Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana

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Abstract

The structure of woody vegetation was studied in little disturbed arid savanna and in adjacent over-grazed vegetation. In the over-grazed areas density and cover of woody plants were higher than in the less disturbed vegetation. The difference was accounted for by one species, *Acacia mellifera*, which was strongly dominant in the overgrazed vegetation. In the open savanna, the woody species varied in height from small shrubs to trees, while the dense shrub vegetation was of uniformly low stature.

It is suggested that, while the differences in total abundance of woody species depend on differences in the amount of soil water available for woody growth, differences in species composition and height distribution are governed by the spatial and temporal distribution of water in the soil profile.

Introduction

Change of open savanna vegetation into shrub and thicket has been described from many semi-arid and arid regions (Walter 1954; Acocks 1964, 1975; Buffington & Herbel 1965; Blackburn & Tueller 1970; Werger & Leistner 1975; van Vegten 1981, 1983; Madany & West 1983; Hacker 1984; Tolsma *et al.* 1987; Archer *et al.* 1988). In most cases the encroachment of woody species has been attributed to human activities, primarily to over-grazing by livestock and related disturbances (Walter 1954; Acocks 1964, 1975; van Vegten 1981, 1983; Noy-Meir 1982; Madany & West 1983; Skarpe 1990).

A theory of shrub invasion in overgrazed savanna was presented by Walter (1954) and further developed by Walker & Noy-Meir (1982) and Noy-Meir (1982). This model describes savanna as a system of two functionally separate soil layers and two vegetation components with different life forms. Both woody species and grasses have access to water in the surface soil, although a healthy grass layer may outcompete woody species in that zone. Water penetrating deeper in the soil is exclusively available for woody growth. A decrease in grasses, e.g., from overgrazing, results in more water being available in both soil layers for consumption by shrubs and trees.

This model can explain the increase in total

woody growth, but not the simultaneous changes in species composition and height frequencies. Only certain species become encroachers while others are unaffected (van Vegten 1981, 1983; Tolsma et al. 1987; Skarpe 1990). In areas with shrub invasion, the woody layer remains fairly low and uniform in stature, also when the same species grows much taller in nearby less disturbed vegetation (van Vegten 1981).

This study presents data on the structure of woody vegetation in little disturbed grass dominated savanna and in adjacent overgrazed areas with bush encroachment. Soil water quantity and temporal and spatial distribution in the soil profile is discussed in relation to the vegetation structure.

Study area

The study was carried out in the Kalahari in western Botswana at about 23° 07′ S, 20° 32′ E (Fig. 1). The mean annual rainfall is ca 300 mm and its coefficient of variation ca 50% (Pike 1971). Rain fall almost entirely during summer, from November to April (Schultze & McGee 1978). The soi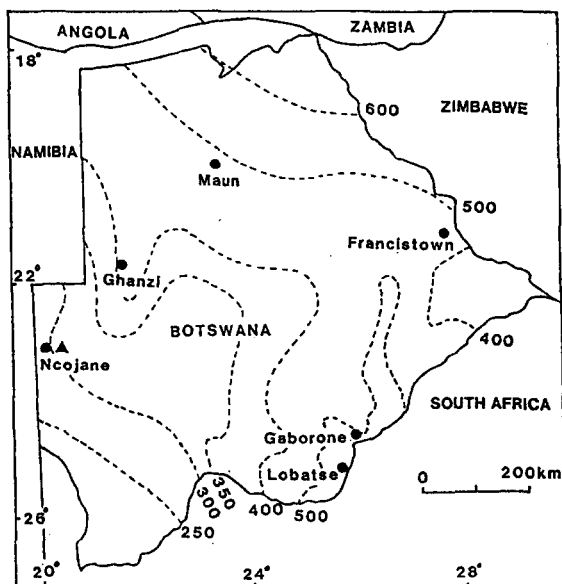l consists of nutrient poor, fairly homogeneous Kalahari sand (Bergström & Skarpe 1985). The vegetation is a shrub savanna of perennial tufted grasses, shrubs and scattered low trees.

The Kalahari vegetation is described by Leistner (1967), Werger & Coetzee (1978), Skarpe (1986).

Methods

In January 1989 woody vegetation was analysed in seven plots, mostly 50*50 m (see Table 1). The plots included more or less undisturbed savanna (plots 1–3), areas overgrazed for 12 years (plots 4 and 5) and for >30 years (plot 6) and one area (plot 7) with unknown history. The areas sampled were subjectively selected according to known land use history and/or vegetation conditions, while the exact positions of the plots therein were decided by random selection of distance and direction from the point of access. In the plots all woody specimens > 0.2 m heigh were recorded by species, and height and two maximum canopy diameters (N-S and E-W) were measured. Total cover of the herbaceous layer was estimated in percent (Table 1).

Cover of the shrubs was calculated from the measured diameters; height and density were taken directly from the records.

Regression of vegetation composition on time for overgrazing was studied by direct gradient analysis (Canonical Correspondence Analysis, ter Braak 1987) for the six plots (1–6) with known land use history. To emphasize the relative differences in species composition rather than the total increase in shrub abundance, relative cover was used instead of absolut.

To illustrate differences in dominance-diversity conditions, importance-value curves (Whittaker 1975) were drawn for each plot using relative cover (%) as importance value.

For the four plots (4–7) with bush encroachment, where crowding occurred in stands of largely one species, Acacia mellifera ssp. detinens (hereafter called Acacia mellifera), the self-thinning coefficient (Yoda et al. 1963) was calcu-

Fig. 1. Situation of the study area (▲) and some isohyets.

lated using the function

$$V = kN^a$$

where V is average volume (cover*height) per plant, N is population density, k is a species dependent proportionality constant and a is the self-thinning coefficient.

Little data are available on soil water distribution in the studied area and under the vegetation types concerned. As a base for discussion, existing data on rainfall, soil properties, fytomass in different vegetations and estimations of water consumption rates were used to calculate water behavior in surface and deeper soil under different conditions (see Appendix).

Table 1. Density (above, no ha^{-1}) and cover (below, %) in the plots.

	Plot number						
	1	2	3	4	5	6	7
Plot size (m^2)	2500	2500	2500	2500	2500	1250	128
Acacia erioloba	120	44	28	16	68	40	78
E. Meyer	5	0	0	0	1	0	0
Acacia lüderitzii	24	4	28	52	36	16	78
Engler	2	2	0	7	3	0	0
Acacia mellifera	232	104	100	224	280	2216	14688
Vahl Bentham	9	8	9	21	27	41	75
ssp. detinens							
Burch. Brenan							
Boscia albitrunca	108	76	68	192	88	72	–
Burch. Gilg &	0	1	1	2	0	0	–
Benedict							
Catophractes	–	–	–	–	–	40	–
alexandri D. Don	–	–	–	–	–	1	–
Ehretia rigida	20	8	28	28	20	8	–
Thunb. Druce	0	0	0	0	0	0	–
Grewia flava DC.	144	124	184	432	388	184	–
	5	2	2	2	2	2	–
Grewia retinervis	8	8	4	–	–	–	–
Burret	0	0	0	–	–	–	–
Lycium hirsutum	12	–	–	–	60	–	–
Dunal	0	–	–	–	0	–	–
Lycium namaquense	40	48	52	140	212	48	–
Dammer	0	0	0	1	2	0	–
Rhus tenuinervis	60	144	76	20	36	8	313
Engler	0	0	0	0	0	0	1
Total woody layer	768	560	568	1104	1188	2632	15157
	21	13	12	33	35	44	76
Total field layer							
cover	25	35	30	<1	<1	<1	<1

14

Results

The cover and density of woody species were lowest in the little disturbed plots (1–3), higher in those overgrazed for 12 years (plots 4 and 5) and
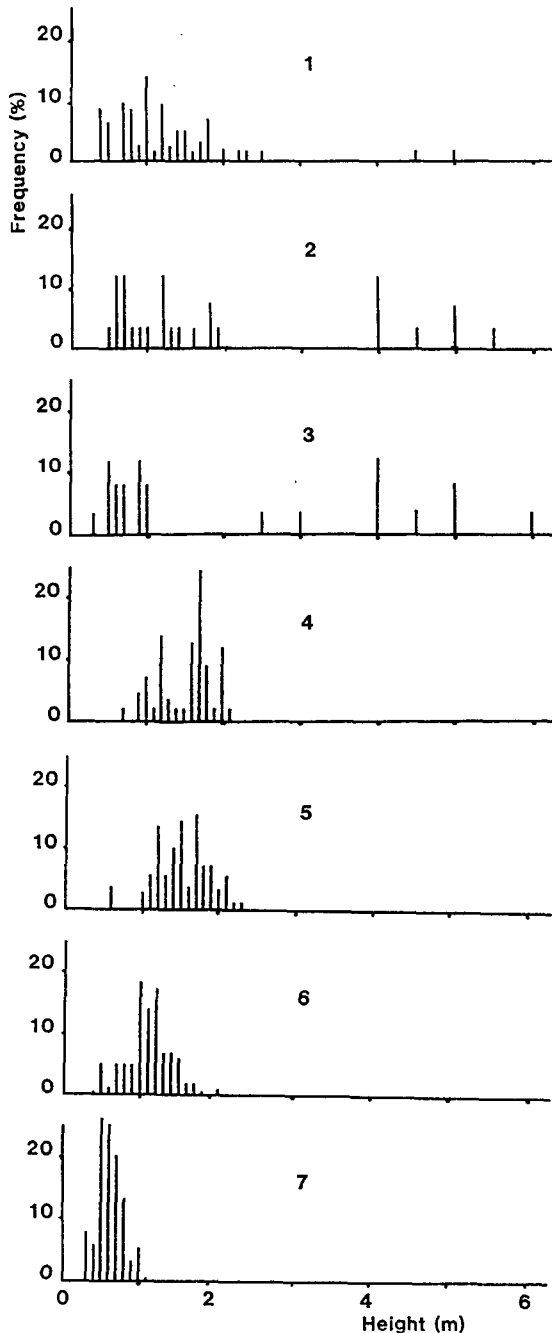
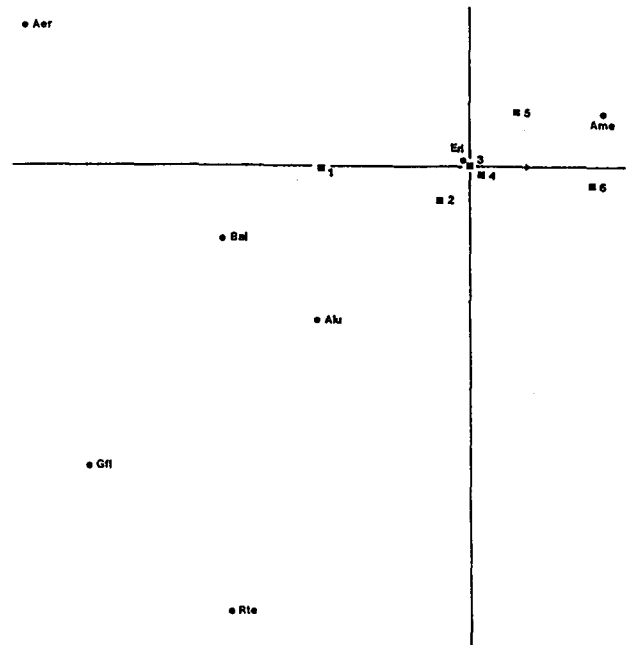*Fig. 2.* Height frequency distributions for *Acacia mellifera* in plots 1–7.

Fig. 3. Canonical Correspondence Analysis ordination diagram of plots 1–6 (■), showing axes 1 and 4 with the time for overgrazing represented by the arrow on the first axis. Species (•) shown are *Acacia erioloba* (Aer), *A. lüderitzii* (Alu), *A. mellifera* (Ame), *Boscia albitrunca* (Bal), *Ehretia rigida* (Eri), *Grewia flava* (Gfl) and *Rhus tenuinervis* (Rte). Abundance is relative cover (%).

even higher in plot 6, overgrazed for > 30 years. Plot 7 with unknown landuse history and encroachment of small, presumably young shrubs had the highest cover and density (Table 1).

The height distribution of lignoses in the open savanna showed a peak in the low shrub layer, roughly 0.5 to 1.5 m, but also included, e.g., *Acacia lüderizii* trees and polycorm *Acacia mellifera* of up to 6 m. In the areas with bush encroachment, the taller component was virtually absent, and the shrubs were mainly below 2 m, in plot 7 below 1 m. The height frequency distributions for *Acacia mellifera* are shown in Fig. 2.

The Canonical Correspondence Analysis shows regression (Canonical coefficient 3.13, $P < 0.05$) of relative species abundance (cover) in the plots on the time-for-overgrazing gradient on the first axis (Fig. 3). Of the 10 species occurring in more than one plot, only *Acacia mellifera* was positively correlated with the first axis.
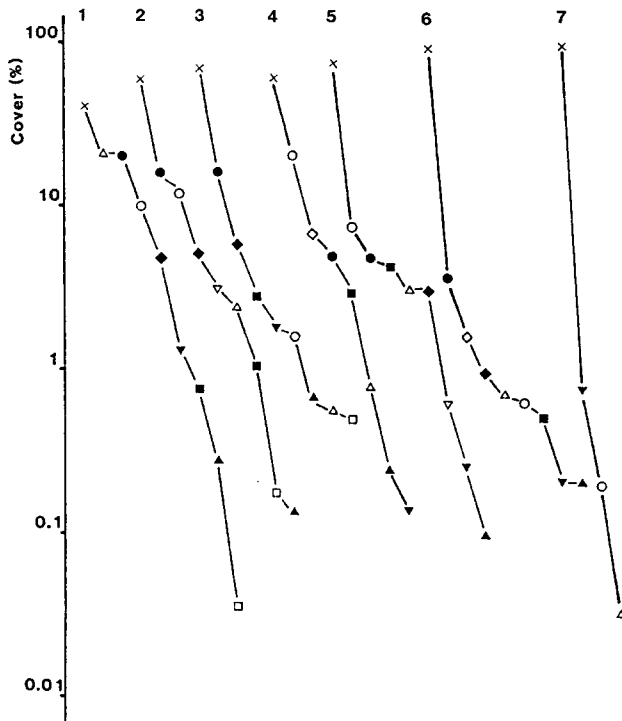
Fig. 4. Importance-value curves (cover%) for woody species in plots 1–7. Species are *Acacia erioloba* (△), *A. lüderitzii* (○), *A. mellifera* (×), *Boscia albitrunca* (◆), *Catophractes alexandri* (◇), *Ehretia rigida* (▲), *Grewia flava* (●), *G. retinervis* (□), *Lycium namaquense* (■), *L. hirsutum* (▽) and *Rhus tenuinervis* (▼).

The dominance-diversity curves show increased dominance by *Acacia mellifera* in the plots with bush encroachment, where it contributes > 90% of the cover of woody species (Fig. 4).
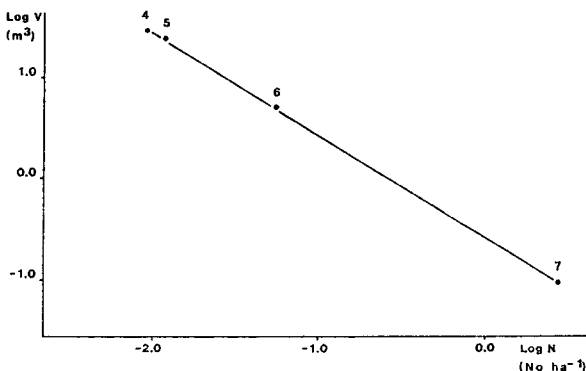

Fig. 5. Relationship between volume (V) and density (N) for woody vegetation in the plots with bush encroachment (4–7). The equation is the logaritmic form, $\log V = a*\log N + k$, of the self thinning function $V = kN^a$.

The self thinning coefficient calculated for the four plots (4–7) with dense *Acacia mellifera* shrubs assumed a value of -1.03 with a regression coefficient of 0.999 (Fig. 5).

Discussion

Vegetation structure

The increase in total cover and density of the woody layer in the overgrazed plots (Table 1), may be explained as a result of increased water availability for woody species following the reduced competition from the grass layer (Walter 1954; Walker & Noy-Meir 1982).

The difference in relative abundance of species between areas with and without bush encroachment, as illustrated by the Canonical Correspondence Analysis (Fig. 3) and the dominance-diversity diagrams (Fig. 4), is not explained by increased water availability. Only *Acacia mellifera* increased in relative cover and density, although there was an increase in absolut density also in *Grewia flava* and *Lycium namaquense* (Table 1). In a previous study in the same area (Skarpe 1990), *Acacia mellifera* and *Grewia flava* increased significantly during the first 5 years of overgrazing. *Acacia mellifera* is frequently regarded as a main encroacher in over-grazed savanna in Southern Africa (van Vegten 1981, 1983; Tolsma *et al.* 1987). It is recorded to have shallow lateral roots (Adams 1967; Leistner 1967; Timberlake 1980; van Vegten 1981 and Tolsma *et al.* 1987). Also *Acacia lüderitzii* and *Grewia flava* (van Vegten 1981) and *Lycium sp.* (Cole & Brown 1976) have been reported to be largely shallow rooted.

Tolsma *et al.* (1987) attribute the success of shallow-rooted acacias as compared to deeprooted species in encroaching overgrazed areas to their better access to nutrients, including N_2-fixation by *Rhizobium*. This probably is of significance in a nutrient poor environment as the Kalahari, but access to water is likely to be at least as important. Of course, the two factors have interactive effects (Penning de Vries *et al.* 1982; Frost *et al.* 1986).

Rains in this area are frequently only enough to wet the surface soil. After the dominance of the grasses has been broken, this water is, to a higher degree than before, available to shrubs and trees. In that situation woody species with shallow lateral roots, have an added advantage compared to those with root systems more restricted to deeper layers. The former can make use of small showers and were observed to start the vegetation period earlier than the same species in grass dominated vegetation.

In the plots with bush encroachment the height of the shrubs was fairly even and much below the species' maximum height in the area. Van Vegten (1981) reported similar conditions and speculated in the occurrence, in encroachment situations, of a special genotype with stunted growth and short life span. Another explanation may be found in the spatial and temporal pattern of competition for water between the crowded shrubs.

The self thinning coefficient was found to be − 1.03, which is significantly different from the common − 1.5 for growth with geometric similarity and − 1.9 for elastic similarity (Norberg 1988). Norberg (1988) calculates a thinning coefficient of − 1.0 for populations where the vertical growth above or below ground has stagnated, resulting in two dimensional, radial growth. He further states that the thinning pattern in a population is dictated by the growth geometry of the plant part involved in the limiting competition. As light is unlikely to be limiting under the present conditions, the critical competition can be presumed to take place between roots for water and/or nutrients. If water is available mainly in the surface soil, root penetration will, in effect, be restricted, and soon result in predominantly two dimensional growth.

Soil moisture calculations

The structure of the vegetation suggests that most soil water is taken up from the surface soil by grasses or shallow rooted shrubs. As a base for discussions, calculations of daily soil moisture conditions were made (cf. Bate et al. 1982), based on real (Botswana Weather Bureau, unpublished)

and modified rainfall data, field capacity of the soil (Bergström & Skarpe 1985), relations between cover of shrubs and total and leaf masses (Skarpe 1990) and between cover and weight of grasses (Skarpe unpublished). Water consumption rates were taken from Whitmore (1971) and Bate et al. (1982). They are presumed to be constant as long as water is available, and to depend on leaf weight.

The model proved to be more sensitive to changes in timing and size of rains than to moderate differences in total seasonal rainfall or to realistic changes in vegetation parameters (see appendix for assumptions). Results from one typical simulation is shown in Fig. 6.

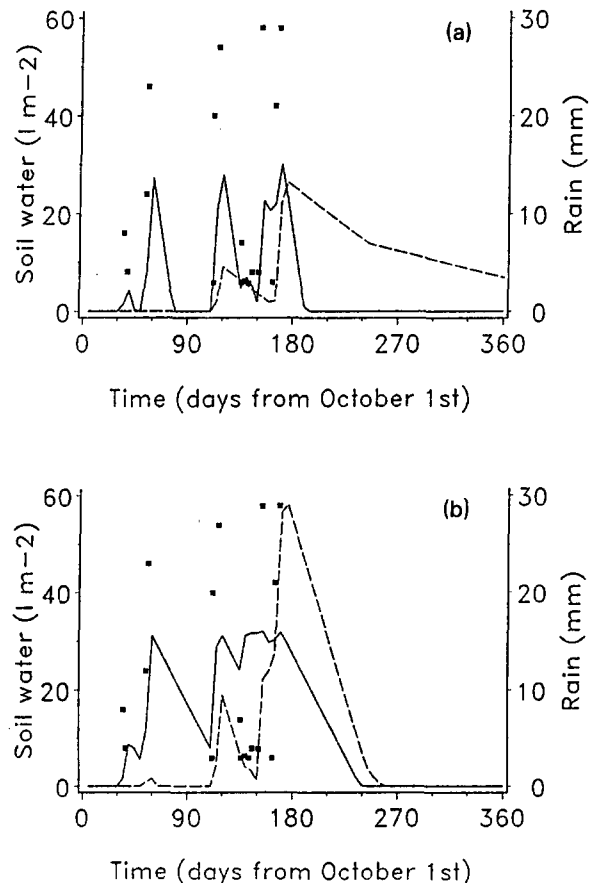In little disturbed savanna real distributions of

Fig. 6. Rain (■) and simulated water content $(l\,m^{-2})$ in topsoil (————) and subsoil (– – – –) as means for 5-days periods in a) in natural savanna and b) under bush encroachment. For assumptions see appendix.

rains resulted in $^2/_3$ to $^3/_4$ of the total soil moisture being used in the uppermost 0.5 m of the soil, which was depleted of moisture, mainly by grasses, 2 to 3 weeks after saturation. Little water penetrated to deeper soil layers. However, the low transpiration from these layers by the sparse woody vegetation caused the moisture to last long, in most cases throughout the year. This would form a reasonable reliable moisture supply to meet the requirements by woody species in the dry season (Walter 1973). If soil water is carried over from one year to the next, the soil might be moistened to a considerable depth, allowing normal root development. It would further mean a certain buffer for dry years. The relative sparseness of shrubs and trees in this vegetation may depend on difficulties for woody seedlings to establish in competition with the grasses (van Vegten 1981).

With dense shrub vegetation and no grass, still most water was used in the top soil by shallow rooted shrubs. The water extraction was, however, slower than with an intact grass layer, and the soil was moist for most of the rainy season. Between $^1/_3$ and $^1/_2$ of the water percolated beyond the top 0.5 m, but was transpired at a much faster rate than under the grass, leading to depletion of soil moisture in the beginning of the dry season. In reality, with water consumption rates decreasing with decreasing availability, some water may be left for longer time. Still, there seems to be a pronounced shortage of water during the dry season, possibly hampering height growth (cf. Diniz & Aguiar, 1972 ex Werger & Coetzee 1978).

Acknowledgements

Appendix

A model was constructed to simulate water content in two soil layers under given rainfall and vegetation. The model runs for 365 days starting with 0 soil moisture in both layers on October 1st. Water input is by effective rain and loss is by consumption by vegetation.

The model is based on the following assumptions:

1. The soil consists of homogeneous sand with a field capacity of 6.5% on a volume basis.
2. Maximum available water is at field capacity, minimum is set to 0.
3. Effective rain is measured rain minus $^1/_3$ that evaporates from soil or vegetation. (This is a smaller loss than is usually estimated (Bate *et al.* 1982), but is motivated by the coarse substrate). Rains <5 mm do not contribute to effective rain.
4. The soil consists of an upper (0.5 m) and a lower layer with independent water budgets, except for recharge of water to the lower layer through the upper.
5. The water reaching the lower soil layer at each rainfall is the difference between the effective rain and the amount required for the surface layer to restore its moisture content to field capacity.
6. The vegetation consists of grasses, with access only to the surface soil, and woody species with access to both soil layers.
7. Woody species are further divided into shallow rooted encroachers and others.
8. Grasses take all their water from the surface soil.
9. Encroachers take X% of their water from the surface soil and (100-X)% from deeper soil layers. (X was varied between 50 and 85; in Fig. 6. X = 75)
10. Other shrubs take Z% of their water from the surface soil and (100-Z)% from deeper soil layers. (Z was varied between 0 and 25; in Fig. 6. Z = 25)
11. All species consume water – if available – at a constant rate of 15 g H_2O g^{-1} leaf day^{-1} from November to May (inclusive).
12. Woody species loose water, from the subsoil, corresponding to 2% of their leafless weight through twig respiration throughout the year (cf Walter 1973).

18

References

Acocks, J. P. H. 1964. Karoo vegetation in relation to the development of deserts. In: D. H. S. Davis (ed), Ecological studies of southern Africa, pp. 100–112. Junk, The Hague.

Acocks, J. P. H. 1975. Veld types of South Africa. Memoirs of the botanical survey of South Africa 40: 1–128.

Adams, M. E. 1967. A study of the ecology of Acacia mellifera A. Seyal and Balanites aegyptica in relation to land-clearing. Journal of Applied Ecology 4: 221–237.

Archer, S., Scifres, C. & Bassham, C. R. 1988. Autogen succession in a subtropical savanna: conversion of grass-land to thorn woodland. Ecological Monographs 58: 111–127.

Bate, G. C., Furniss, P. R. & Pendle, P. G. 1982. Water re-lations in southern African savannas. In: B. J. Huntley & B. H. Walker (eds), Ecology of tropical savannas, pp. 336–358. Springer-Verlag, Berlin.

Bergström, R. & Skarpe, C. 1985. Characteristics of the Kalahari sand in western Botswana. Meddelande från Växtbiologiska Institutionen 1985: 3.

Blackburn, W. H. & Tueller, P. T. 1970. Pinyon and Juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51: 841–848.

Buffington, L. C. & Herbel, C. H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological monographs 35: 139–164.

Cole, M. M. & Brown, R. C. 1976. The vegetation of the Ghanzi area of Western Botswana. Journal of biogeogra-phy 3: 169–196.

Diniz, A. C. & Aguiar, F. Q. 1972. Os solos e a vegetação do planalto ocidental da Cela. Inst. Inv. Agron. Angola, Sér. Cien. 26: 1–24.

Frost, P., Medina, E., Menaut, J. -C., Solbrig, O., Swift, M. & Walker, B. 1986. Responses of savannas to stress and disturbance. Biology International 10: 1–82.

Hacker, R. B. 1984. Vegetation dynamics in a grazed mulga shrubland community I. The mid-storey shrubs. Australian Journal of Botany 32: 239–250.

Leistner, O. A. 1967. The plant ecology of the southern Kalahari. Botanical Survey Memoir 38: 1–172.

Madany, M. H. & West, N. E. 1983. Livestock grazing – fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64: 661–667.

Norberg, R. Å. 1988. Theory of growth geometry of plants and self-thinning of plant populations: geometric similari-ty, elastic similarity and different growth modes of plant parts. The American Naturalist 131 (2): 220–256.

Noy-Meir, I. 1982. Stability of plant-herbivore models and possible applications to savanna. In: B. J. Huntley & B. H. Walker (eds), Ecology of tropical savannas, pp. 591–609. Springer Verlag, Berlin.

Penning de Vries, F. W. T. & Djiteye, M. A. 1982. La produc-tivité des pâturages sahéliens. Centre for Agricultural Pub-lishing and Documentation, Wageningen.

Pike, J. G. 1971. Rainfall over Botswana. In: Anonymus (ed), Proceedings of the conference on sustained production from semi-arid areas, pp. 69–76. The Botswana Society, Gaborone.

Schulze, R. E. & McGee, O. S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. In: M. J. A. Werger (ed), Biogeography and ecology of southern Africa, pp. 19–54. Junk, The Hague.

Skarpe, C. 1986. Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. Vegetatio 68: 3–18.

Skarpe, C. 1990. Shrub layer dynamics under different herbi-vore densities in an arid savanna, Botswana. Submitted ms.

Ter Braak, C. J. F. 1987. The analysis of vegetation-environ-ment relationships by canonical correspondence analysis. Vegetatio 69: 69–77.

Timberlake, J. 1980. Handbook of Botswana Acacias. Ministry of Agriculture, Botswana, Gaborone.

Tolsma, D. J., Ernst, W. H. O., Verweij, R. A. & Vooijst, R. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. Journal of Ecology 75: 755–770.

Van Vegten, J. A. 1981. Man-made vegetation changes: an example from Botswana's savanna. National Institute of Development and Cultural Research, Gaborone, Botswana.

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

Walker, B. H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. In: B. J. Huntley & B. H. Walker (eds), Ecology of tropical savannas, pp. 556–590. Springer Verlag, Berlin.

Walter, H. 1954. Die Verbuschung, eine Erscheinung der subtropischen Savannengebiete, und ihre ökologischen Ursachen. Vegetatio 5/6: 6–10.

Walter, H. 1973. Die Vegetation der Erde; I. Die tropischen und subtropischen Zonen. (3rd ed.) Fischer, Stuttgart.

Werger, M. J. A. & Coetzee, B. J. 1978. The Sudano-Zambezian Region. In: M. J. A. Werger (ed), Biogeogra-phy and Ecology of Southern Africa, pp. 301–462. Junk, The Hague.

Werger, M. J. A. & Leistner, O. A. 1975. Vegetations-dynamik in der südlichen Kalahari. In: W. Schmidt (ed), Sukzessionsforschung, pp. 135–158. Cramer, Vaduz.

Whitmore, J. S. 1971. South Africa's water budget. South African Journal of Science 67: 166–176.

Whittaker, R. H. 1975. Communities and ecosystems. (2nd ed.) MacMillan, New York.

Yoda, K., Kira, T., Ogawa, M. & Hozumi, K. 1963. Intra-specific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of Biology 14: 107–129.