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Invasion of *Chromolaena odorata* in the Lowveld Region of Swaziland and its Effect on Herbaceous Layer Productivity

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Abstract: A study was conducted to investigate pattern of Chromolaena odorata invasion and its effect on grass layer in three land use systems (communal, government ranch and game reserve) and two soil classes (lithosol and raw mineral soil). Six sites (2 ha each) were selected, one on each of the two common soil classes for each land use system. The communal land had significantly lowest (p<0.05) density (465 SE ha-1) of C. odorata compared to the game reserve and there was no significant difference in total density in the two soil classes (mean = 691 SE ha⁻¹). The greatest proportion occurred in height class of >1-1.5 m and the lowest in >0-0.5 m. Shrub (>0.5-3 m) and seedling (>0-0.5 m) densities were significantly (p<0.05) highest in the game reserve and commercial ranch, respectively. Total dry matter (DM) grass production within and outside invaded areas showed significant differences (p<0.05) in many sites. More pronounced trends of DM production were observed for the most dominant palatable species which included *Urochloa mozambicensis*, Panicum deustum and P. maximum. It is concluded that the invasion of C. odorata was rated to be moderate or high while past land management may be the major factor in the difference between land use systems. The effect of invasion of C. odorata on the grass layer was also severe to constitute a threat to livestock and game industries. Adaptive control strategies are therefore recommended while further work will be required to identify the causes of difference between land uses, to determine soil characteristics and overall productivity potential as affected by C. odorata invasion as well as interaction effects between biotic and abiotic factors.

Key words: Chromolaena odorata, land use, soil class, rangeland, invasion, dry matter

INTRODUCTION

Southern Africa savanna rangelands support large, diverse and dynamic ecosystems which sustain both wildlife and agricultural enterprises. In several cases, however, alien shrubs have been noted to invade these rangelands. Such invasion has been known as a recent ecological phenomena characterized by a plant density of invasive shrubs beyond the level the ecosystem can carry under a climax equilibrium condition. *Chromolaena odorata* is a perennial scrambling shrub of neotropical origin forming a dense tangled bushes of up to 3 m (Strathie-Korrubel, 2000) and produces copious quantities of efficiently dispersed seeds capable of establishing even in undisturbed habitats. It forms a dense, permanent thickets over large areas, thereby suppressing other vegetation. Solomon *et al.* (2006) contended that the invasion of savannas by *C. odorata* appears to be episodic in nature and the change from savannas to shrub land can happen very rapidly. The population of *C. odorata* in southern Africa is commonly associated with high rainfall areas and annual rain as little as 500 mm or below (Foxcroft and Martin, 2002).

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Chromolaena odorata has been reported to be a major threat to livestock, game farming and biodiversity conservation with a negative impact on the productivity of the grassland ecosystem in southern Africa. The productivity and long term economic viability of agriculture as well as the ecological integrity of savannas can be undermined by the invasion of such plants at the expense of the herbaceous cover, especially grasses. In Swaziland, savannas represent a valuable economic resource as a means of sustenance to the people. There are two main types of land tenure and usage in this ecosystem namely; the Swazi National Land which is mainly the communal land and the Title Deed Land which is mainly private ranching (Sweet and Khumalo, 1994). In both tenures, livestock production is the most valuable activity and in recent time, an invasion of C. odorata has been reported in the lowveld savannas of Swaziland (Solomon, 2006; Solomon et al., 2006). However, information on the extent of infestation and the magnitude of its associated problems in the different land uses and soil types has not been fully understood. This study was therefore designed to investigate the pattern of C. odorata invasion and its effect on the grass layer productivity under three land use systems (game reserve, commercial cattle ranch and communal grazing land) and at two soil classes (lithosol and raw mineral soil).

MATERIALS AND METHODS

Study Area

This study was conducted in Simunye area in the lowveld of the Kingdom of Swaziland which represents about 33% of the total land area of the country. The landscape is undulating with the co-ordinates of approximate center of the study area are 26°05′ S, 31°58′ E and the altitude ranges between 250-500 m above sea level. The climate is generally semi-arid and mean annual rainfall ranges between 400-600 mm with most of the rainfall occurring between October and March. The mean monthly temperature in January and July are 26 and 18°C, respectively (Monadjem and David, 2005). The vegetation has been classified as lowveld savanna (Acocks, 1988) with broad leaved woodland predominating in the West, microphyllous (acacia) savanna in the East and the riverine forest along the rivers and major drainage lines (Hess *et al.*, 1990; Sweet and Khumalo, 1994). Basal and sandstone-claystone are the geological features of this area, while raw mineral soil and lithosol are the most common soil classes. The raw mineral soil is shallower and sandier with a higher content of gravel and sand than the lithosol (Murdroch, 1970).

Site selection, sampling procedure and data collection

Three land use systems, namely; communal grazing land, commercial government ranch and game reserve located adjacent to each other were identified. Shewula land represents the communal grazing land; Nkalashane ranch and Mlawula represent the commercial government ranch and game reserve, respectively (Fig. 1). Six sites (2 ha each) were selected, one on each of the two common soil classes for each land use system. The sites were identified with the help of the geographical information system of the country (GIS) which included patches of land invaded by C. odorata and the adjacent non-invaded area. Three 100 m transects were laid out randomly along the invaded patch on each site, giving a total of 18 transects. Along each transect $3\times100~\text{m}^2$ quadrats were evenly spaced to record the density of C. odorata. All the rooted Chromolaena species were counted in each $100~\text{m}^2$ quadrat and recorded into one of the five height classes of >0-0.5; >0.5-1; >1-1.5; >1.5-2 and >2-3 m. An arbitrary decision was made to count a stem as a separate individual if it is > 50~cm from the nearest stem. The plant data were then standardized to shrub equivalent (1 SE = 1 shrub, 1.5 m high) for determining the total density per unit area of land. Shrub equivalent height was assumed to be the average height for the shrub. This method was chosen because the distribution of C. odorata was impossible to detect using remote sensing techniques (Abaye, 2003).

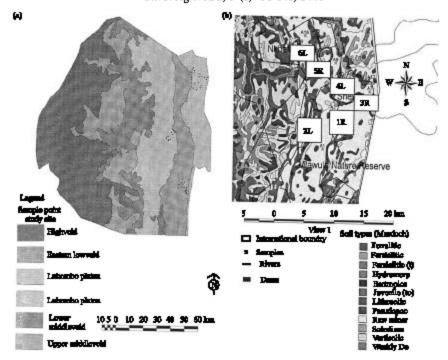


Fig. 1: Map of Swaziland (a) and location of the study sites in the lowveld of Swaziland (b) 1 and 2 Game reserve, 3 and 4: Communal grazing land, 5 and 6: Commercial government cattle ranch; L: Lithosol, r: Raw mineral soil

Dry Matter yield (DM) and botanical composition of the grass layer were determined from 7×0.25 m² quadrats laid randomly within each 100 m² quadrat invaded patches and the adjacent non-invaded areas. The quadrat samples were cut to stubble height of 2 cm and dried in the oven at 72°C for 48 h. All vegetation data were collected towards the end of the rainy season (March-April, 2006).

Soil Sampling and Analysis

Topsoil samples to a depth of 200 mm were taken from each transect at 15 random locations per transect. Each set of 15 samples was bulked, thoroughly mixed, air dried and sieved through a 2 mm mesh screen prior analysis. Soil texture of the experimental samples was determined by means of standard Bouyoucos (hydrometer) method (Day, 1965). Soil pH was measured in a 1:2.5 soil water relation extract method while the Kjeldahl method was used to determine percentage total Nitrogen (N) (Van Reeuwijk, 1992). Percentage Organic Carbon (OC) was analyzed using colorimetric method (Baker, 1976). Sodium (Na) and potassium (K) were determined by emission spectroscopy and magnesium (Mg), calcium (Ca), zinc (Zn), copper (Cu) and iron (Fe) using atomic absorption spectroscopy (Jackson, 1970). Phosphorous was detected by the ultra violet Spectrophotometer (Olsen and Sommers, 1982).

Statistical Analysis

Since quadrat data on density and height distribution of the study plant were not normally distributed, the non-parametric Whitney U-test for two independent samples was used (Kent and Coker, 1992). Soil and herbaceous data were normally distributed and analysed using the GLM of SAS software (SAS, 1987). Herbaceous data for the invaded and non-invaded area were compared using a simple t-test.

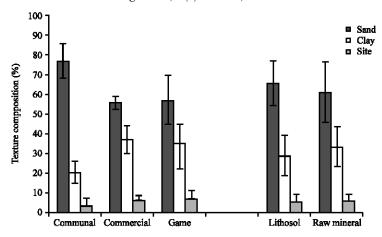


Fig. 2: Texture composition (%) of topsoil sampled from the three land use systems and two soil classes

Table 1: Soil pH, organic carbon (OC), nitrogen (N), macro (cmol_c kg⁻¹) and micro elements (Mean±SE ^h) of top soil

	Land uses			Soil classes		
Elements	Communal	Commercial	Game	Lithosol	Raw mineral	
Soil pH	5.92±0.52	5.37 ± 0.14	5.49±0.38	5.59±0.39	5.59±0.50	
Ca	0.12 ± 0.09^a	5.46±1.18 ^b	$2.08\pm0.47^{ab}***$	2.51 ± 1.20	2.60 ± 1.11	
Mg	2.66 ± 0.51	3.03 ± 0.41	2.81 ± 0.71	2.75 ± 0.60	2.91 ± 0.51	
K	0.98 ± 0.58^a	$0.41\pm0.06^{\circ}$	1.12±0.09°**	0.85 ± 0.28	0.82 ± 0.31	
Na	6.91 ± 1.80^{a}	4.34 ± 1.14^{b}	6.37±0.61 ^{ab} *	5.99±1.98	5.74 ± 0.53	
Zn (ppm)	1.38 ± 0.14	1.26 ± 0.16	1.42 ± 0.13	1.21 ± 0.11	1.47 ± 0.11	
P (mg kg ⁻¹)	1.53±0.64°	4.90 ± 2.32^{b}	2.84±1.03 ^{ab} *	2.96±1.20	3.22 ± 1.34	
OC (%)	3.06 ± 0.18	2.80 ± 0.43	2.48 ± 0.44	2.58 ± 0.27	2.98 ± 0.40	
N (%)	0.10 ± 0.02^a	0.22 ± 0.03^{b}	0.19±0.04 ^b **	0.17 ± 0.02	0.18 ± 0.03	

 1 : Standard error, Means with the different superscripts in the same row are statistically different, *: p<0.05; **: p<0.01, ***: p<0.001

RESULTS

Soil Analysis

Results on soil texture as presented in Fig. 2 revealed that the sand, silt and clay contents were not remarkably different in the three land use systems and the two soil classes. There were no significant (p>0.05) variations in the soil pH among land use systems and soil classes. Copper and Fe were below detectable level in all the study sites. Calcium was significantly (p<0.001) highest in the commercial ranch but lowest in the communal grazing land (Table 1). Potassium and Na were lower (p<0.05) in the ranch than in the game reserve and communal land.

Phosphorus was significantly lowest (p<0.05) on communal land than in the ranch, where as the game reserve did not differ (p>0.05) from both land use systems. Nitrogen was significantly lowest (p<0.01) on communal land. All soil variables did not show significant differences between lithosol and raw mineral soils in the study area as shown in Table 1.

Density and Height Distribution of Chromolaena odorata

Marked difference (p<0.05) in the total SE density of C. odorata existed between the communal land and game reserve. The difference between the two soil classes (lithosol and raw mineral soil) was not apparent and less pronounced compared to the patterns observed among the land use systems (Table 2). Most of the study sites had largest proportion of height class >1-1.5 m and lowest in height range >0-0.5 m.

Table 2: Total density of *Chromolaena odorata* (mean shrub equivalent per ha as well number of individuals per ha) under the three land use systems and the two soil classes

		Height clas	ss (m) (%)					
	Shrub density							
Land use systems	SE/ha±SE (Shrub ha ⁻¹)	>0-0.5	>0.5-1	>1-1.5	>1.5-2>	2-3		
Communal grazing land	465±197 (604) ^a	4.80	28.97	41.39	14.49	10.35		
Commercial ranch	618±243 (662)ab	9.43	18.87	28.30	26.42	16.98		
Game reserve	990±218 (1237) ^b	2.02	4.04	39.39	37.37	17.17		
Soil classes								
Lithosol	738±199 (965)	3.42	12.95	43.11	26.73	13.78		
Raw Mineral	644±174 (708)	7.06	15.25	28.25	31.78	17.66		

SE: Standard Error, Means with the different superscripts in the same column are statistically different (p<0.05)

Table 3: Density (mean number of individuals per ha) of the seedlings and shrubs of Chromolaena odorata

	Density (mean number of individuals per na±8E)			
Land use systems	Seedlings (>0-0.5) m	Shrub density (>0.5-3) m		
Communal grazing land	25±5a	0575±187°		
Commercial ranch	62±8 ^b	0600±220°		
Game reserve	25±3ª	1212±213 ^b		
Soil classes				
Lithosol	58±13	933±192		
Raw Mineral	50±8	658±161		

Means with different superscripts in the same column are statistically different (p<0.05)

There was a significantly (p<0.05) more shrubs (>0.5-3 m) in the game reserve than in the ranch and communal land (Table 3). There was a significantly (p<0.05) more seedlings (>0-0.5) in the ranch than on communal land and game reserve.

Grass Layer Productivity

A total of 26 grasses were identified, of which 23 were perennials, 6 classified as highly palatable, 12 moderately palatable and the remaining ones as less palatable. Six species each were present only under and outside the invaded areas (Table 4).

Data on grass DM yield indicated that the ranch had significantly (p<0.001) the highest production. With regard to soil class, DM production was remarkably higher (p<0.01) on lithosol than raw mineral soil (Fig. 3).

Grass DM yield within and outside invaded areas did not show marked difference on lithosol soil of the communal sites, but differed significantly (p = 0.05) on the raw mineral soil (Table 5). On the commercial government ranch, DM yield of grass within and outside the invaded areas was similar on the raw mineral soil, while there was significant (p<0.01) difference on the lithosol soil class. In the game reserve sites DM yield approached significant variations (p=0.06) within and outside the invaded areas on both soil classes (Table 5).

Dominant and common grass species were also examined for their DM production within and outside the invaded areas. The following grass species were found to be dominant/common to the study sites: *Aristida sciurus*, *Heteropogon contortus*, *P. deustum*, *P. maximum*, *U. mosabicensis* and *Melinis repens*.

In the communal land under the lithosol soil, DM yield of *U. mosabicensis* and *P. deustum* were significantly lower (p<0.05) under the invaded area than outside the invaded area. *Panicum maxiumum* was significantly lower (p<0.05) within the invaded area on both lithosol and raw mineral soil. Except for *U. mosabicensis* which showed non-significant variation under the ranch-lithosol site, these three species showed similar patterns of variation within and outside invaded areas on the raw mineral soil in the ranch and game reserve. Nevertheless, *H. contortus* and *M. repens*, which were dominant on raw mineral soil in the ranch did not show marked difference (p>0.05) within and outside the invaded areas. Similarly, *A. sciurus* was dominant on lithosol of the game reserve but did not show significant difference within and outside the infested areas (Table 6).

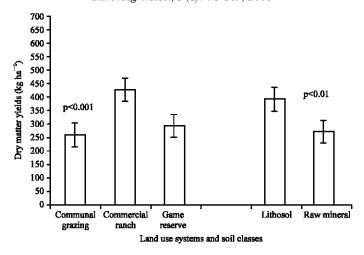


Fig. 3: Dry matter yield of grasses in three land use systems and two soil classes

Table 4: Life forms and ecological grouping of grass species identified in the study sites

			Status	
Species name	Life forms ¹ (palatability)	Ecological groups ²	Invaded	Non-invaded
Aristida bipartita	A(LP)	Inc IIc		
Aristida sciurus	P(LP)	Inc IIc		
Bothrichloa insculpta	P(MP)	Inc IIa		
Bothriochloa radicans	P(LP)	Inc IIb	X	
Brachiaria nigropedata	P(HP)	De	X	
Cenchrus ciliaris	P(HP)	De		X
Chloris virgata	P(MP)	Inc IIc		
Dactyloctenium aegypticum	A(MP)	Inc IIb		
Digitaria eriantha	P(HP)	De		
Digitaria longiflora	P(MP)	Inc IIb		
Digitaria sp. (1)	P(MP)	-		
Diplanche eleusine	P(MP)	Inc IIa	X	
Enneapogon cenchroides	P (LP)	Inc IIc		X
Eragrostis lehmanniana	P(MP)	Inc IIa	X	
Eragrostis superba	P(LP)	Inc IIb	X	
Eustachys paspaloides	P (HP)	de		
Heteropogon contortus	P(MP)	Inc IIa		
Hyparrhenia cymbaria	P(MP)	De	X	
Melinis repens	P(LP)	Inc IIb	X	
Panicum deustum	P(HP)	de		
Рапісит тахітит	P(HP)	de		
Panicum natalense	P(LP)	de		
Setaria sagittifolia	A(MP)	Іпс Пс		X
Sporobulus africanus	P(LP)	Inc IIb		X
Und. (SN64)	P(MP)	-		X
Urochloa mosabicensis	P (MP)	Inc Iia		

 Urochloa mosabicensis
 P (MP)
 Inc Iia

 1: LP = Less
 palatable;
 MP = Moderately
 palatable;
 HP = Highly
 palatable;
 A = annual;
 P = Perennial;
 2: Inc II a = Increaser IIa; Inc IIb = Increaser IIb; Inc IIc = Increaser IIc (Foran, 1976; Tainton et al., 1980; Vorster, 1982)

Table 5: Grass dry matter yield (kg ha⁻¹±SE) under and outside invaded areas by *Chromolaena odorata*

yield (Kg Ha +BL) dilde	and outside invaded area	s by Chromotacha oachaa	
Soil class	Under invaded area	Outside invaded areas	p-value
Lithosol	198.80±32.10	269.20±32.10	0.20
Raw mineral soil	178.13±29.34	381.73±29.34	0.05
Lithosol	441.76±32.14	715.20±32.14	0.02
Raw mineral soil	310.27 ± 29.00	289.80±29.00	0.40
Lithosol	251.94±31.10	472.36±32.10	0.06
Raw mineral soil	151.24±29.34	325.04±29.34	0.03
	Soil class Lithosol Raw mineral soil Lithosol Raw mineral soil Lithosol	Soil class Under invaded area Lithosol 198.80±32.10 Raw mineral soil 178.13±29.34 Lithosol 441.76±32.14 Raw mineral soil 310.27±29.00 Lithosol 251.94±31.10	Lithosol 198.80±32.10 269.20±32.10 Raw mineral soil 178.13±29.34 381.73±29.34 Lithosol 441.76±32.14 715.20±32.14 Raw mineral soil 310.27±29.00 289.80±29.00 Lithosol 251.94±31.10 472.36±32.10

Significant at p = 0.06

Table 6: Dry matter yield (kg ha⁻¹±SE) of most common grasses under and outside invaded areas by

<u>Chomolaena od</u>	lorata				
	Communal grazing	land			
	Soil classes				
	Lithosol		Raw mineral soil		
Species	Invaded area	Outside invaded area	Invaded area	Outside invaded area	
Urochloa mosambicensis Panicum maximum Panicum deustum	33.10±11.1 ^a 9.20±2.00 ^a 4.60±2.52 ^a Commercial ranch	157.13±52.31 ^b *** 068.73±23.39 ^b *** 012.47±1.65 ^b ***	55.04±20.33°	101.36±27.08°***	
	Soil classes				
	Lithosol		Raw mineral soil		
Species	Invaded area	Outside invaded area	Invaded area	Outside invaded area	
Urochloa mosambicensis Panicum maximum	120.7±32.99 ^a 211.04±46.64 ^a	225.73±38.96 ^b ** 422.96±41.54 ^b **			
Panicum deustum			025.2±13.00	059.60±17.66	
Heteropogon contortus			97.47±36.31	170.27±44.00 024.80±04.10	
Melinis repens	Game reserve		22.07±11.33	024.80±04.10	
	Soil classes				
	Lithosol		Raw mineral s		
Species	Invaded area	Outside invaded area	Invaded area	Outside invaded area	
Urochloa mosambicensis	30.32±3.49 ^a	59.04±11.32 ^b *			
Aristida sciurus	44.08±12.95°	30.96±14.35 ^b *			
Panicum maximum	18.32±4.48°	92.24±29.00 ^b **			
Panicum deustum			19.52±5.22a	38±7.80°*	

Means with the different superscripts in the same raw are statistically different at p<0.05(*) and at p<0.01 (**)

DISCUSSION

Information on soil texture and pH of the raw mineral soil has been unavailable from the previous report in the lowveld areas (Murdoch, 1970; Sutcliffe, 1975). Results of the soil texture on lithosol in the current study indicated that the sand and silt content were 65 and 6% disagreed with the previous report of 53 and 17%, respectively (Sutcliffe, 1975). The findings also suggested that the soil in the two classes fall under sandy-clay-loam texture. Soil elements analysis indicated that most exchangeable cation levels are distinguishable and not consistent among the three land use systems and the reasons are not clear. With the exception of Ca, whose level was very low, soil levels of all macro elements across the study areas were fairly above critical values for plant growth (Mtimuni, 1982; Katyal and Randhawa, 1983; McDowell, 1985). The level of phosphorous reported in this study was within the optimum plant requirement (Lemma et al., 2002) for semi-arid rangelands. However, previous analysis (Sutcliffe, 1975) indicated that the amount of phosphorous in the study areas was far lower than the present, while OC and N were reported to be similar. Among the soil properties total OC is a sensitive soil quality indicator suggesting that within a narrow range of soil, it may serve as a suitable indicator of soil fertility (Murage et al., 2000). Furthermore, soil OC fraction offers further insight into soil fertility changes and the sustainability of land use and management (Barrios et al., 1996; Du Preez and Snyman, 2003). Total N analysis indicated the significantly lowest content on communal land, but overall values suggest that the area was remarkably deficient in N. There are evidences that deficiency of N in rangelands can severely limit the productivity of the grass layer (Barnes and Smart, 1991; Solomon et al., 2007).

As previously discussed, the game reserve had a significantly greater density of C. odorata than the other land use systems. This might be due to past management and stocking rate differences of the area. The game reserve represents an area with a history of more severe grazing pressure than the other land uses. Prior to establishment (before 1986), the reserve area was divided into four cattle ranches on freehold land and intensively used with an average stocking rate of 4.4 ha/LSU, which was well above that of the other land uses and the recommended stocking rate of 6-8 ha/LSU (FAO, 1994; SNTC, 1996) . The later shift to the present land use was associated with the depletion of the herbaceous resources and the progress of bush/shrub encroachment that lowered the grazing capacity below the economic optimum number of cattle over long term utilization. Mlawula reserve has been sparsely populated in recent times. The current finding agreed with Abaye (2003) that, land use system has detrimental effect on the abundance of Chromolaena in the Kwazul-Natal province of South Africa and further pointed out that conservation and forest areas were most affected compared to the communal grazing land. However, Smet and Ward (2005) had a contrary report in Kimberly thorn bushveld of South Africa that shrub densities were the highest in the communal grazing lands, while game reserves had the lowest. Annika (2000) reported that significant differences in shrub densities were absent between the communal land and private rangelands in the North-east District of Botswana.

In the current study the density of C. odorata was rated moderate (<250-550 ha⁻¹) on communal grazing land, high (>550-850/ha) in the ranch and very high (>850 ha) in the game reserve. The invasion of this alien plant was also visually observed at various levels in a number of grazing sites outside the study areas. The increase in shrub density of alien plants which can be termed as bush/shrub invasion has been contentious just as other woody plants in rangeland ecology and management. Different researchers suggested that the main causes of shrub invasion are grazing (Solomon, 2003); fire (Van Auken, 2000), rainfall (Kraaij, 2002) and the nature of soil (Wiegand et al., 2006). These factors influence the structure and function of the arid and semi-arid savannas of southern Africa. Grazing and fire act partly by influencing the availability of and competition for water and nutrients. According to Abaye (2003), the low disturbance of grazing land due to light stocking rate contributed to the low level of Chromolaena abundance on communal land in KwaZulu-Natal Province of South Africa. Joshi (2001) reported that any increase in disturbance of an ecosystem leads to increased probability of alien plants invasion. The degradation of natural grasslands in terms of loss of herbaceous cover due to overstocking provides conducive environment for alien species to establish and become invasive. Several alien invasive plants identified in Southern Africa are colonizing at the rate of species that benefit from reduced competition that follows habitat degradation (Abaye, 2003).

Although all the study sites were dominated by shrubs (>0.5-3 m), the patterns of height class distribution were different. The height class represents the age of a plant, while its pattern of distribution explains the different stages of invasion. Therefore, control of C. odorata invasion may require a thorough understanding of different growth stages and life cycle of the plant. Germination of C. odorata seed occurs from the seedbank and may be favored by episodic heavy rainfall or fire. Survival of seedlings is influenced by moisture stress, competition from trees/shrubs and grasses and trampling by animals. The effective stage at which C. odorata can be controlled is at seedling establishment. In later reproductive stage the likelihood of control becomes difficult since the plant has already produced seeds which will remain as seed bank in the soil for the next generation.

Three states of vegetation (Fig. 4) leading from savannas to shrub climax (invasion climax) may illustrate the state and transition model of shrub encroachment in the semi-arid savannas of Africa. As illustrated in the figure, a change from savanna state to early invasion and shrub establishment state may be reversed with minimum control inputs. Nevertheless, further advancement in the invasion will eventually lead to shrub/bush climax, which at this state will be unlikely to reverse without huge investment in range rehabilitation projects. In developing countries, control of *C. odorata* at the climax stage can be further constrained by limited financial resources.

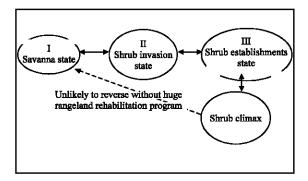


Fig. 4: State-and-transition model showing invasion of Chromolaena odorata

The commercial government ranch had higher total DM grass production than the other land uses. Some years ago, the ranch was closed down and grazing was excluded because of the invasion of *C. odorata* in some grazing camps. In a study conducted in the high veld of Swaziland, Tsabedze and Solomon (2006) observed that, game reserve had the highest DM grass production. The significantly lower DM production of grass on the raw mineral than lithosol soil was expected because the former is characterized by outcrops with discontinuous soil cover and occasionally buried soil sandwiched between stone mantle and consolidated rock which might not favor abundant grass production.

In this study significant difference in the total and individual grass DM production were noted under and outside the invaded areas. Similarly, lower productivity of herbaceous layer under the shrubs/trees as opposed to the nearby open grasslands was reported elsewhere (Grünow *et al.*, 1980; Dye and Spear, 1982; Walker and Noy-Meir, 1982). In another instance, grassland productivity was found to be higher under canopies than in the adjacent open grasslands (Smit and Swart, 1994; Jiménez-Labato and Vaverde, 2006). The present study indicated that the differences in biomass of grass species increased dramatically at higher shrub densities with the corresponding increase in the amount of bare ground litter cover beneath the shrub. Increased grassland productivity under the invaded area may be associated with low-shrub density and decreased productivity -with high shrub density. The decline of grassland productivity under the invaded areas suggest that the invasion by such shrubs competes for soil moisture and nutrients which presumably alters the microclimate features of the herbaceous layer (Hobbs and Mooney, 1985)

Walter (1971) postulated savannas as a two layer soil water system in which grasses are superior competitors for water and nutrients on top soil with woody plants having exclusive access to a lower (subsoil) water supply. According to Walker and Noy-Meir (1982) model, the zero isocline for woody plants is always below that of grasses. The current study and the finding of Wiegand *et al.* (2006) support neither of these models because relatively even distribution and high densities of *C. odorata* roots were observed on the top soil where most of the herbaceous plant root existed suggesting that some woody/semi-woody plants can be equally or more competent than grasses for water on the top soil.

CONCLUSION

It is concluded from this study that the invasion of *C. odorata* ranges from moderate to high and that history of land use systems may be the major determining factor for invasion. All the study sites were dominated by shrubs and at advanced stage, control of the invasion may require a huge investment in the form of range rehabilitation projects. The effect of *C. odorata* on grass composition and production was severe and could threaten livestock and game industries. In most cases, dry matter

production within the invaded areas was significantly lowest and dominant palatable species such as *U. mosabicensis*, *P. maximum* and *P. deustum* were most affected. Adaptive control strategies are therefore recommended while further work will be required to identify the causes of difference between land uses, to determine soil characteristics and the overall productivity potential as affected by *C. odorata* invasion as well as its interaction effects.

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