
Short-term responses of rehabilitating coastal dune forest ground vegetation to livestock grazing

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Abstract

We investigated the responses of the ground vegetation in a 17-year-old coastal dune forest plant community to four levels of experimentally applied livestock grazing (three grazing levels and one ungrazed control) from May 1994 to March 1996. The effects of grazing were apparently subordinate to site-specific intrinsic vegetation change and there were some indications that rainfall interacted with grazing level. Grazing had some apparent but no significant effects on plant species composition, significantly affected plant species richness over time, and significantly increased the range of species richness and vegetation cover values as well as the relative abundance and numbers of plant species with erect growth forms. Vegetation cover changed significantly over time, independently of grazing. Our results point to two important, easily measured mechanisms for the conservation management of coastal dune forests – the interaction of disturbance type with plant growth form and the increase of variation in community structural variables under disturbance. These mechanisms, although they potentially have wide application and predictive power, have not been studied adequately.

Key words: disturbance, growth form, species richness, variability

Résumé

Nous avons étudié les réponses de la végétation terrestre d'une plantation forestière de 17 ans sur une dune côtière à quatre niveaux expérimentaux de pâturage par du bétail (trois niveaux de pâturage et un contrôle non pâturé) entre mai 1994 et mars 1996. Les effets du pâtu-

rage dépendaient apparemment des changements de végétation intrinsèques spécifiques des sites, et certains indices laissent penser qu'il y a des interactions entre les chutes de pluies et le taux de pâturage. Le pâturage qui avait certains effets apparents, mais non significatifs sur la composition spécifique des plantes, affectait significativement la richesse en espèces avec le temps, et augmentait significativement l'étendue de la richesse en espèces végétales et la couverture végétale ainsi que l'abondance relative et le nombre d'espèces végétales de forme érigée. Le couvert végétal changeait significativement au cours du temps, quel que soit le pâturage. Nos résultats indiquent deux mécanismes importants, faciles à mesurer, pour la gestion conservatoire des forêts de dunes côtières – l'interaction du type de perturbation avec la forme de la croissance des plantes, et l'accroissement de la variation des variables structurelles de la communauté végétale en cas de perturbation. Ces mécanismes, même s'ils peuvent avoir une large application et une valeur prédictive, n'ont pas encore été convenablement étudiés.

Introduction

Two main factors are relevant to grazing in African coastal dune forests. The first of these is that large herbivores can influence the organization of almost every plant community at many different scales and on all hierarchical levels (Glenn-Lewin & van der Maarel, 1992; van de Koppel, Rietkerk & Weissing, 1997). Although coastal dune forests are generally regarded as a resilient habitat type with a fairly predictable development from grassland to mature dune forest (Weisser, 1978; Weisser & Muller, 1983), current insights into community development stress the existence of multiple possible stable states (Sutherland, 1990; see also von Maltitz, van Wyk & Everard, 1990).

Secondly, few vertebrate herbivores inhabit the coastal dune forests of the southeast coast of Africa (Skinner & Smithers, 1990). Of the 26 mammal species listed by

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Ferreira (1993) for the coastal dune forests north of Richards Bay, KwaZulu-Natal, South Africa, only three herbivores (the bushpig *Potamochoerus porcus* [Linnaeus 1758], the red duiker *Cephalophus natalensis* [Smith 1834] and the bushbuck *Tragelaphus scriptus* [Pallas 1766]) are large enough to cause significant disturbance to vegetation. Both red duiker and bushbuck occur in relatively low numbers and are highly selective in their feeding habits, while the distribution of the bushpig is typically patchy and they are not common anywhere (Skinner & Smithers, 1990). Livestock grazing, which is therefore likely to be an 'unnatural' type of disturbance for coastal dune forests, could thus have far-reaching implications, not only for the conservation of coastal dune forests, but also for their post-disturbance development.

The mining company Richards Bay Minerals (RBM) has been mining and subsequently rehabilitating a strip of coastal sand dunes on the northeast coast of South Africa since July 1977 (Camp, 1990; van Aarde *et al.*, 1996). The mining lease and rehabilitating areas are situated in a regional development node with large influxes of people (23% increase from 1980 to 1991) and their associated domestic livestock. This has led to illegitimate grazing of regenerating forests, and concerns over its possible effect on the rehabilitation programme.

We expected livestock grazing to significantly affect the restoration of coastal dune forest in the short term through its effect on ground vegetation community structure. The present study therefore examines the short-term effects of cattle on ground vegetation (i) species richness and vegetation cover (ii) species composition, and (iii) numbers and abundances of species in two plant growth form groups in a 17-year-old rehabilitating coastal dune forest.

Materials and methods

Study area

The study was conducted in the oldest regenerating part of an area of mined dunes north of Richards Bay, KwaZulu-Natal, South Africa (28°43'S and 32°12'E), which has been under ecological rehabilitation since 1977 (Stand I in Ferreira & van Aarde, 1996). The area is characterized by longitudinal sand dunes, lying parallel to the coastline, and rising to an elevation of 40–90 m above sea level. Soils (fine to medium-grained aeolian sands)

are uniform throughout the area, with little horizontal differentiation (Avis, 1992). Most rain falls from January to March (peak in February; annual mean 1292 mm). Extended droughts are uncommon and approximately 30% of annual precipitation occurs in the winter. Daily maximum temperatures range from 22.6 °C to 30.0 °C and minimum temperatures from 10.0 °C to 20.6 °C in June and January, respectively (Ferreira, 1996).

The regenerating forest consists of an *Acacia karroo* (Hayne) woodland 9–12 m high, with secondary dune forest tree species colonizing. Compared to a mature forest there is relatively little vertical stratification. The herb layer (\approx 1 m or less) is dominated by a number of stoloniferous grasses, creepers and decumbent herbs. Van Aarde *et al.* (1996) provide a detailed description of the study area and vegetation.

Experimental design and data recording

Grazing was applied to 0.125 ha fenced paddocks, arranged in four blocks with a Control, Low, Medium and High grazing level in each (i.e. four replicates per grazing level). Blocks were randomly placed within the study site and grazing levels randomly assigned to paddocks within each block. In this instance the term 'grazing' includes all other forms of disturbance by cattle to the vegetation, i.e. trampling, defecating, etc. Five grazing cycles were applied over 16 months (Fig. 1), the period between grazing cycles varying from 90 to 150 days. A grazing cycle consisted of 2 days' grazing in the low grazing level paddocks, 4 days in the medium level paddocks and 8 days in the high level paddocks. For each grazing cycle, eight heifers (200–300 kg) were sorted into four pairs (so that mean pair-weight \approx mean group-weight) and each pair randomly assigned to one of the four replicates in a grazing level every day.

Species presence and vegetation cover were recorded at six 1 m² quadrats per paddock prior to each grazing cycle. Vegetation cover was recorded with a point-bridge adapted from Barbour, Burk & Pitts, (1987). Plant species were assigned to one of two categories: (i) decumbent (all species, excluding lianas, with mostly horizontal vegetative growth, i.e. creepers and stoloniferous grasses), and (ii) erect (large and small annual and perennial forbs, tussock grasses, juvenile trees and shrubs). Rainfall was measured using standard rain gauges at two points situated halfway between the four blocks of grazing paddocks.

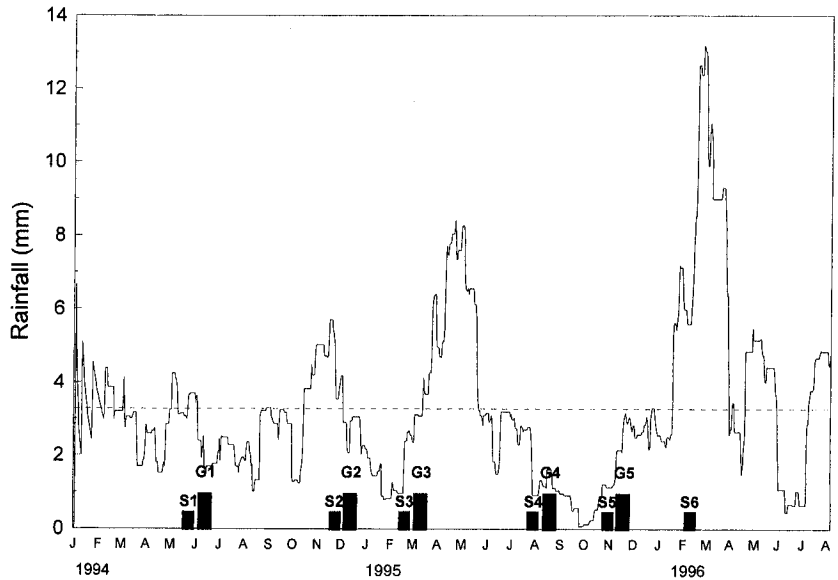


Fig 1 Mean ($n = 3$) daily rainfall in the rehabilitating area from January 1994 to August 1996 and schedule of plant surveys and grazing cycles. The dotted line represents the mean daily rainfall over a 10-year period, including the period of our study. S1–S6 represent plant surveys and G1–G5 grazing applications

The data were used to calculate species density (SD or species/m²), vegetation cover below 10 cm (VC), relative abundance of growth form (Erect/Decumbent[Ab]) and number of species per growth form (Erect/Decumbent[Sp]), as well as species composition. For species composition analysis we defined three Bray–Curtis similarity classes (Ludwig & Reynolds, 1988): (i) temporal similarity (Tsim): similarity of a paddock to itself over time; (ii) close spatial similarity (CSsim): similarity between paddocks in the same block, but from different grazing levels; and (iii) far spatial similarity (FSsim): similarity between paddocks in the same grazing level, but from different blocks.

To determine whether the microhabitats at the quadrats were similar, we recorded the structure of the canopy vegetation surrounding each quadrat (name, height, stem diameter and number of stems of closest species of canopy tree in each of four quarters surrounding the quadrat), percentage canopy cover at each quadrat (measured on a colour negative of the underside of the canopy with a Quantimet 520 image analyser; Cambridge Instruments, London), and the light intensity (lux) on the forest floor (Measuring Instruments Technologies, Pretoria).

Statistical analysis

We tested for differences in microhabitat between paddocks with analysis of variance (ANOVA) and the

Kruskal–Wallis test where applicable, for the overall effect of cattle on VC (arcsine transformed) and SD with multivariate analysis of variance for repeated measures (MANOVA; Potvin, Lechowicz & Tardif, 1990), and for comparisons between grazing levels we used Tukey's honestly significant difference test (T-HSD; Sokal & Rohlf, 1995). We used least squares linear regression (LSLR) to test for the effect of cattle on the range in VC and SD values as well as on all growth form variables and similarity changes over time (independent variable: days since start of first survey). A significant difference between the slopes of control and any of the other grazing levels indicated a grazing effect, and a slope significantly different from zero for any of the grazing levels indicated a time effect. Analysis of similarity (ANOSIM; Clarke, 1993) was used to test for differences in species composition between grazing levels, paddocks and sequential surveys.

Results

Microhabitat

There were no significant differences between grazing levels in canopy tree structure and density (Kruskal–Wallis: all H -values ≤ 3.22 , all P -values > 0.05), incandescent light (overall mean \pm SE = 21.40 ± 1.43 lux; ANOVA: $F = 1.31$, $P = 0.20$) and percentage canopy cover (overall mean \pm SE = $84.9 \pm 0.78\%$; ANOVA: $F = 1.18$, $P = 0.36$). Only one species of canopy tree was recorded, namely

A. karroo. We therefore assumed that differences in microclimatic conditions at each quadrat were small enough for the herb layer vegetation not to have been affected by it. Furthermore, although precipitation was not measured at all survey points, we assumed that paddocks were close enough to each other not to have been influenced by spatial variation in rainfall patterns. Rainfall followed a seasonal pattern during the study period, although daily rainfall was below the 10-year average for a considerable period before the third survey (Fig. 1). It increased somewhat after the second survey and at the time of the fourth survey increased above the 10-year average.

Plant species density (SD)

Mean SD decreased over time in Control, while it stayed at the same level in Low, Medium and High (Fig. 2). The

time–grazing level interaction (linear) and time effect (quadratic) were significant (MANOVA; overall time × level: Roy's GR = 0.34, $F = 6.20$, $P < 0.001$, overall time: Roy's GR = 1.94, $F = 34.20$, $P < 0.001$; linear (time × level): $F = 4.26$, $P = 0.01$; quadratic (time): $F = 10.48$, $P = 0.002$). Control differed from Low and High over all surveys (T-HSD, $msd_{(0.05,20)} = 1.87$). During survey 2 Control and High differed significantly ($msd_{(0.05,12)} = 1.803$), during survey 4 Control differed from both Low and High ($msd_{(0.05,12)} = 2.35$), during survey 5 ($msd_{(0.05,12)} = 2.37$) and survey 6 ($msd_{(0.05,12)} = 1.97$) Control differed from Low, Medium and High.

Increased grazing level apparently increased the range of SD values at each survey over time; in contrast the range decreased in Control (Fig. 3). The slope of the relationship between time and range of values at each survey was significant for Control (ISLR;

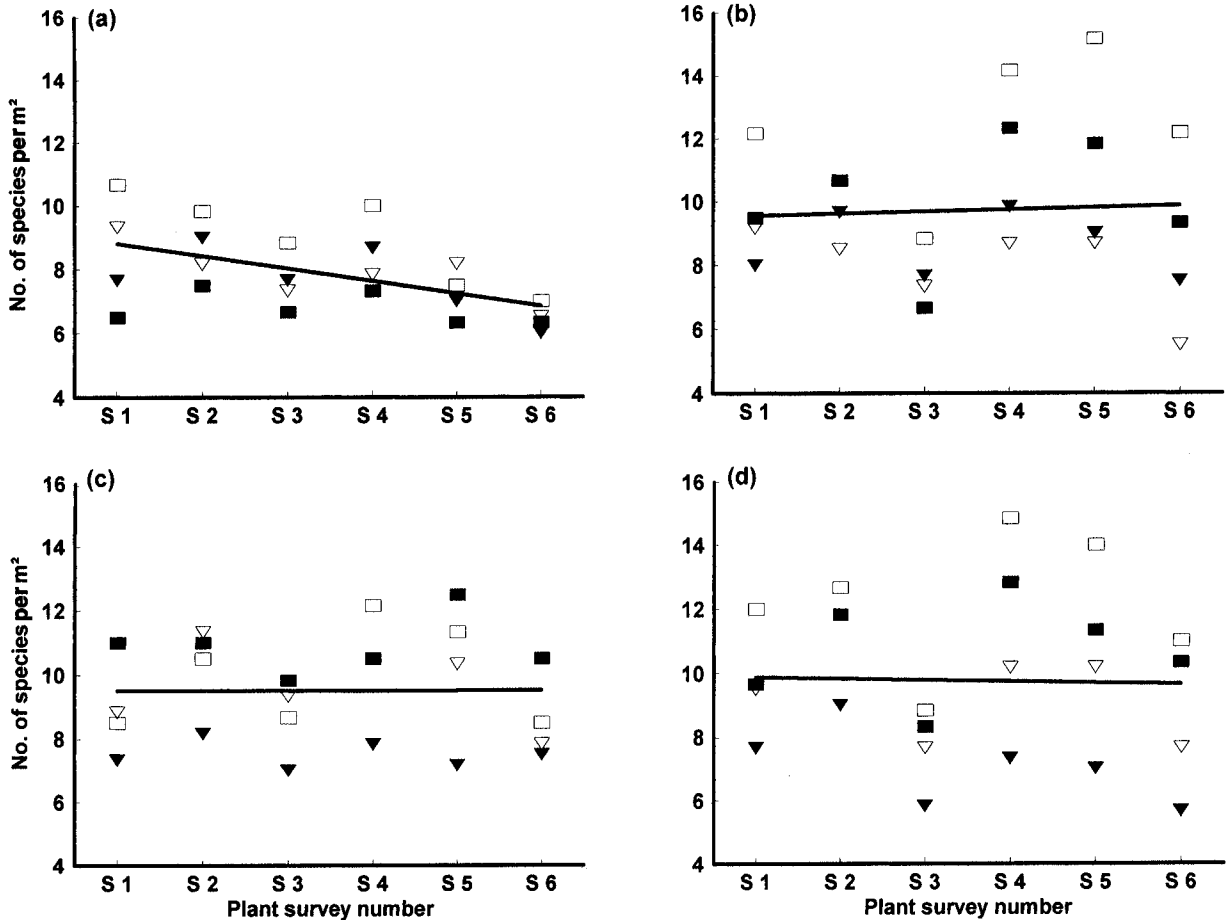


Fig 2 The number of species per 1 m² quadrat (species density or SD – see text) over 6 plant surveys in (a) Control (b) Low (c) Medium and (d) High. Symbols represent different paddocks. Lines were fitted with least squares linear regression on the mean values per survey

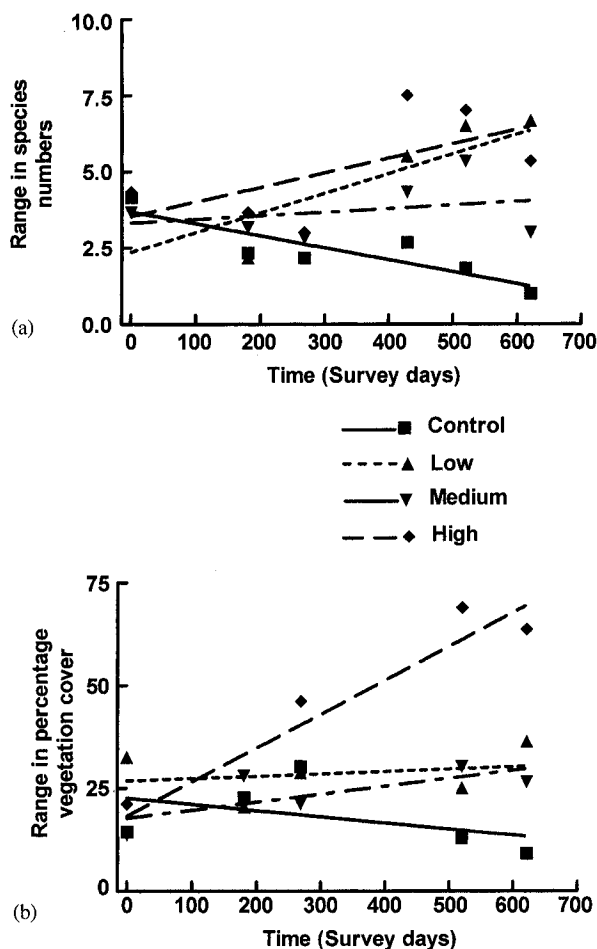


Fig 3 The relationship between time (days since start of first plant survey) and range in values (difference between minimum and maximum for each survey) of (a) SD and (b) VC. Least squares linear regression models are described in the text

$y = 3.70 - 0.004x$, $P = 0.03$, $r^2 = 0.74$), but not for Low to High (slopes from 0.001 to 0.006, all $P > 0.05$; r^2 from 0.08 to 0.53). Slopes were significantly different overall ($F = 3.47$; $P = 0.04$), with Control differing from Low.

Vegetation cover (VC)

Mean VC apparently increased over time in Control, but decreased slightly in High (Fig. 4). There was a significant quadratic time effect, but no significant time–grazing level interaction or grazing effect (MANOVA; overall time:

Roy's GR = 3.96, $F = 8.91$, $P = 0.003$, quadratic (time): $F = 26.81$, $P < 0.001$). The range of values per survey increased with grazing level (Fig. 3), but none of the slopes differed significantly from zero (slopes from -0.004 to 0.06 , all $P > 0.05$, r^2 from 0.006 to 0.30) or from each other ($F = 0.44$; $P > 0.05$).

Growth form

Decumbent[Ab] values for Control remained higher than Low, Medium and High throughout and apparently increased more over time (Fig. 5a). Slopes were not significantly different ($F = 1.07$, $P = 0.39$). In contrast Erect[Ab] values for Control remained lower than the other grazing levels throughout (Fig. 5b), the slope for Control differing significantly from High (Control: $y = 15.69 - 0.008x$; $P = 0.15$, $r^2 = 0.44$; High: $y = 23.84 + 0.009x$; $P = 0.06$, $r^2 = 0.63$; $F = 3.90$, $P = 0.03$). The slope of the relationship between time and Erect[Sp] was significant only for Low and High (Low: $y = 18.53 + 0.009x$; $P = 0.04$, $r^2 = 0.70$; High: $y = 15.29 + 0.01x$; $P = 0.04$, $r^2 = 0.70$). Both Erect and Decumbent species were apparently lost faster from Control (Fig. 5c,d). Differences were more pronounced in Erect plants however (Fig. 5d), where the slope for Control differed significantly from High ($F = 5.39$, $P = 0.009$).

Similarity/species composition

Species composition of Control paddocks apparently changed faster over time (similarity to initial species composition, or Tsim, declined faster; Fig. 6a) and stayed more similar to each other than the other grazing levels (mean similarity within grazing level, or FSsim, was higher; Fig. 6b). For Tsim, slopes were significant in Control ($y = 94.06 - 3.57x$, $P = 0.05$; $r^2 = 0.79$, $P = 0.05$) and Low ($y = 86.66 - 1.51x$, $P = 0.01$; $r^2 = 0.93$, $P = 0.01$), but there were no overall significant differences between the slopes ($F = 1.22$, $P = 0.35$). Slopes for FSsim (Fig. 6b) were not significantly different from zero or from each other (range = -1.56 to -0.11 , all P -values > 0.05 ; all r^2 -values ≤ 0.40 ; $F = 0.35$, $P = 0.79$). Similarity within blocks (CSSim) (Fig. 6c) in two of the blocks decreased significantly over time (Block 2: $y = 66.45 - 0.01x$, $P = 0.009$, $r^2 = 0.18$; Block 4: $y = 71.16 - 0.02x$, $P = 0.007$, $r^2 = 0.20$), but the slopes for the different blocks did not differ significantly ($F = 1.26$, $P = 0.29$). Mean Tsim (over all grazing levels) stayed higher than both mean CSSim

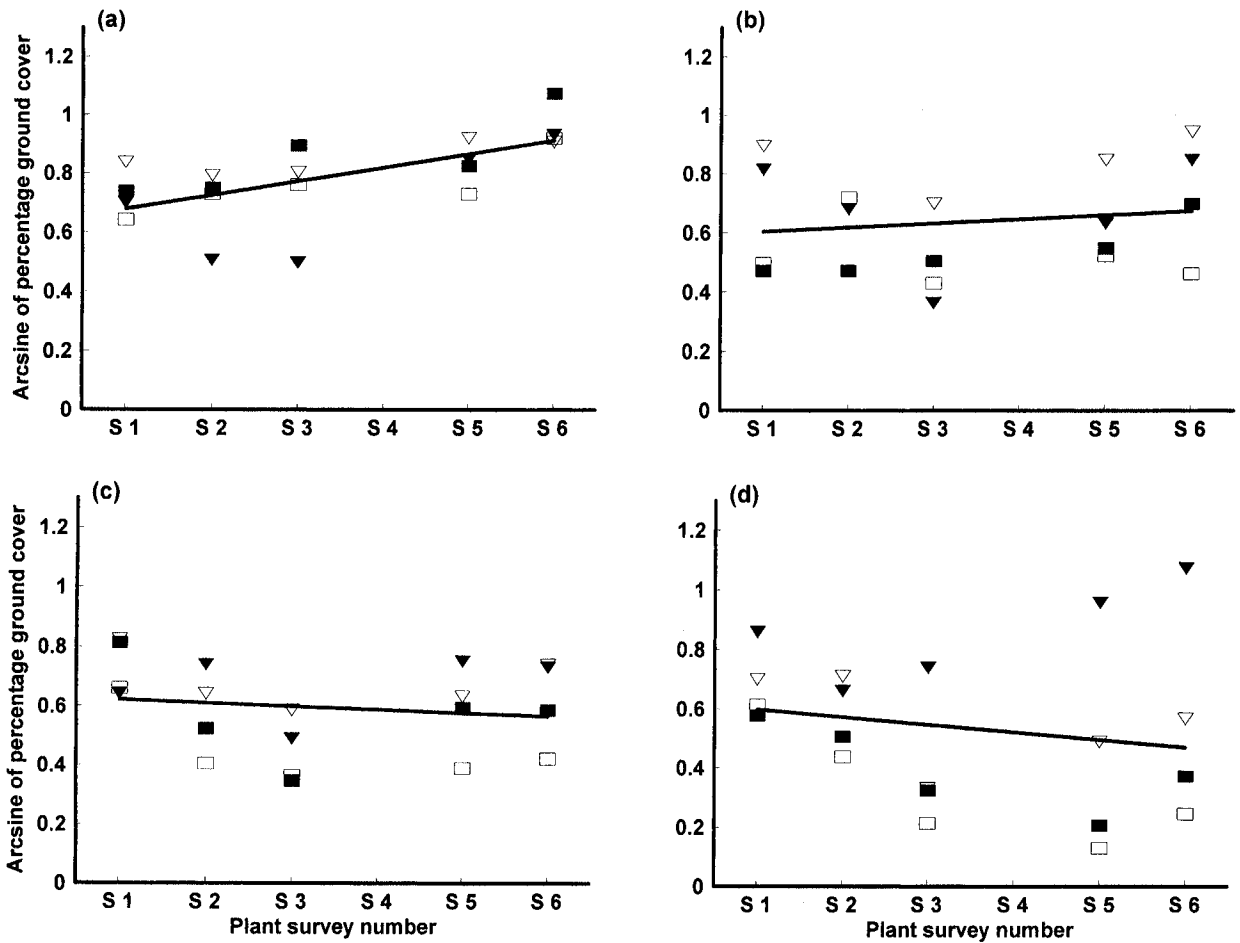


Fig 4 The percentage ground cover (VC – see text) (arcsine transformed) over 5 plant surveys in (a) Control (b) Low (c) Medium and (d) High. Symbols represent different paddocks. Lines were fitted with least squares linear regression on the mean values per survey

and mean FSsim, and CSsim stayed higher than FSsim throughout the study period (Fig. 6d).

There were no significant differences between either the grazing levels or the different surveys in species composition (two-way crossed ANOSIM; $R = -0.004$, $P = 0.52$ and $R = -0.09$, $P = 0.98$, respectively). There were also no significant differences between the grazing levels within any of the surveys (one-way ANOSIM; global R -values range -0.11 to 0.11 , all P -values > 0.05). Blocks of paddocks on the other hand differed significantly over all (global $R \geq 0.45$, $P \leq 0.001$ in all surveys). In these comparisons the pair of blocks situated closer to each other were never significantly different ($R \leq 0.46$, $P > 0.05$ in all cases), while the other blocks, situated further away from each other, were always different ($R \geq 0.43$, $P < 0.05$ in all cases).

Discussion

Site and climate

Our study was conducted over a relatively short time-scale, with an emphasis on the effects of grazing on ground vegetation community variables. Results suggest that grazing had some effects on plant community structure, although these were not always significant and appeared to be subordinate to both intrinsic vegetation change (i.e. site effects) and rainfall effects. Site effects can clearly be seen in the significant differences in species composition between the blocks of paddocks at all times, while at the same time none of the grazing levels differed. Furthermore, if grazing had an effect over and above site and environment, there would have been a change in

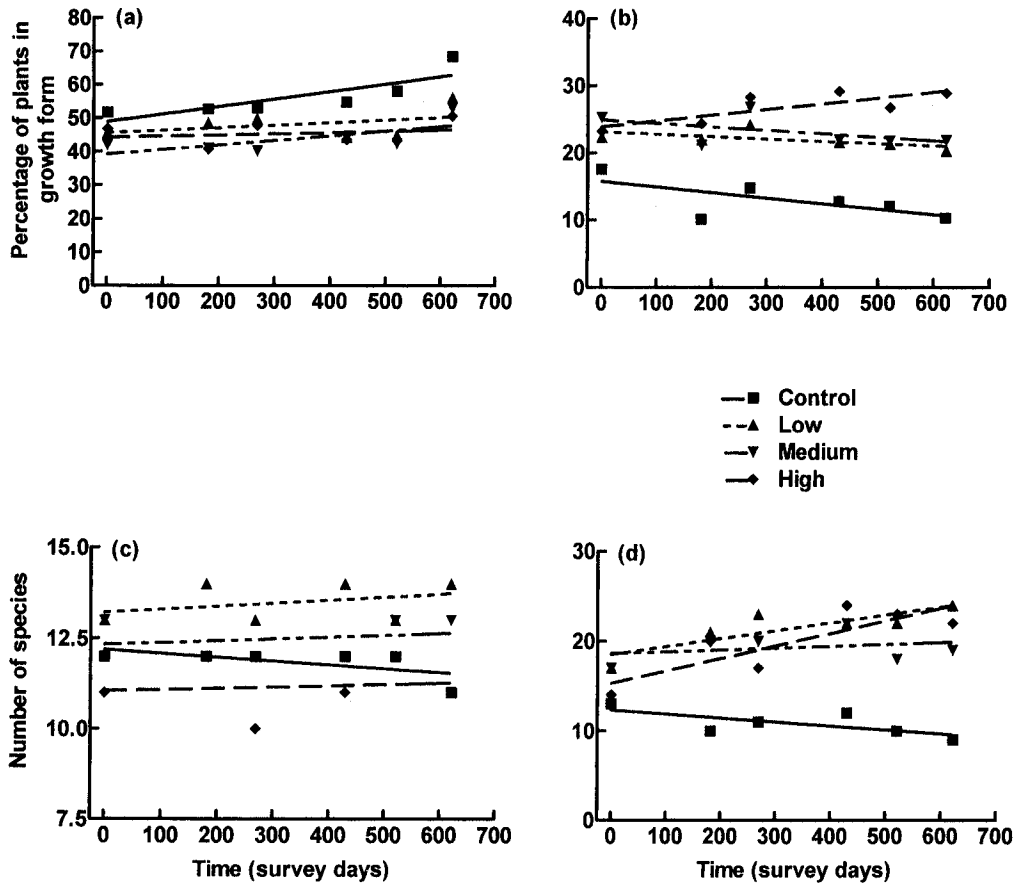


Fig 5 The relationship between time (days since start of first plant survey) and (a) relative abundance of decumbent plants, (b) relative abundances of erect plants, (c) number of decumbent species, and (d) number of erect species; in four grazing levels. Least squares linear regression models are described in the text

the site-dependent theoretical ranking of temporal (Tsim; highest) – close spatial (CSSim) – and far spatial (FSSim) similarity over time, and/or a difference between control and treatment in this pattern. This did not happen, nor did paddocks within the same grazing level and paddocks within the same block become more (i.e. increased FSSim) and less (i.e. decreased CSSim) similar to each other, respectively, as expected. Also, although CSSim did decrease in two of the blocks, FSSim, contrary to expectation, actually decreased. Grazing could therefore not overcome the high Tsim and CSSim, or the low FSSim, which suggests that the ground vegetation community of these coastal dunes is relatively resistant to grazing disturbance in the short term.

Rainfall effect was not specifically investigated, but the drop in almost all variables and grazing levels during survey 3 followed on and was probably the result of a

relatively dry preceding period (Fig. 1). Furthermore, there were some indications of a possible interaction between grazing level and rainfall effect, because the magnitude of the drop in both SD and VC during survey 3 (Figs. 2 and 4) was apparently dependent on the level of grazing. It is well known that rainfall (and climate in general) can have a strong influence on plant community variables, overshadowing other abiotic and biotic disturbances (e.g. Walker & Knoop, 1987; O'Connor, 1991; Peel, Grossman & van Rooyen, 1991).

Grazing

In contrast to our study, earlier studies noted decreases in vegetation cover under grazing (e.g. Belsky & Blumenthal, 1997, cites several examples in western US forests). Presumably our result was due to a combination

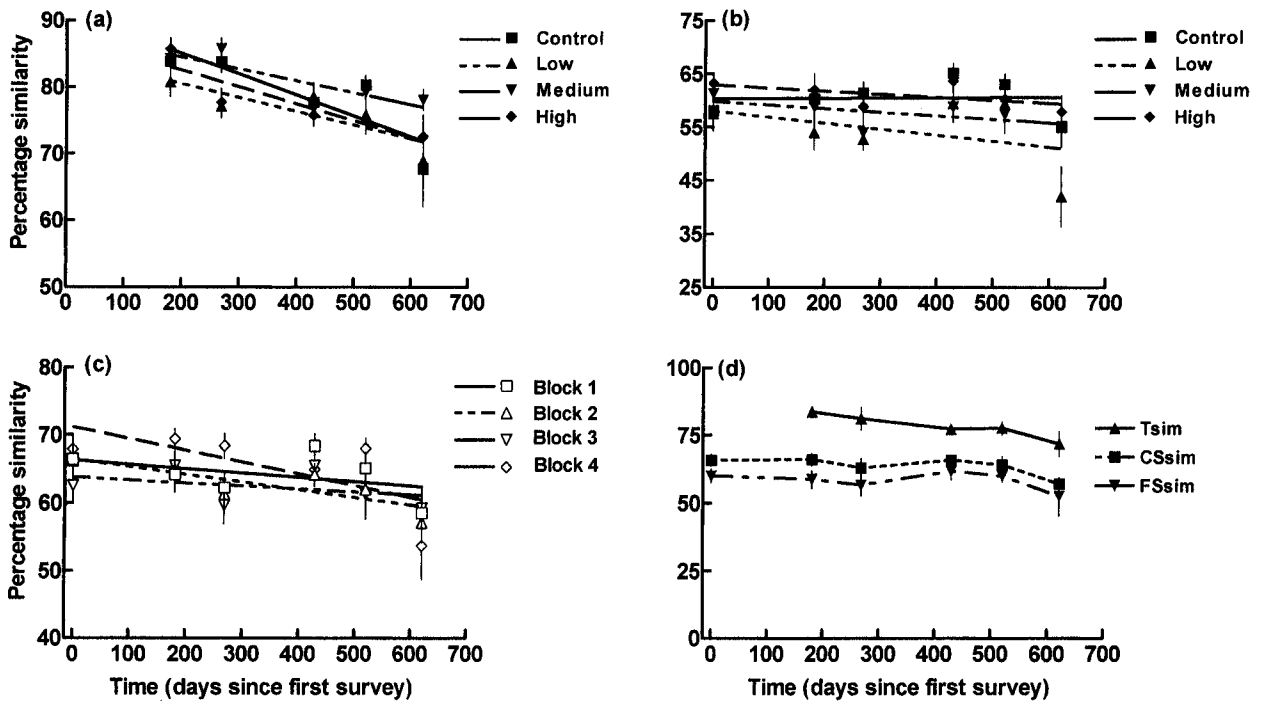


Fig 6 The relationship between time (days since start of first plant survey) and (a) temporal similarity (Tsim = similarity to initial species composition), (b) far spatial similarity (FSsim = paddocks in the same grazing level but in different blocks), (c) close spatial similarity (CSsim = paddocks in the same block but in different grazing levels), and (d) a summary of changes in mean similarity over all grazing levels (for Tsim and FSsim) and over all blocks (for CSsim); in four grazing levels. Least squares linear regression models are described in the text

of (possibly) too light a grazing pressure and relatively long intervals between successive surveys, providing the fast-growing herbaceous vegetation sufficient time to recover. However, grazing had a significant level-dependent effect on SD (species density, an index of richness), which evidently became progressively more intense with time, mostly because of a progressive decrease in mean SD in the ungrazed Control. Grazing itself apparently maintained mean species richness (Smith & Rushton, 1994; Wilson, 1994), in our case probably as a result of an increase in the number of erect forb species as they were released from competition with the dominant decumbent plants (see also Gibson, Watt & Brown, 1987; Smith & Rushton, 1994).

The highest grazing level we applied, although initially estimated to be sufficient to emulate high grazing intensity, was probably not high enough to decrease species richness in the short term. Decreased richness/diversity apparently occurs only in long-term overgrazing situations (Barker, Herlocker & Young, 1989 [grassland]; McIntyre & Lavorel, 1994 [grassland]). Many studies (of

varying duration) in fact report higher species richness under grazing (Gibson *et al.*, 1987 [moist grassland], O'Connor, 1991 [savanna], Pandey & Singh, 1992 [seasonally dry savanna], Bullock *et al.*, 1994 [grassland], Ash & McIvor, 1998 [tall grassland]), usually as a result of increases in annual grasses and forbs. A distinction should however be made between grazing effect and exclusion effect – in those studies carried out in a background of free-range grazing (as our own was), species richness does not increase under grazing, it rather decreases where grazing has been excluded (e.g. Pandey & Singh, 1992; Smith & Rushton, 1994). This suggests that plant species numbers in the area affected by free-range grazing are maintained by grazing. Depending on the vegetation type, grazing may thus be an important tool in managing plant diversity.

In contrast to most other studies (e.g. Smith & Rushton, 1994), in our study grazing had relatively little direct influence on species composition. With the exception of CSsim, which decreased significantly in two of the blocks (because of either grazing or intrinsic succession), none

of the effects were significant. Nevertheless, there were some indications of a grazing effect in that the average similarity in a grazing level (FSsim), tended to decline faster in grazed than ungrazed paddocks, while at the same time Tsim decreased faster in Control than in other grazing levels. This indicates a faster average species turnover across blocks in the absence of grazing. If turnover is a measure of the rate of succession, then livestock grazing may 'retard' succession (Davidson, 1993). This may be because grazing-tolerant plant species persist longer (Tsim declines relatively slowly, explaining the grazed results), or it may be an artefact of the decrease in number of species in Control (Tsim declines relatively fast, explaining the ungrazed results), or both.

A level-dependent effect on the range of both SD and VC values was the most noticeable and also most interesting grazing effect. For instance, exclusion of grazing apparently decreases any *a priori* site differences in SD, suggesting that there is a general limit to species richness in the absence of disturbance. Furthermore, the increased range of SD values under grazing was site-specific, some sites within the same grazing level remaining relatively unaffected (Figs. 4 and 5). Given that each site has its characteristic complement of species (evidenced by relatively low FSsim), the resistance of particular species to grazing is probably crucial in determining the response of a site to grazing. A site that originally consisted of a few patch-dominant plant species might become more heterogeneous in response to grazing and consequently allow a more even spread of species (in effect decreasing the scale of patchiness). On the other hand a site that was heterogeneous before the start of grazing may react in exactly the opposite way – a few robust plants may become dominant at the cost of a number of more disturbance-sensitive plants. Also, a differential response of the woody and herbaceous plants to a disturbance by cattle may lead to increases or decreases in species numbers.

We know of no other studies that have looked at the effect of grazing on variation in plant species numbers and vegetation cover. Indeed, apart from Warwick & Clarke (1993), who used increased variability as an indication of ecosystem stress in a marine environment, we were unable to find any references to this phenomenon.

Finally, grazing tended to increase the proportion of erect compared to decumbent plants. The ground vegetation in our study area was dominated by decumbent plants (from 40% to 65% frequency over all grazing levels,

compared to 10% to 35% erect plants; Fig. 5). This is probably because the strategy of colonization by horizontal vegetative growth has a competitive advantage in a dynamic and large-scale patchy resource environment (Dushyantha & Hutchings, 1997). Coastal dune vegetation may therefore be adapted to disturbance on several different evolutionary and ecological time-scales (Mentis & Ellery, 1998). However, this adaptation is likely to be specific to relatively large disturbances, in the size range of tree-falls to cyclonic blowouts (although there is some evidence that disturbances larger than tree-falls are uncommon in African forests; Chapman *et al.*, 1999), and not to disturbances by large gregarious herbivores. 'Natural' disturbances in this type of environment are typically intense, of short duration and cause a large-scale (relative to plant size) mosaic of open areas (Mentis & Ellery, 1998), while cattle disturbance is low-grade, cumulative and causes a small-scale patchy resource environment [implicit in McNaughton's (1984) argument].

Scale-dependent effects of disturbance on plant communities have often been recorded (Coffin & Lauenroth, 1988; Walker, Langridge & McFarlane, 1997). Furthermore, a survey of the literature on grazing and its effects on vegetation suggests that there is a strong effect on plant life attributes, particularly in environments that do not have a long history of grazing by large herbivores (for some recent examples see McIntyre *et al.*, 1995; Belsky & Blumenthal, 1997; Fensham, Holman & Cox, 1999). Our study tends to confirm this.

Conclusion

Our results point to two important, easily measured mechanisms with wide application in coastal dune forest management – the interaction of disturbance type with plant growth form (Adámoli *et al.*, 1990; Díaz, Acosta & Cabido, 1992; McIntyre, Lavorel & Tremont, 1995), and the increase in variation in community structural variables under disturbance (Warwick & Clarke, 1993). However, on the east coast of Africa where livestock numbers are increasing, these mechanisms have not been studied adequately – there is for instance no quantitative information available on the levels and effects of anthropogenically-derived disturbances (including cattle) in any coastal forested areas in southern Africa. In view of increased development and increasing human population pressures in the coastal regions, a trend that occurs not just in South Africa but also across the

African continent, this is a factor that warrants urgent investigation.

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