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 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 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°23S´, 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.

CHAPTER 2

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 m^2 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 m^2). 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:

SSL = stem length/stem mass, and SRL = 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.

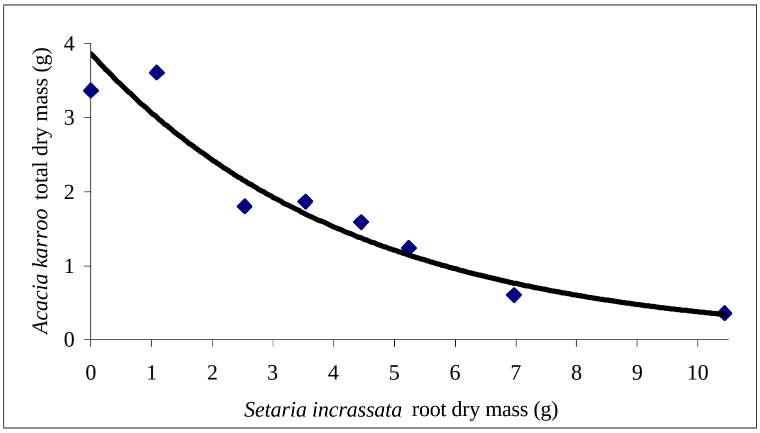

Figure 1. The relationship between *Acacia karroo* and *Setaria incrassata* root biomass production

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}

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).

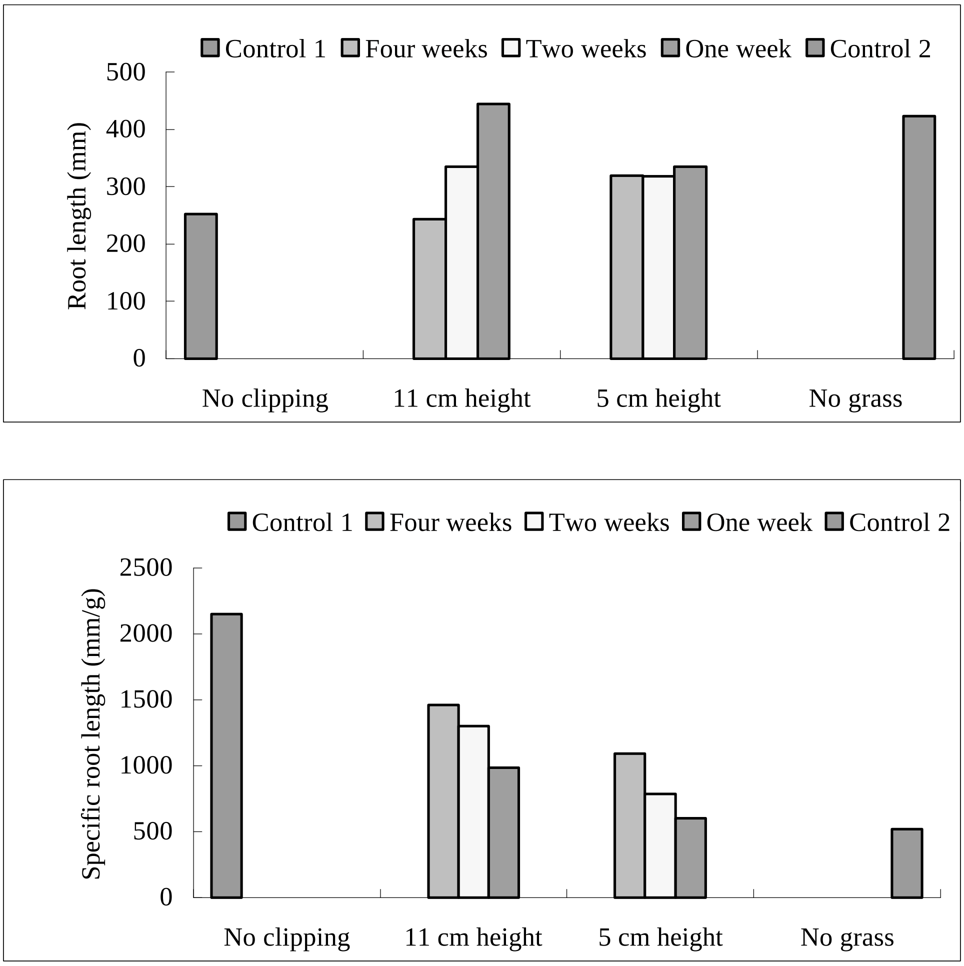

Figure 2. Root extension of *Acacia karroo* seedlings competing with grass clipped at different regimes indicating (a) absolute root length and (b) specific root length.

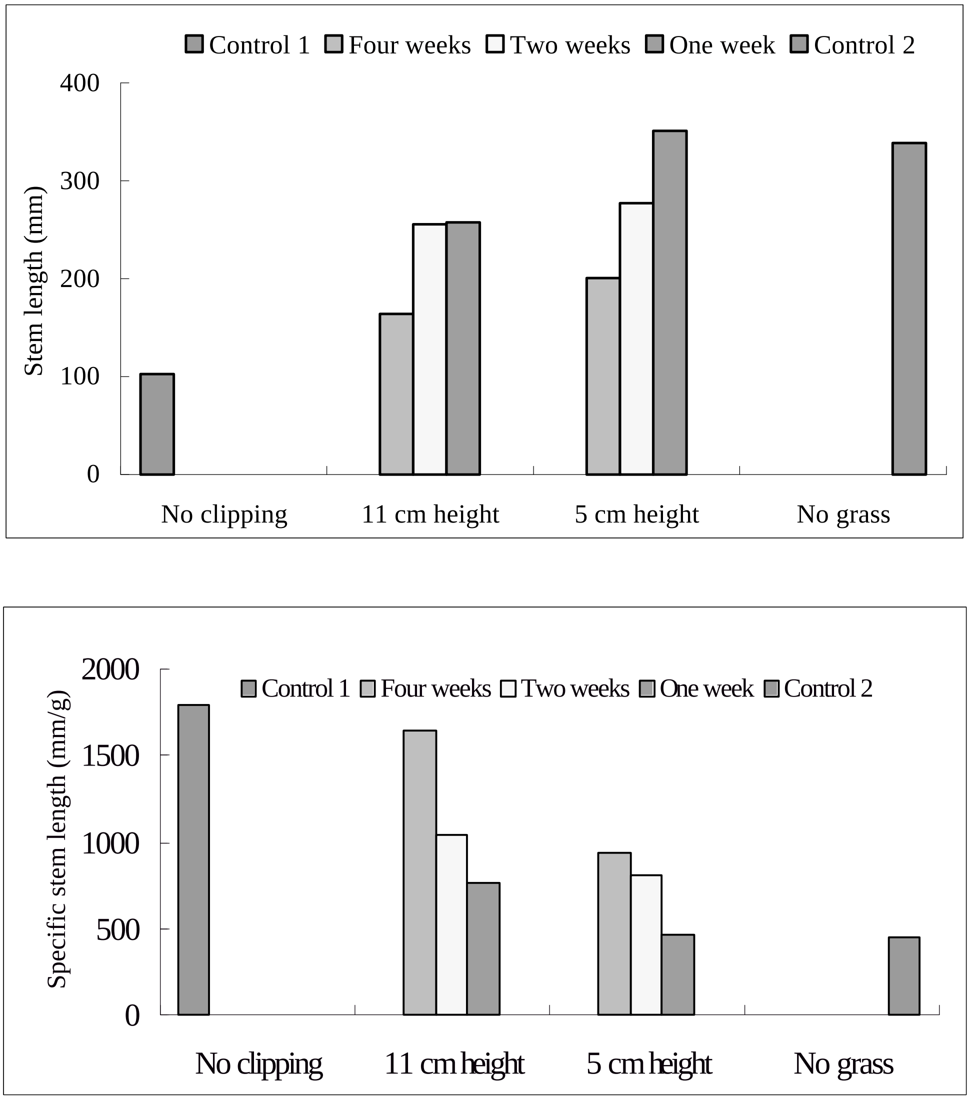

Figure 3. Stem extension of *Acacia karroo* seedlings competing with grass clipped at different regimes indicating (a) absolute stem length, and (b) specific stem length.

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
Between paddocks	0.85	0.379	0.49	0.499
Within paddocks				
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

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

	Lightly-grazed paddock				Heavily-grazed paddock			
Clipping treatment	1993/4	1994/5	% change	Total	1993/4	1994/5	% change	Total
I 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 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 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.

Acknowledgements

C. Chirara is thankful to the Department of Plant Ecology and Evolutionary Biology, Utrecht University, for funding, and to Matopos Research Station for providing the study sites. We are also grateful to B. Mandizvidza, A. Hlathwayo, D. Mpofu, C. M., and J. Nkomo for helping in the field. We would like to thank J. Stuefer and W. Dijkman of Utrecht University for their comments on draft manuscripts.

References

Chapin, F.S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics 11*, 233-260.

Chapin, F.S. and Slack, M. 1979. Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited Tundra graminoids. *Oecologia 42*, 67-79.

Clement, C.R., Hopper, M.J., Jones, L.H.P. and Leafe, E.L. 1978. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution: ii. Effect of light, defoliation, and relationship to carbon dioxide flux. *Journal of Experimental Botany 29*, 1173-1183.

Dalton, F.N., Herkelbrath, W.N., Rawlins, D.S. and Roades, J.D. 1984. Time domain reflectometry: simultaneous assessment of the soil water content and electrical conductivity with a single probe. *Science 224*, 989-990.

Dye, P.J. 1983. *Prediction of variation in grass growth in a semi-arid induced grassland.* DPhil Thesis, University of Witwatersrand, Johannesburg.

Dye, P.J. and Spear, P.T. 1982. The effects of bush clearing and rainfall variability on grass yield and composition in southwest Zimbabwe. *Zimbabwe Journal of Agricultural Research 20*, 103-118.

Fahnestock, J.T. and Knapp, A.K. 1994. Plant responses to selective grazing by bison: interactions between light, herbivory and water stress. *Vegetatio 115*, 123-131.

Frost, P.G.H. and Robertson, F. 1987. The ecological effects of fire in savannas. In: Walker, B.H. (ed), *Determinants of Tropical Savannas.* IRL Press Limited, Oxford, UK.

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

Kelly, R.D. and Walker, B.H. 1976. The effects of different forms of land use on the ecology of a semi-arid ecosystem in south eastern Rhodesia. *Journal of Ecology 64,* 553-576.

Kennan, T.C.D. 1966. Veld management in the medium and low rainfall areas of Rhodesia. Parts 1 & 2. *Rhodesia Farmer 37(31)*, 11-12 & 20 and *37(32)*, 27-28 & 30.

Kennan, T.C.D., Staples, R.R. and West, O. 1955. Veld management in Southern Rhodesia. *Rhodesia Agricultural Journal 52*, 4-21.

McNaughton, S.J. and Chapin, F.S.III. 1985. Effects of phosphorous nutrition and defoliation on C_4 graminoids from the Serengeti Plains. *Ecology 66*, 1617-1629.

McNaughton, S.J., Wallace, L.L. and Coughenour, M.B. 1983. Plant adaptation in an ecosystem context: effects of defoliation, nitrogen, and water on growth of an African C_4 sedge. *Ecology 66*, 307-318.

O'Connor, T.G. 1995. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia 103*, 214-223.

Plowes, D.C.H.. 1956. Bush or grass: which do we want? *Rhodesia Agricultural Journal 53*, 589-595.

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

Smith, T.M. and Shackleton, S.E. 1988. The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. *South African Journal of Botany 54*, 375-379.

SPSS/PC+. 1988. SPSS for the IBM PC/XT/AT. SPSS, Chicago, Illinois, USA.

Van Vegten, J.A. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio 56*, 3-7.

West, O. 1947. Thornbush encroachment in relation to the management of veld grazing. *Rhodesia Agricultural Journal 44*, 499-497.

West, O. 1958. Bush encroachment, veld burning and grazing management. *Rhodesia Agricultural Journal 55*, 407-425.

Withers, J.R. 1979. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove , Victoria. IV. The effect of shading on seedling establishment . *Australian Journal of Botany 27*, 47-66.