (0.2)	7.7 ^a (0.8)	0.017 ^b (0.002)	0.060 ^{cd} (0.007)
Light	Light	0%	586.3 ^{cd} (28.9)	65.5 ^{ab} (5.83)	6.0 ^a (0.7)	8.3 ^a (0.3)	0.139 ^f (0.023)	0.152 ^{fg} (0.017)
		50%	557.2 ^{bcd} (26.5)	66.5 ^{ab} (9.65)	6.0 ^a (0.7)	11.0 ^b (1.3)	0.139 ^{ef} (0.046)	0.184 ^g (0.037)
		90%	619.8 ^d (29.4)	74.0 ^{ab} (9.82)	5.7 ^a (0.2)	11.7 ^b (1.3)	0.125 ^{ef} (0.027)	0.171 ^g (0.018)
F-Values								
Previous environment (Prev.)			19.73***	7.14**	183.52***	18.36***	73.2***	338.5***
Present environment (Pres.)			42.23***	2.87 ^{NS}	0.07 ^{NS}	16.21***	156.4***	260.2***
Defoliation (D)			0.01 ^{NS}	2.29 ^{NS}	0.53 ^{NS}	0.24 ^{NS}	31.0***	9.9***
Pres. x Prev.			0.53 ^{NS}	2.44 ^{NS}	0.89 ^{NS}	1.08 ^{NS}	3.6 ^{NS}	43.0***
Prev. x D			0.29 ^{NS}	2.46 ^{NS}	1.39 ^{NS}	3.91*	3.8*	4.1*
Pres. x D			1.53 ^{NS}	4.42*	2.85 ^{NS}	2.63 ^{NS}	7.8*	0.3 ^{NS}
Prev. x Pres. x D			0.71 ^{NS}	1.99 ^{NS}	2.57 ^{NS}	1.85 ^{NS}	1.0 ^{NS}	2.9 ^{NS}

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Table 2. Primary data showing size characteristics of (nine-week old) *A. karroo* seedlings at the time of defoliation and four weeks after a single defoliation treatment. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's New Multiple Range Test. ^{NS} = p>0.05; * = p<0.05; ** = p<0.01; *** = p<0.001

Irradiance environment		Clip. level	Dry mass (g)				
Prev.	Pres.		Stem	Total plant	Clipped leaves	Cumulative leaf mass	Cumulative plant mass
Shade	Shade	0%	0.010 ^b (0.001)	0.056 ^b (0.005)	0.000	0.032 ^b (0.003)	0.056 ^b (0.005)
		50%	0.004 ^a (0.001)	0.021 ^a (0.002)	0.007 ^a (0.001)	0.015 ^a (0.003)	0.028 ^a (0.003)
		90%	0.004 ^a (0.001)	0.018 ^a (0.001)	0.010 ^b (0.001)	0.015 ^a (0.001)	0.028 ^a (0.002)
Shade	Light	0%	0.039 ^{de} (0.005)	0.235 ^{de} (0.025)	0.000	0.092 ^{de} (0.001)	0.235 ^{de} (0.025)
		50%	0.020 ^{bc} (0.004)	0.120 ^c (0.020)	0.008 ^{ab} (0.001)	0.054 ^{bc} (0.011)	0.128 ^c (0.020)
		90%	0.021 ^{bc} (0.004)	0.118 ^c (0.016)	0.010 ^b (0.001)	0.050 ^{bc} (0.007)	0.117 ^c (0.016)
Light	Shade	0%	0.033 ^{cd} (0.012)	0.195 ^d (0.018)	0.000	0.064 ^{cd} (0.004)	0.195 ^{de} (0.018)
		50%	0.019 ^{bc} (0.004)	0.129 ^c (0.011)	0.015 ^c (0.002)	0.052 ^{bc} (0.005)	0.145 ^{cd} (0.011)
		90%	0.017 ^{bc} (0.002)	0.094 ^c (0.010)	0.022 ^d (0.002)	0.039 ^{bc} (0.002)	0.116 ^c (0.009)
Light	Light	0%	0.048 ^{de} (0.010)	0.339 ^e (0.046)	0.000	0.139 ^e (0.023)	0.339 ^{fg} (0.046)
		50%	0.065 ^e (0.012)	0.388 ^e (0.090)	0.020 ^{cd} (0.001)	0.159 ^e (0.046)	0.408 ^g (0.089)
		90%	0.054 ^{de} (0.012)	0.349 ^e (0.056)	0.023 ^d (0.002)	0.148 ^e (0.029)	0.372 ^g (0.058)
F-Values							
Previous environment (Prev.)			67.2***	229.6***	117.0***	93.0***	231.8***
Present environment (Pres.)			88.6***	250.9***	2.7 ^{NS}	134.0***	229.6***
Defoliation (D)			6.2**	24.8***	13.1**	10.1** ^{NS}	13.9***
Pres. x Prev.			5.6*	19.0***	0.3 ^{NS}	1.5 ^{NS}	14.8***
Prev. x D			4.1*	7.2**	0.1***	3.7 ^{NS}	5.8**
Pres. x D			1.1 ^{NS}	3.8*	1.3 ^{NS}	1.2 ^{NS}	1.3 ^{NS}
Prev. x Pres. x D			0.4 ^{NS}	0.7 ^{NS}	0.2 ^{NS}	0.7 ^{NS}	1.4 ^{NS}

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Table 3. Morphology and leaf characteristics of *A. karroo* seedlings five weeks after a single defoliation treatment. Standard error values are in parentheses. Means in the same column with different superscript letters were different by Duncan's New Multiple Range Test. ^{NS} = p>0.05; * = p<0.05; ** = p<0.01; *** = p<0.001

Previous	Present	Clip. level	LAR (cm ² g ⁻¹)	SLA (cm ² g ⁻¹)	Root/shoot ratio (g/g)	RMR	LMR	SMR	
Shade	Shade	0%	321.84 ^g (10.99)	560.79 ^d (16.10)	0.34 ^a (0.04)	0.25 ^a (0.03)	0.58 ^d (0.02)	0.17 ^{ab} (0.01)	
		50%	215.75 ^f (14.91)	506.43 ^d (12.03)	1.08 ^b (0.05)	0.44 ^b (0.07)	0.37 ^{bc} (0.07)	0.19 ^{ab} (0.04)	
		90%	150.06 ^e (15.86)	572.90 ^d (44.19)	1.02 ^b (0.26)	0.47 ^{bc} (0.05)	0.29 ^b (0.03)	0.24 ^b (0.03)	
	Shade	Light	0%	53.97 ^{ab} (8.01)	134.44 ^{ab} (11.88)	0.81 ^{ab} (0.07)	0.44 ^b (0.02)	0.39 ^{bc} (0.02)	0.16 ^{ab} (0.01)
			50%	61.59 ^{bc} (10.92)	182.82 ^{abc} (22.61)	0.87 ^{ab} (0.10)	0.46 ^{bc} (0.03)	0.39 ^{bc} (0.03)	0.15 ^{ab} (0.02)
			90%	95.30 ^d (17.49)	249.86 ^{bc} (27.74)	0.82 ^{ab} (0.01)	0.44 ^b (0.03)	0.37 ^{bc} (0.02)	0.19 ^{ab} (0.02)
Light	Shade	0%	113.11 ^d (1.93)	317.14 ^c (25.09)	1.07 ^b (0.13)	0.50 ^{bc} (0.04)	0.34 ^{bc} (0.02)	0.16 ^{ab} (0.05)	
		50%	87.91 ^d (8.95)	276.85 ^{bc} (33.21)	1.41 ^{bc} (0.22)	0.57 ^{cd} (0.03)	0.29 ^b (0.02)	0.14 ^a (0.02)	
		90%	55.94 ^b (4.91)	284.87 ^c (20.13)	1.81 ^c (0.15)	0.64 ^d (0.02)	0.18 ^a (0.01)	0.18 ^{ab} (0.02)	
Light	Light	0%	35.80 ^{ab} (4.02)	79.56 ^a (10.68)	0.87 ^{ab} (0.09)	0.46 ^{bc} (0.03)	0.41 ^c (0.03)	0.13 ^a (0.02)	
		50%	22.09 ^a (6.76)	66.78 ^a (17.78)	1.03 ^b (0.15)	0.50 ^{bc} (0.03)	0.32 ^{bc} (0.06)	0.19 ^{ab} (0.04)	
		90%	29.64 ^{ab} (3.57)	84.61 ^a (3.59)	1.07 ^b (0.12)	0.51 ^{bc} (0.03)	0.35 ^{bc} (0.02)	0.14 ^a (0.02)	
F-Values									
Previous environment (Prev.)			242.31***	47.80***	12.5***	26.63***	21.43***	2.79 ^{NS}	
Present environment (Pres.)			329.69***	117.54***	3.6 ^{NS}	0.78 ^{NS}	2.09 ^{NS}	1.27 ^{NS}	
Defoliation (D)			23.53***	0.77 ^{NS}	5.1**	8.36**	17.84**	1.22 ^{NS}	
Pres. x Prev.			74.59***	7.17*	4.2*	10.53**	10.66**	0.66 ^{NS}	
Pres. x D			3.20 ^{NS}	0.75 ^{NS}	0.5 ^{NS}	0.48 ^{NS}	0.85 ^{NS}	0.66 ^{NS}	
Pres. x D			41.34***	0.73 ^{NS}	2.6 ^{NS}	4.47*	8.06**	0.83 ^{NS}	
Prev. x Pres. x D			15.91***	0.20 ^{NS}	0.5 ^{NS}	1.11 ^{NS}	4.16*	0.82 ^{NS}	

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The previous irradiance conditions and defoliation had a significant effect on the root/shoot ratio ($p < 0.01$) and there was an interaction between the previous and the present irradiance conditions. Clipped seedlings in LS had the highest root/shoot ratio (Table 3). The lowest root/shoot ratio was found in unclipped plants growing in SS conditions. Defoliation resulted in increases in root/shoot ratio in SS and LS treatments, but had no effect in the other treatments (Figure 2). The RMR and LMR were affected by the defoliation regime and the previous irradiance conditions (Table 3, $p < 0.001$). Seedlings in SS and LS that were clipped to 90% had significantly lower LMR than the unclipped plants in these treatments. Those seedlings that ended in light (LL and SL) recovered well from defoliation and so there were no differences in LMR between clipped and unclipped treatments ($p > 0.05$).

At five weeks, shaded *A. karroo* seedlings had less leaves than those in full light (Table 1). After defoliation, there was production of new leaves in all treatments. As Table 2 shows, LL seedlings that were defoliated produced at least 11 leaves but plants in the rest of the treatments had significantly fewer leaves (between 6 and 8). Defoliation, and both the previous and the present irradiance conditions significantly affected the LAR (Table 3, $p < 0.05$). Seedling in shade throughout had the highest LAR, and it was lower with defoliation. The lowest LAR was found in plants that grew in light for the whole period and defoliation under this irradiance treatment did not result in a lower LAR. The SLA was significantly influenced by both the previous and the present irradiance environments (Table 3, $p < 0.001$). Defoliation did not have a significant influence on SLA.

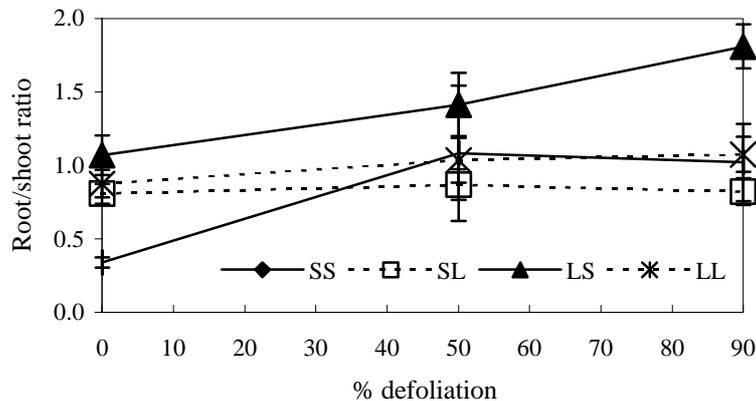


Figure 2. The effects of defoliation on the root/shoot ratio of *A. karroo* seedlings. Bars indicate standard errors.

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Discussion

Acacia karroo is an invader of grassland in semi-arid savannas where rainfall is seasonal. Seeds germinate during the wet season when the seedlings are likely to be shaded by perennial and annual grasses, and by moribund material from previous seasons. Grazing creates light gaps that result in abrupt and dramatic increases in irradiance reaching establishing seedlings. In addition, grazing might also be accompanied by selective or non-selective defoliation of the tree seedlings. This study investigated the ability of defoliated *A. karroo* seedlings to recover under different defoliation regimes and irradiance circumstances.

Root growth is an important process for water and nutrient intake. Defoliation has been reported to reduce root length in some graminoid species (Richards 1984). The results of this study however show that the ability of *A. karroo* seedlings to elongate their root system is not affected by defoliation. The seedlings of this species have been reported to put down deep root systems during their early developmental stages, even under shaded conditions (Chapter 5). Though shaded seedlings had shorter roots at five weeks, they had grown to at least 39 cm by the end of the study. Such seedlings can access moisture from deeper levels when the water table drops during the dry season.

Growth in height is a useful indicator of the young plant's fitness because it measures seedling response to competition for light (Fetcher *et al.* 1983). Defoliation of seedlings that were under shade throughout resulted in reduced stem length. Under field conditions, such plants would therefore remain within the grass stratum for a longer period than those that are not defoliated. In previous experiments, it has been demonstrated that *A. karroo* seedlings can survive in deep shade of about 4% of full light (Chapter 4, Chirara in press) and they can therefore persist in the grass sward despite their slow growth rate. O'Connor (1995) also reports that seedlings of this species can form seedling banks within the grass matrix and utilize periods of favourable conditions to grow.

Defoliation reduces the size of the plant's photosynthetic area and hence carbon acquiring capacity (Anderson and Lee 1995, Lovelock *et al.* 1999), which may result in reduced growth or mortality. This study has shown that in terms of biomass production, *A. karroo* seedlings recover well from a single defoliation if they were growing continuously in full daylight. In this treatment, defoliation apparently quickly led to exact compensation (Belsky 1986), since cumulative dry weight of the clipped plants equalled that of controls. Such compensation occurs through the development of new leaves. In addition, it has been reported that partial defoliation usually leads to high photosynthetic rates per remaining leaf area (McNaughton 1979b). Presumably this process allows *A. karroo* seedlings in full light to compensate for the biomass actually removed after a single defoliation treatment. However, seedlings growing in shade after defoliation were unable to fully recover within 4 weeks from the removal of part of the leaves. Their leaf biomass and total biomass were

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reduced after defoliation in comparison with unclipped seedlings. Even in plants transferred from shade to full light upon defoliation, leaf and total biomass at the final harvest were affected by the defoliation treatment, presumably because they had been unable to store sufficient reserves in the shade to allow fast recovery of leaf area.

Complete and partial leaf defoliation leads to a drastic reduction of carbohydrate synthesis (Brouwer 1983). This results in reduced growth of the plants and alteration of resource partitioning (Detling *et al.* 1979). In addition, changes in irradiance conditions lead to changes in resource allocation patterns. In this study, defoliated *A. karroo* seedlings growing continuously in light and those transferred from shade to light restored the root/shoot ratio to the same level as in control (unclipped) plants within four weeks. Apparently, plants in these treatments successfully invested in shoot growth to enhance light harvesting and hence carbon assimilation. Seedlings that remained or were transferred to shade after defoliation had higher root/shoot ratios than control plants. For these seedlings, the combination of low irradiance and a reduced leaf area restricted net carbon assimilation, and thereby limited the plants' ability to adjust their root/shoot ratios to suit the present irradiance conditions.

Generally, LAR and SLA are higher under shade than higher irradiance conditions. Changes in LAR may arise from changes in either of its components – SLA and LMR (Lambers and Poorter 1992). In this experiment, plants growing in shade throughout had high LARs that, obviously, initially decreased with increasing defoliation intensity. When compared with values at the time of defoliation, SLA decreased when seedlings were transferred from shade to light and increased when transferred from light to shade. This morphological plasticity of *A. karroo* seedlings has been reported also in earlier experiments (Chapter 5).

In conclusion, *A. karroo* seedlings can partly compensate for leaf area loss resulting from a single defoliation, depending on the irradiance conditions before and after the defoliation. Only for seedlings growing continuously in full daylight, defoliation did not reduce the seedlings' ability to utilize the available irradiance. Defoliated seedlings continuously growing in shade, as may happen after insect herbivory, or suddenly exposed to full daylight after defoliation, as may happen if a large grazer removes part of the seedling together with the grasses shading it, will at least temporarily show reduced growth. Yet, no seedling died even after 90% defoliation, and since the formation of a long tap root was not impaired by defoliation, *Acacia karroo* seedlings are well adapted for growth in semi-arid regions where soil moisture is the principal factor affecting recruitment and defoliation by herbivores is common.

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7

General Discussion

Bush encroachment in semi-arid savannas occurs when seeds of invasive woody species are dispersed, germinate and the seedlings successfully establish and grow to juvenile or mature trees, or when new stems sprout from rhizomes in clonal woody species. In savanna areas where trees are still spaced, indiscriminate cutting of the trees often leads to a multi-stemmed tree where a single stem grew before (Robinson and Robertshaw 1975). This effectively results in increased tree density and can render some areas inaccessible to both browsers and grazers. High tree densities reduce grass productivity and lead to changes in species composition. The physiognomic shift from grassland vegetation to woodland is therefore undesirable for savanna land use and is thus regarded as an indication of land degradation. The problem of bush encroachment has been attributed to the introduction of cattle as the predominant grazing species (Walter 1954, Van Vegten 1983). Many experiments that have addressed the problem of bush encroachment have primarily focused on the adult trees, apparently because the problem was already there and had to be dealt with in order to increase grass productivity.

The success of woody plants in grasslands depends on factors influencing the several stages of the life cycle of the tree species involved like seed production, seed dispersal and germination, seedling establishment and their growth to adult stages. The germination, emergence and establishment phase is critical in the life cycle of plants and any factors that affect this growth phase potentially influence the population dynamics of a species. Survival of tree seedlings that emerge during a particular season depends on water availability in the topsoil, which is the domain of the roots of the herbaceous layer (Medina and Silva 1991) and where competition for soil moisture is strongest (Bertiller *et al.* 1996). In this study, factors influencing seedling recruitment in *Acacia karroo*, an invasive species in semi-arid ecosystems in southern Africa, are investigated under both controlled and field conditions. Having evaluated the effect of grass defoliation on grass productivity, the main aims of the study are:

- 1) to investigate the effect of grass on soil moisture availability and how this affects woody seedling survival and growth,
- 2) to evaluate the response of *A. karroo* seedlings to availability of and changes in irradiance and soil moisture conditions,
- 3) to investigate the response of the tree seedlings to defoliation. This chapter summarises and discusses the main findings of this study.

CHAPTER 7

Grass defoliation

It is generally accepted that a high grass biomass can suppress tree seedlings (Brown and Booyesen 1967, Walker *et al.* 1981, Knoop and Walker 1985). Rushworth (1975) reports that over 50% of the biomass of many perennial savanna grasses may be belowground. When such grasses are intensely defoliated, some re-growth still occurs in the following season, albeit with reduced vigour. Continued intense defoliation results in death of the plants. Scholes (1985) recorded massive death of perennial grasses during two years of drought and heavy grazing. Savanna theories have taken this up and singled out reduction in grass vigour due to overgrazing as a factor affecting water availability in the top soil. This, in interaction with rainfall, was considered as the most important factor influencing bush encroachment. In this study, defoliation of grasses under field conditions during one season resulted in reduced aboveground biomass production in the following season in an area dominated by perennials (Chapter 2). This was however partly influenced by a decrease in annual rainfall from 558 mm to 406 mm. Such a depleted grass biomass resulting from defoliation in the previous season would reduce the effectiveness of fire, a useful tool in the control of bush encroachment in semi-arid savannas (Trollope 1980, Higgins *et al.* 2000). Greenhouse studies proved that repeated and heavy defoliation of grasses reduces their productivity even under wet conditions (Chapters 2 & 3). In dry tropical savannas, grazing has been reported to reduce belowground grass biomass by 41-55% (Pandey and Singh 1992). The reason for this is that removal of the shoot results in depletion of the storage reserves and less translocation of current photosynthate to the roots. The overall result is a reduced grass root system that supports a smaller shoot biomass and consequently utilises less resources than a vigorously growing grass sward.

... But does this translate into higher recruitment rates of *A. karroo* vis-à-vis seed germination and seedling survival?

Seed germination

Although most plants produce large quantities of seeds and are usually dispersed for considerable distances, only a small proportion of these seeds produce mature plants (Kozlowski and Gunn 1972). Animals are an important means of dispersal of the seeds of *Acacia* species. Dry pods of *Acacias* are a significant item in the diet of both wild animals (Coe and Coe 1987) and livestock (Hauser 1994). Seeds in the pods can be destroyed by chewing and digestion and the remainder are subsequently passed in dung (Miller 1994). *Acacias* are hard-seeded and the seed coat needs to be scarified to break the seed dormancy. It has been suggested that passage of seeds through the guts of herbivores scarifies the seeds (Lamprey 1967). In preliminary experiments to this thesis, seeds of *A. karroo* and *A. nilotica* were scarified using concentrated sulphuric acid. The seeds still

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germinated even after one hour in the acid (Figure 1). These results suggest that *Acacia* seeds need a strong acid to break dormancy and so may withstand abrasion by weaker acids. Though germination may vary depending on the time the seeds are retained in the gut of herbivores (McKey 1975), it is unlikely that gastric acids alone can scarify seeds of *A. karroo*. Indeed, Coe and Coe (1987) report that passage of *Acacia* seeds through the gut of ungulates did not result in enhanced germination of the surviving seeds. It is possible that chewing damages the seed coat and thus breaks seed dormancy. This may however damage the seeds in the process, rendering them unviable.

In semi-arid regions, soil moisture is the most important factor influencing seed germination. Due to the erratic distribution of rainfall and high evaporation rates in these regions, the soil surface is watered infrequently and may dry out too rapidly for a seed to germinate or for a germinating seedling to extend its root downward to deeper layers where soil moisture is found. In this study the highest germination rates, as determined by seedling emergence, were in those treatments where the grass was unclipped (Chapter 2). This enhanced germination of *Acacia* seeds under undefoliated sward also has been found in other southern African savannas (O'Connor 1995). A grass cover therefore provides a suitable microclimate for germination as its shade reduces rapid evaporation of surface moisture.

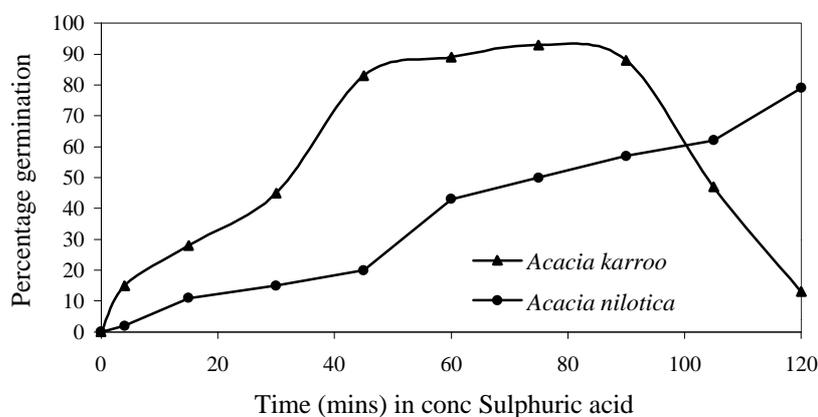


Figure 1. The effect of concentrated sulphuric acid on the germination of seeds of *A. karroo* and *A. nilotica*.

Seedling survival and growth

Grass swards have been shown to be 'safe sites' for seed germination, moreso when unclipped (Chapter 2). The central question in this thesis is, are the same sites conducive for *A. karroo* seedling establishment? Although grass-clipping frequency had a strong

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effect on seedling survival during the wet season under field conditions, the grass defoliation regime had no effect on the survival of the tree seedlings at the end of the dry season (Chapter 2). During the wet season, seedling survival was highest in the bare and more frequently clipped treatments. The reason for this could be that frequent clipping reduces the grass growth and thus biomass, which consequently leads to less soil moisture being utilised and is therefore made available to establishing *A. karroo* seedlings. There was however also a high survival rate of seedlings when the grass was unclipped. This is attributed to the positive effect of grasses in reducing soil moisture loss compared to the less frequently clipped treatments where lower survival rates were recorded. There is therefore a complex combination of positive and negative interactions operating between *A. karroo* seedlings and grasses via soil moisture. From previous studies in other savanna ecosystems, there is evidence for both the suppression (Brown and Booysen 1967, Walker *et al.* 1981, Knoop and Walker 1985) and facilitation (Brown and Archer 1989, Holmgren *et al.* 1997) of tree seedling establishment and growth by grasses.

In greenhouse studies however, grass biomass strongly influenced the growth and survival of *A. karroo* seedlings (Chapters 2 & 3). Grass biomass has also been shown to reduce the growth and survival of other woody seedlings (Knoop 1982). In this study, there was a negative relationship between grass root biomass production and tree seedling biomass. Unclipped grass swards had the highest biomass and, during a prolonged drought, they rapidly depleted much of the topsoil moisture, causing woody plant seedling mortality (Chapter 3). In their work in a semi arid savanna, Knoop and Walker (1985) demonstrated that during dry periods, topsoil water is depleted at a higher rate in situations with unclipped grasses than where there is no grass. Thus, although grasses can facilitate woody plant establishment by ameliorating soil moisture, this seems to be a short-term respite as the grasses will compete strongly with tree seedlings in the event of wet season droughts.

Dry season seedling survival was very low and was not influenced by the grass defoliation regime. Then, does herbaceous competition play any role in bush encroachment in semi-arid savannas? Low survivorship of *A. karroo* seedlings during the dry season has been recorded in other southern African savannas (O'Connor 1995). The annual rainfall during the time of this study was 406 mm in an area whose long-term average is 600 mm. In addition, its distribution was erratic. It is apparent that soil moisture had an overriding effect on the dry season seedling survival. This is because during this period, the topsoil dries out and the water table recedes to deeper layers. To survive during the dry season, roots of young *A. karroo* plants need permanent access to soil moisture until the start of the next rainy season (Loth 1999). Any factor therefore that causes rapid drying of the topsoil or delays root development can be detrimental to *A. karroo* seedlings (Du Toit 1966).

Most of the plant's active growth occurs during the wet season. It is important that plants put down deep roots during this period. When grown in porous soils, *A. karroo* seedlings put down deep roots within a few weeks of emerging (Chapters 5 & 6), irrespective of the

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soil moisture and irradiance conditions. In less porous soils however, unclipped grasses significantly reduced rapid root elongation (Chapters 2 & 3), mainly due to increased soil strength and the associated low penetrability of drier soils. The longer the time the roots take to reach the moister soil horizons, the more the plants are subjected to moisture fluctuations in the topsoil which can be drastic during long intra-seasonal dry spells. Plants whose roots are restricted to the surface soil horizons where grass roots are densest have reduced RGR. Smaller woody plant seedlings resulting from reduced RGR are more likely to die than those growing with clipped, less competitive grasses.

In general, grasses reduced the growth of *A. karroo* seedlings, even under continuously wet conditions (Chapter 3). This is contrary to the findings of Brown *et al.* (1998) who argue that herbaceous competition does not influence the growth of *Acacia nilotica* seedlings, another encroaching species in southern African ecosystems. This study has shown that in the absence of defoliation, grasses are capable of reducing *A. karroo* seedling biomass production. Decrease of grass biomass through defoliation led to increases in available soil moisture and thus growth of the woody seedlings. Hence, any factor that reduces the biomass of perennial grasses increases the frequency of woody seedling establishment and thus bush encroachment. Therefore, overgrazing by cattle, together with other determinants (Chapter 1), contribute to the problem of bush encroachment in semi-arid savanna ecosystems.

Above- vs. belowground competition

Grazing reduces both the above-ground and below-ground biomass of grasses. Lack thereof leads to accumulation of biomass and litter which shade tree seedlings. A high grass root biomass had a negative effect on *A. karroo* seedlings (Chapter 3). From field studies, we know that dense grass sward can reduce irradiance at ground level to as low as 6% (Chapter 4). Grasses therefore compete with establishing woody plants for both light and soil moisture. Reduction in root growth may result from increased resource allocation to the shoot or overall reduced growth of the seedlings. Such plants might not survive as they cannot access soil moisture from deeper layers during dry spells between rainfall events or during the dry season.

Acacia karroo seedlings growing in deep shade (4% of full light) produced low biomass, short roots and low root/shoot ratios under both low and high soil moisture conditions (Chapter 4). *Acacia karroo* has been described as light demanding (Du Toit 1966). Yet, the plants survived the 12-week duration of the experiment, which can be equivalent to the length of the wet season in the semi-arid savannas of southern Africa (Frost *et al.* 1986). The seedlings responded to shade by allocating more biomass to aboveground parts and etiolating. Higher investment of biomass into leaf and stem growth at the expense of the root even under dry conditions suggests that deep shade has a more negative effect to growth than low soil moisture. However, above this level of irradiance under dry

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conditions, biomass production is limited more by water than by light and the seedlings allocate more resources to root growth. The seedlings also morphologically adjust their growth pattern by producing high LARs and SLAs when grown under low irradiance conditions (Chapter 4).

From the results of Chapter 4, it is concluded that *A. karroo* seedlings adjust their biomass allocation in response to both light and soil moisture limitation to maximise capture of resources. Under field conditions, grass canopies reduce the amount of irradiance reaching tree seedlings and also alter their soil moisture environment. There is therefore an interaction between aboveground and belowground competition in the semi-arid savannas of southern Africa.

Acclimation to changes in irradiance and soil moisture conditions

In the absence of grass defoliation, tree seedlings in the natural environment are subjected to the shade of the herbaceous vegetation. During the rainy season, soil moisture is generally high though it decreases during prolonged dry spells. Grazing opens up the grass matrix and increases irradiance reaching emerging seedlings. In addition, at the onset of the dry season, grasses die back and soil moisture recedes to deeper layers. Thus, establishing seedlings are subjected to changes, at times drastic, in their irradiance and soil moisture environment. An adaptation to the highly temporally variable environmental conditions of semi-arid savannas is important for plants growing in these regions.

In this study, seedlings of *A. karroo* acclimated to both irradiance and soil moisture changes (Chapter 5). The seedlings survived shifts to new conditions mainly because of the long roots developed during the first few weeks of establishment, and also by adjusting their leaf characteristics and resource allocation patterns to suit their new environments. The development of long roots and the limited horizontal root development by *A. karroo* points to niche differentiation that reduces competition with herbaceous plant roots (Anderson and Sinclair 1993).

Acacia karroo seedlings are morphologically plastic and can adapt to short-term changes in both above- and belowground resource limitation (Chapter 5). The tree seedlings changed their LAR and SLA to adapt to their new irradiance environment. There were no mortalities recorded, mainly because the plants had access to a deeper and more lasting soil volume. As a result, seedlings of *A. karroo* are tolerant of low irradiance levels and have been recorded to persist in dense grass swards for at least a year (O'Connor 1995).

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Herbivory

Acacia karroo seedlings are vulnerable to herbivory from both vertebrate and invertebrate animals. The tree seedlings can be defoliated either as individual plants or eaten along with grasses. The herbivores might change the seedling's microenvironment in the process, e.g. grazing improves the irradiance condition of the seedlings. Regeneration of the defoliated seedlings is influenced by the immediate micro-conditions. Seedlings exposed to insect herbivory when growing beneath the canopy of grasses will regenerate under shade and those that are eaten together with grasses are suddenly exposed to full daylight.

Defoliation of *A. karroo* seedlings, even by 90% of the leaves, did not impair the formation of a long taproot (Chapter 6). This means that in porous soils, the seedlings will be able to extend their roots to deeper, moister horizons and enhance their chances of surviving the dry season drought. Seedlings that continued to grow in, or were exposed to full light after defoliation restored their root/shoot ratio to the level of unclipped plants. This is probably because defoliation in *A. karroo* results in increased photosynthesis in the remaining leaves, as has been reported in other tree species (Nowak and Caldwell 1984).

The seedlings of *A. karroo* had reduced biomass when defoliated, except in plants that grew continuously in shade where there was exact compensation. There were no differences in biomass production for plants defoliated at 50% and 90% in all irradiance treatments. However, *A. karroo* seedlings can at least partly compensate for leaf loss resulting from a single defoliation. No seedlings died as a result of defoliation. Therefore, *A. karroo* seedlings are well adapted to survival in savanna grasslands where defoliation by both vertebrate and invertebrate herbivores is common.

Conclusions and implications for management

Grasses have been shown to reduce both topsoil moisture and irradiance just above the soil surface. Defoliation of the grasses increases the availability of these resources. However, an unclipped grass sward provides a conducive microenvironment for tree seed germination but immediately subjects the emerging seedlings to competition for light and, under prolonged droughts, soil moisture. Although a large grass biomass reduces the accumulation of biomass by the tree seedlings, the plants can still access the water available in deeper soil layers and survive, though this depends on other soil characteristics. The results of this study indicate that *Acacia karroo* seedlings are well adapted to escaping grass competition by niche differentiation through root growth, biomass partitioning or morphological changes. Since *A. karroo* can establish and survive in dense swards, the findings of this study do not support the generalisation that a high grass biomass can suppress tree seedlings, at least during the first season of establishment. There is no indication therefore, that reduction in grass competition resulting from

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overgrazing is the sole cause of bush encroachment in the semi-arid savannas of southern Africa. In addition, seedlings of *A. karroo* recover well from a single defoliation and thus are well adapted to surviving herbivory in both bare and grassed areas.

Evidence from African and other tropical savannas indicate a close link between the problem of bush encroachment and increases in the density of grazing herbivores. The results of this study do not make light of such evidence, but rather suggest that there are mechanisms of encroachment other than mere facilitation of tree seedling survival and growth through reduced grass competition. In African savannas, cattle have been proved to play a significant role in the dispersal of *Acacia* seeds into grasslands (Miller 1994). These seeds germinate under the influence of dense grass swards. Overgrazing in such instances reduces the intensity and frequency of savanna fires that have been proven effective in controlling bush encroachment (Trollope 1974, 1980, Van de Vijver 1999). As shown in this study, grass competition limits the development, biomass accumulation and absolute height growth of the seedlings and keeps them within the grass layer for longer periods. Such seedlings are therefore susceptible to damage or kill by fire.

Rainfall is also important in bush encroachment in semi-arid savannas of southern Africa. The amount of rainfall and the length of the wet season can influence the fraction of tree seedlings that survive the dry season drought. Soil characteristics like penetrability and soil depth are also important as they determine root elongation and access to soil moisture. In less penetrable soil seedlings may not survive the dry season as the roots remain above the water table. From the plasticity and growth strategies displayed by *A. karroo* in this study, it is possible that once these seedlings have grown their roots to zones of permanent or near-permanent moisture availability, they can persist within the grass layer and utilise episodes of resource availability to grow. Having said this, and considering the complex web of factors that influence savanna structure and function, it is perceptible that maintenance of healthy grass swards through grazing management is still an important factor in the maintenance of tree-grass balances in savannas. It is suggested that management such as that of stocking rate and the grazing regime should be aware of and be able to adapt to variation in natural phenomena such as rainfall and natural fires.

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SAMENVATTING

In de Afrikaanse savanne neemt de dichtheid van struiken en kleine bomen plaatselijk zeer sterk toe en dat leidt tot ondoordringbare bossages met weinig ondergroei. Men zou dat met een modern woord ‘verstruiking’ kunnen noemen, homoloog aan het Duitse ‘Verbuschung’ (Walter 1954) of het Engelse ‘bush encroachment’, maar hier zal de term ‘dichtgroeien’ worden gebruikt. Halfdroge savannes groeien dicht als er zaden van oprukkende houtige soorten kiemen en de kiemplanten met succes tot jonge, en later tot volwassen, struiken en bomen opgroeien, of als die houtige soorten clonaal nieuwe uitlopers vanuit hun rhizomen produceren. Als die struiken en bomen hoge dichtheden bereiken wordt het veld plaatselijk voor grazende en knabbelende grote planteneters ontoegankelijk. Hoge dichtheden van de houtige planten gaan samen met een lage productie van de grassen en kruiden en dit kan ook een verandering in de plaatselijke soortensamenstelling met zich mee brengen. Voor veeboeren is het dichtgroeien van de savanne dus een slechte zaak en het wordt dan ook als een teken van landdegradatie beschouwd.

De grootschalige introductie van koeien als de veruit belangrijkste grazers in de savanne wordt traditioneel als de oorzaak van het dichtgroeien van de savanne gezien (Walter 1954, Van Vegten 1983). Het is ook onderwerp van veel veldexperimenten geweest, maar deze experimenten hebben bijna allemaal betrekking op de volwassen bomen en struiken gehad, klaarblijkelijk omdat het probleem van het dichtgroeien ergens zijn kop op stak en daar dan ook moest worden opgelost, zodat er weer meer gras ging groeien.

Maar het succes van de houtige soorten hangt natuurlijk van een hele reeks factoren af, die tijdens de verschillende levensfasen van een boom of struik van belang zijn, zoals de productie van zaad, de zaadverspreiding, de kieming ervan en de vestiging van de kiemplant, en de groei naar volwassenheid. Kieming, uitlopen van de kiemplant en vestiging ervan zijn de levensfasen waarin er in plantenpopulaties zeer veel sterfte optreedt en het is dus van belang de factoren die dan een rol spelen te onderzoeken. De overleving van de kiemplanten hangt van de waterbeschikbaarheid in de bovenste bodemlaag af, maar dat is ook de laag waarin de grassen wortelen en daar zal dus de concurrentie om water erg sterk zijn (Medina & Silva 1991, Bertiller *et al.* 1996).

Deze dissertatie doet verslag van onderzoek naar de groei en het succes van kiemplanten en hele jonge boompjes (‘juvenielen’) van *Acacia karroo*, een sterk opdringende boomsoort in de halfdroge savannes van zuidelijk Afrika. Het onderzoek doet verslag van veld- en kas-onderzoek. Nadat de gevolgen van het afknippen van gras op de grasproductie is vastgesteld richt dit onderzoek zich vooral op:

1) het effect van een grasdek op de beschikbaarheid van water in de bodem en de effecten hiervan op de overleving en groei van de kiemplanten en juvenielen van *Acacia karroo*,

- 2) een evaluatie van de reactie van *Acacia karroo*-juvenielen op de beschikbare hoeveelheid licht en bodemvocht waarin ze moeten opgroeien en op veranderingen daarin, en
- 3) de reactie van *Acacia karroo*-juvenielen op ontbladering.

Grasknippen en grasproductie

Vaak neemt men aan dat een dicht en dik grasdek kiemplanten van de bomen verstikt (Brown & Booyesen 1967, Walker *et al.* 1981, Knoop & Walker 1985). Bij de overjarige savannegrassen zit meer dan 50 % van de biomassa onder de grond (Ruthword 1975) en als die grassen worden afgeknipt of afgevreten kunnen ze toch weer uitlopen, ook al is dat even wat minder uitbundig. Herhaald en volledig afknippen leidt echter tot het afsterven van de grassen. Scholes (1985) vond in een veldonderzoek, dat een heel groot aantal overjarige grasplanten na twee jaar van droogte en sterke beweiding dood was. Dit gegeven is ook verwerkt in verschillende oecologische savannetheorieën, die stellen dat een afname in de groei­kracht van de grassen door overbeweiding van invloed is op de waterbeschikbaarheid in de bovenste bodemlaag. En dit, tezamen met de hoeveelheid regenval, zou dan de belangrijkste verklaring voor het dichtgroeien van de savanne met struiken en bomen zijn.

Ons onderzoek liet zien, dat het gedurende een heel groeiseizoen afknippen van de grassen in het veld een lagere productie van grasbiomassa in het volgende seizoen tot gevolg had (hoofdstuk 2). Maar dit kwam minstens ten dele doordat de regenval afnam van 558 mm in het eerste jaar tot 406 mm in het tweede.

Als er minder gras is, zijn savannebranden minder verwoestend. En vuur wordt als een instrument voor het bestrijden van het dichtgroeien van de halfdroge savanne gebruikt (Trollope 1980, Higgins *et al.* 2000).

Kasproeven lieten zien dat het herhaaldelijk afknippen van grassen hun biomassa­productie ook onder natte omstandigheden deed verminderen (hoofdstukken 2 en 3), terwijl beweiding van savannes tot een afname van de ondergrondse grasbiomassa met 41-50 % leidde (Pandey & Singh 1992). Dit komt, omdat het afknippen van de halmen tot een verminderde translocatie van reserves naar wortels leidt. Daardoor wordt het wortelstelsel kleiner en vervolgens ook het bovengrondse deel en het resultaat is dat zo'n grasplant minder hulpbronnen verbruikt dan een krachtig groeiend gras.

... Maar leidt dat ook tot een groter succes voor *Acacia karroo* wat betreft de kieming van zijn zaad en de overleving van zijn kiemplanten en juvenielen?

Kieming

Acacia-zaden worden vaak door grotere dieren verspreid, zowel wilde dieren als vee, als ze de droge peulen eten (Coe & Coe 1987, Hauser 1994). Een aantal zaden in de peul worden door het kauwen en de spijsvertering vernietigd, maar andere komen onbeschadigd met de mest weer in het veld terecht (Miller 1994). Het is echter nog niet helemaal duidelijk hoe groot het belang van de passage van de zaden door het darmkanaal van de dieren voor de kieming precies is.

In de halfdroge savanne is bodemvocht echter erg belangrijk voor de kieming. Omdat de regen erratisch verspreid valt en de evaporatiesnelheden hoog zijn, wordt het bodemoppervlak infrequent vochtig en droogt het daarna wellicht weer te snel uit voor een kiemend zaad of voor een kiemplant die zijn jonge wortel in de bodem omlaag moet laten groeien naar de iets dieper liggende lagen waar bodemvocht beschikbaar is. In dit onderzoek waren de kiempercentages het hoogst in de behandeling waarin het gras niet geknipt werd (hoofdstuk 2). Hoge kiempercentages van *Acacia*-zaden zijn ook gevonden in andere savannes in zuidelijk Afrika, wanneer het gras er niet werd gemaaid of afgegraasd (O'Connor 1995). Een dicht grasdek lijkt dus een geschikt microklimaat voor de kieming van *Acacia*-zaden te bieden, waarschijnlijk omdat dat de evaporatie aan het bodemoppervlak beperkt.

Overleving en groei

Hoofdstuk 2 liet zien dat een grasmat een 'veilige omgeving' is voor kiemende zaden, vooral als het gras niet geknipt wordt. Een centrale vraag in deze dissertatie is of dit ook een gunstige omgeving is voor de vestiging van de kiemplant en voor de groei ervan? In het veld had de frequentie waarmee het gras geknipt werd een grote invloed op de overleving van de kiemplant gedurende het regenseizoen, maar de grasbedekking had geen effect op de overleving van de kiemplanten van *Acacia* aan het eind van het droge seizoen (hoofdstuk 2). Gedurende het regenseizoen was de overleving van de kiemplanten op geheel kale bodem en in de frequent geknipte grasmat het best, wellicht omdat daar het meeste bodemvocht voor de zich vestigende *Acacia*-kiemplanten beschikbaar was, omdat de grasplanten er immers weinig water verbruikten. Maar ook in de niet-geknipte grasmat overleefden veel kiemplanten. Dit is misschien het gevolg van de verminderde evaporatie aan het bodemoppervlak onder deze behandeling in vergelijking met de af en toe geknipte behandelingen, waar er veel minder kiemplanten overleefden. Het bodemvocht is dus blijkbaar in een complexe combinatie van positieve en negatieve interacties werkzaam op het succes van *Acacia*-kiemplanten. Eerder onderzoek in andere savannes hebben zowel onderdrukking (Brown & Booyen 1967, Walker *et al.* 1981, Knoop & Walker 1985) als facilitatie van kiemplantvestiging (Brown & Archer 1989, Holmgren *et al.* 1997) in een grasmat laten zien.

In kasexperimenten had de hoeveelheid gras grote invloed op de overleving van *Acacia karroo*-kiemplanten, waarbij de biomassa van de kiemplanten kleiner was naar gelang de biomassa van de graswortels groter was (hoofdstukken 2 en 3). Niet-geknipte grasmatten hadden de meeste biomassa en tijdens een langdurige droogte verbruikten die al gauw een heel groot deel van het water in de bovenste bodemlaag, waardoor de *Acacia*-kiemplanten afstierven (hoofdstuk 3). Knoop & Walker (1985) hebben laten zien, dat in de droge savanne het water van de bovenste bodemlaag ook sneller op raakt als het gras er niet geknipt is dan wanneer er helemaal geen grasbedekking is. Grassen kunnen dus de vestiging van houtige kiemplanten wel faciliteren doordat ze de beschikbaarheid van water in de bodem verhogen, maar deze gunstige invloed is maar van korte duur, omdat de grassen spoedig hard met de kiemplanten om datzelfde water zullen gaan concurreren als er een droge periode tijdens het regenseizoen optreedt.

Gedurende het droge seizoen was er heel weinig overleving van de kiemplanten of het gras nu geknipt was of niet. De vraag is dan, speelt de concurrentie met grassen nu wel of niet een rol in het dichtgroeien van de savanne? Het is duidelijk dat de hoeveelheid bodemvocht van heel groot belang is voor het percentage kiemplanten dat het droge seizoen overleeft. De bovenste bodemlaag droogt dan uit en water is alleen nog in de wat diepere lagen beschikbaar. Om het droge seizoen te overleven hebben de wortels van de *Acacia karroo* juvenielen permanente toegang tot dat water nodig en daarom kan elke factor die de uitdroging van de bodem versnelt of de wortelontwikkeling van de jonge planten vertraagt van catastrofale betekenis zijn. De kiemplanten groeien vrijwel uitsluitend tijdens het regenseizoen en dan moeten ze de diepere bodemlagen zien te bereiken. In poreuze grond kunnen *Acacia karroo*-kiemplanten, onafhankelijk van de hoeveelheid bodemvocht en licht die beschikbaar zijn, binnen een paar weken na kieming diepreikende wortels produceren (hoofdstukken 5 en 6). In minder poreuze grond heeft niet-geknipt gras echter een negatieve invloed op de bereikte worteldiepte, vooral als gevolg van de hogere bodemweerstand en de lagere bodemdoordringbaarheid die dat voor de wortels met zich meebrengt (hoofdstukken 2 en 3). Hoe langer de wortels nodig hebben om diepere, vochtigere bodemlagen te bereiken, hoe meer de planten aan fluctuaties in de waterbeschikbaarheid in de bovenste bodemlagen onderhevig zijn. Tijdens wat langere droge perioden in het regenseizoen kunnen die fluctuaties drastisch zijn.

Kiemplanten die niet dieper wortelen dan de graswortels hadden lagere relatieve groeisnelheden (RGR), en een grasmat remde in alle gevallen de groei van *Acacia karroo*-kiemplanten, zelfs onder voortdurend natte omstandigheden (hoofdstuk 3). Dit strookt niet met de resultaten van Brown *et al.* (1998), die rapporteerden dat de groei van kiemplanten van *Acacia nilotica*, ook een soort die savannes in zuidelijk Afrika dichtgroeit, niet door concurrentie met grassen werd beïnvloed. Vooral als het gras niet geknipt werd remde dat in onze proeven de biomassaproductie van de *Acacia karroo*-kiemplanten en geknipt gras leidde tot een hogere beschikbaarheid van bodemvocht en daarmee tot een snellere groei

van de kiemplanten. Het lijkt er dus op, dat elke factor die de biomassa van de overjarige grassen reduceert, de vestigingsfrequentie van de kiemplanten van de houtige gewassen verhoogt en daarmee dan het dichtgroeien van de savanne bevordert. Overbeweiding door vee bevordert dus, samen met andere factoren (hoofdstuk 1), het dichtgroeien van de halfdroge savannes.

Boven- en ondergrondse concurrentie

Begrazing resulteert in een vermindering van zowel de bovengrondse als de ondergrondse biomassa van de grassen. Zonder begrazing hoopt zich biomassa en strooisel op en dat biedt schaduw aan de kiemplanten van de bomen. Een grote wortelmassa van de grassen had een negatief effect op de *Acacia karroo*-kiemplanten. Veldproeven lieten zien dat in een dichte grasmat de lichtintensiteit aan het bodemoppervlak wel tot 6 % van de volle instraling kan zijn gereduceerd (hoofdstuk 4). Grassen concurreren dus zowel om licht als om water met de kiemplanten van de houtige gewassen. Een verminderde groei van de wortel van de kiemplanten kan het gevolg zijn van een verhoogde allocatie van biomassa naar de bovengrondse delen of van een algehele vermindering van de groeisnelheid van de kiemplant of juveniel. Als zulke planten de diepere, vochtigere bodemlagen niet weten te bereiken, zullen ze droge perioden tijdens het regenseizoen of het lange droge seizoen niet overleven.

Kiemplanten van *Acacia karroo*, die in diepe schaduw (4 % van de volle instraling) opgroeiden, produceerden weinig biomassa, korte wortels en een lage wortel/spruitverhouding onder alle omstandigheden van waterbeschikbaarheid (hoofdstuk 4). *Acacia karroo* wordt als lichtbehoevend beschouwd (Du Toit 1966). Desalniettemin overleefden de planten het 12 weken durende experiment (en dat is net zo lang als het hele regenseizoen in de halfdroge savannes van zuidelijk Afrika) en alloceerden in de schaduw een groter deel van hun biomassa naar de spruit en etioleerden. De gebleken hogere investering van biomassa in bladeren en stam ten koste van de investering in de wortel, zelfs onder droge groei-omstandigheden, suggereert dat diepe schaduw een ongunstiger effect op de groei heeft dan een geringe waterbeschikbaarheid. Maar als de lichtomstandigheden ook maar een beetje beter zijn blijkt de biomassa-productie, onder droge groei-omstandigheden, meer door beschikbaarheid van water dan van licht beperkt te worden. De kiem- en juveniele planten investeren dan meer in wortelgroei en passen zich morfologisch ook aan door bij lage lichtintensiteiten een hogere LAR en SLA te produceren (hoofdstuk 4).

Het blijkt dus dat *Acacia karroo*-juvenielen het investeringspatroon van hun biomassa aan de licht- en vochtbeschikbaarheid aanpassen om zodoende de opnamecapaciteit van de noodzakelijke hulpbronnen te maximaliseren. In het veld zorgt het grasdek ervoor, dat de kiemplanten van de bomen minder licht krijgen en wijzigt ook de waterbeschikbaarheid. Er is dus een interactie tussen de bovengrondse en ondergrondse concurrentie tussen de

grassen en houtige kiemplanten en juvenielen in de halfdroge savannes van zuidelijk Afrika.

Acclimatie aan veranderingen in instraling en waterbeschikbaarheid

Als het gras niet geknipt of afgegraasd wordt ondervinden de kiemplanten van de houtige gewassen de schaduw van het grasdek. Tijdens het regenseizoen is er in de halfdroge savannes over het algemeen voldoende water beschikbaar, hoewel dat veel minder kan zijn tijdens vrij langdurige droge perioden tussen regendagen. Begrazing opent het grasdek en zorgt ervoor dat de kiemplanten meer instraling ontvangen. Vanaf het begin van het droge seizoen sterven de grassen bovengronds af en droogt de bovenste bodemlaag uit. De kiemplanten van de houtige gewassen, die zich aan het vestigen zijn worden dan dus blootgesteld aan, soms drastische, veranderingen in instralingsniveau en waterbeschikbaarheid. Het is dus belangrijk dat zulke planten zich aan deze sterke tijdelijke veranderingen in hun omgeving kunnen aanpassen.

Onze experimenten laten zien, dat *Acacia karroo*-juvenielen goed aan veranderingen in instraling en waterbeschikbaarheid acclimatiseren (hoofdstuk 5). De kiemplanten overleefden een plotselinge verplaatsing naar geheel nieuwe groei-omstandigheden voornamelijk doordat ze tijdens de eerste vijf weken van hun vestiging lange wortels hadden laten uitgroeien; ze pasten ook hun bladeigenschappen en hun allocatiepatroon aan de nieuwe omstandigheden aan. De snelle ontwikkeling van lange, diepe wortels en weinig horizontale wortelgroei in *Acacia karroo* wijst op een nisdifferentiatie, die leidt tot een geringere concurrentie met de graswortels (Anderson & Sinclair 1993). De kiemplanten waren morfologisch ook plastisch en pasten zich aan de plotselinge veranderingen in hun bovengrondse en ondergrondse milieu aan met veranderingen in hun LAR en SLA (hoofdstuk 5). Geen van de juvenielen stierf af, want ze waren er allemaal in geslaagd de diepere, vochtigere bodemlagen te bereiken. Juvenielen van *Acacia karroo* blijken dan ook in staat te zijn om minstens een jaar lang in dichte, donkere grasmatten in het veld te overleven (O'Connor 1995).

Begrazing

Kiemplanten en juvenielen van *Acacia karroo* kunnen zowel door grote gewervelde planteneters samen met het gras worden opgegeten, als door kleine ongewervelde dieren individueel worden ontbladerd. Kiemplanten die door insecten zijn kaal gegeten zullen in de schaduw van het gras moeten regenereren, maar kiemplanten, die samen met het gras zijn afgevreten worden plotseling aan het volle daglicht blootgesteld.

Ontbladering van *Acacia karroo*-kiemplanten, zelfs tot 90 % van het totale bladoppervlak, had geen invloed op de vorming van een lange penwortel (hoofdstuk 6). Zulke planten

kunnen in een poreuze bodem de diepere, vochtigere bodemlagen wel bereiken en het droge seizoen overleven. Ontbladerde kiemplanten in het volle licht wijzigden hun wortel/spruitverhouding snel naar het niveau dat normaal is voor niet-geknipte planten, waarschijnlijk omdat ontbladering tot een verhoogde fotosynthetische productie in de overgebleven bladeren leidt.

Ontbladerde *Acacia karroo*-kiemplanten produceerden minder biomassa, behalve wanneer ze voortdurend in de schaduw groeiden; dan werd hun biomassa-productie volledig gecompenseerd. Of de planten nu 50 % of 90 % ontbladerd werden maakte geen verschil. *Acacia karroo*-kiemplanten kunnen een eenmalige ontbladering gedeeltelijk compenseren door nieuwe bladeren te laten uitgroeien. De kiemplanten zijn dus goed toegerust om de gebruikelijke ontbladering door grote of kleine planteneters in de savanne te overleven.

Conclusies

Grassen blijken de beschikbaarheid van water in de bovenste bodemlaag en de hoeveelheid instraling vlak boven het bodemoppervlak te verminderen en ontbladering van de grassen vergroot de beschikbaarheid van deze hulpbronnen. Een niet-geknipt grasdek levert echter een geschikt microklimaat voor de kieming van zaden van houtige gewassen, maar dwingt de kiemplant onmiddellijk tot concurrentie om licht en, tijdens een periode van droogte, om bodemvocht. Hoewel een grote biomassa-productie van de grassen een geringere biomassa-productie van de kiemplanten tot gevolg heeft, kunnen de kiemplanten onder die omstandigheden toch nog wel de diepere, vochtigere bodemlagen bereiken en overleven. Hierbij spelen echter ook andere bodemeigenschappen een rol. Onze resultaten geven aan dat *Acacia karroo*-kiemplanten en -juvenielen, door hun wortelgroei, het allocatiepatroon van hun biomassa en hun morfologische plasticiteit, goed toegerust zijn om de concurrentie met grassen te ontwijken. Omdat we hebben laten zien, dat *Acacia karroo*-kiemplanten zich goed in een dichte grasmat kunnen vestigen en daar kunnen overleven, is het niet waar, zoals algemeen verondersteld wordt, dat een dicht grasdek de kiemplanten kan uitschakelen, in elk geval niet tijdens het eerste seizoen van vestiging. Er zijn dus in het geheel geen aanwijzingen, dat de verminderde concurrentiekracht van grassen in de overbeweide, halfdroge savannes van zuidelijk Afrika de enige oorzaak is voor het dichtgroeien ervan met struiken en bomen. Bovendien blijken de kiemplanten van *Acacia karroo* zich heel goed van een eenmalige ontbladering te herstellen en overleven ze begrazing in kale zowel als grasrijke savannes heel gemakkelijk.

Waarnemingen en onderzoek in Afrikaanse en andere tropische savannes indiceren dat er een nauw verband tussen het probleem van het dichtgroeien van de savanne en de toenemende dichtheid van grazend vee bestaat. De resultaten van ons onderzoek wijzen die bevindingen niet lichtvaardig weg, maar geven aan, dat er bij het dichtgroeien blijkbaar nog andere mechanismen werkzaam zijn dan slechts de bevordering van de

overlevingskansen en groei van de kiemplanten van de houtige gewassen door een verminderde concurrentiekracht van de grassen.

Vee speelt een belangrijke rol in de verspreiding van *Acacia*-zaden in de Afrikaanse savanne (Miller 1994). Die zaden kiemen goed in een dicht grasdek. Onder overbeweiding is er niet zo'n dicht grasdek en daardoor is de intensiteit en de frequentie van savannebranden onder zulke omstandigheden lager, terwijl vuur juist een effectief middel tegen het dichtgroeien van savannes is gebleken (Trollope 1974, 1980). Ons onderzoek heeft laten zien, dat een sterke concurrentie van het gras de ontwikkeling, biomassa-accumulatie en hoogtegroeï van de kiemplanten van *Acacia karroo* belemmert en ze daardoor langer binnen het bereik van het grasdek houdt. Zulke kiemplanten en juvenielen kunnen dus langer door een savannebrand beschadigd of vernietigd worden.

Regenval speelt ook een belangrijke rol. De hoeveelheid regen en de lengte van het regenseizoen beïnvloeden het percentage kiemplanten dat het droge seizoen overleeft. Doordringbaarheid van de bodem en bodemdikte zijn ook belangrijk omdat ze de lengtegroei van de wortel en daarmee de toegang tot bodemvocht beïnvloeden. Met een plasticiteit en groeistrategie zoals de *Acacia karroo*-kiemplanten die in ons onderzoek hebben laten zien lijkt het waarschijnlijk dat ze, als ze met hun wortels eenmaal de diepere bodemlagen met een permanente of bijna-permanente waterbeschikbaarheid hebben bereikt, in het grasdek kunnen blijven overleven en in het gunstige seizoen kunnen uitgroeien.

Dit gezegd hebbend, en het complexe geheel van factoren die de oecologie van de savanne beïnvloeden in ogenschouw nemend, lijkt het toch belangrijk dat door middel van beweidingsbeheer een behoorlijke graslaag in stand wordt gehouden, omdat die van invloed is op de balans tussen bomen en gras in de savannes. Beweidingsbeheer en belading met vee zijn dan ook belangrijke managementinstrumenten, die dynamisch zouden moeten worden gebruikt en op de natuurlijke variatie in regenval en savannebranden zouden moeten inspelen.

(De literatuurverwijzingen in deze Samenvatting worden aan het eind van de General Discussion gespecificeerd.)

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Curriculum Vitae

Chipangura Chirara

I was born on 1st December 1968 in Charter, Zimbabwe. I attended primary school at Matirige in Chivhu. I attended several secondary schools and finally did my 'A-Level' at St Augustines Mission Penhalonga in 1989. I did a Bachelor of Science Honours Degree in Biological Sciences at the University of Zimbabwe from 1990-1992, majoring in Ecology and Microbiology. Between December 1992 and March 1993 I worked as a graduate Research assistant to Professor B.M. Marshall who was working on eutrophication of Lake Chivero. In May 1993 I registered as a Higher Degrees student in the Department of Biological Sciences, University of Zimbabwe. I worked in a project that was funded by Utrecht University and supported by Matopos Research Station. From November 1993 to March 1995 I did field work at Matopos Research Station, in southwestern Zimbabwe under the supervision of Professor Peter Frost and Dr. V. Gwarazimba. At Matopos, I was also attached to several ongoing projects in the Ecology Section. At the beginning of 1995 I briefly joined Matopos Research Station as a Rangeland Ecologist but could not continue with this post as my studies required that I travelled abroad and to the university in Harare for relatively long periods of time. Between June and November 1995 I joined the Department of Plant Ecology and Evolutionary Biology, Utrecht University as a graduate exchange student. Here I attended graduate courses and participated in PhD meetings. In 1996 I registered for a PhD with the University of Zimbabwe and later transferred to Utrecht University, Department of Plant Ecology, to complete my studies on bush encroachment.