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## Seasonal vegetation changes in the Hoanib River catchment, north-western Namibia: a study of a non-equilibrium system

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The numbers of livestock and wildlife that can be supported in an arid environment such as the Hoanib River catchment, north-western Namibia, are determined by annual and seasonal availability of grazing and browsing. The availability and abundance of vegetation was investigated in eight focus-study areas across the catchment. The vegetation of the focus area was observed to behave in a non-equilibrium manner in that it was dependent on annual rainfall rather than intensity of landuse. The Zurich–Montpellier method of vegetation assessment was used for the evaluation of vegetation plots. The amount of dry season grazing was also dependent on the previous season's rainfall, with 'dead grass' and perennial grass only available after an 'above average' rainfall season. Vegetation communities were dominated by mixed *Colophospermum mopane* woodlands in the 100–350 mm rainfall zone, while perennial grasses dominated the 50–100 mm rainfall zone. While the bulk rangeland appeared not to be disturbed by landuse, a 2 km 'sacrifice zone' around water sources was found to have changes in vegetation species and abundance. During below-average rainfall seasons and drought, when there is limited or no grazing, browse becomes the most important source of nutrition for domestic stock and wildlife.

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### Introduction

#### *Equilibrium or non-equilibrium system?*

In order to manage rangelands, it is first necessary to understand how they function and what are the potential impacts of the different management strategies. There are three proposed theories of how a rangeland functions, each relating to the degree and direction of link between plant and herbivore production. Links between biotic factors can be termed density dependent or density independent according to responses of one variable to the other. Definitions of equilibrium, quasi-equilibrium and non-equilibrium systems are crucial if there is to be a clear understanding of how paradigms

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such as these, affect arid and semi-arid lands (Behnke, 1993; Behnke & Scoones, 1993; Behnke *et al.*, 1993).

According to Behnke & Scoones (1993), the paradigms can be defined as follows:

- Equilibrial means that the numbers of livestock strongly affect the forage production from a particular area of land.
- Quasi-equilibrial means the numbers of livestock affect forage production in an area less strongly. Interactions are sometimes equilibrial with biotic interactions, sometimes non-equilibrial with abiotic climatic factors driving the system.
- Non-equilibrial means that the numbers of livestock do not significantly affect the total plant production in an area of land.

The question of whether or not traditional farming methods have contributed to degradation of the land has been the subject of a large volume of literature. According to Dodd (1994), the term 'degradation' was initially used to define the process of change in an ecosystem toward a 'less productive' state. The modern use of the term usually refers to a decrease in productivity or unfavourable changes in species composition, but it does not infer that the changes are permanent or the result 'desert-like'. In addition, Dodd (1994) defines desertification as an irreversible change in the environment and should only be applied to areas where rainfall is between 50 and 300 mm annually. Many authors (e.g. Ellison, 1960; Downing, 1978; Dankwerts & Stuart-Hill, 1988; Mwalyosi, 1992; Dean & Macdonald, 1994; Dodd, 1994) attribute the main driving force of degradation and desertification to human influence, in association with periods of aridity. In response to the United Nations Conference on Environment and Development (UNCED) (1992) which subsequently led to the 1994 Convention to Combat Desertification, Namibia established NAPCOD (Namibia's Programme to Combat Desertification). This programme recognizes that poverty, population growth and desertification are intimately linked and it addresses the political, socio-economic and biophysical aspects related to land degradation (DRFN, 2001).

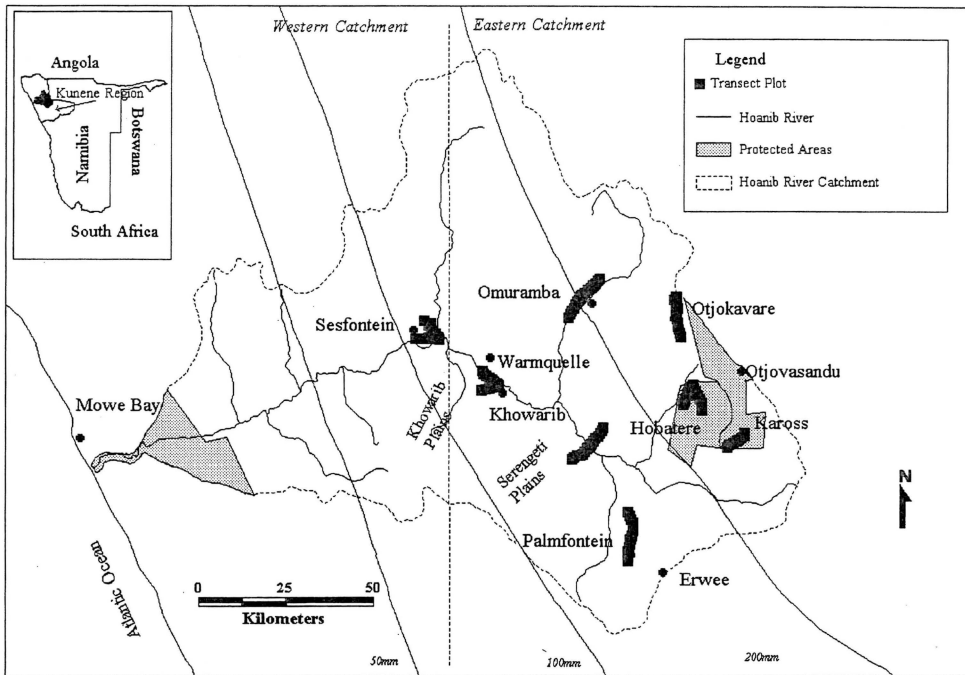
Other authors (e.g. Sandford, 1983; Ellis & Swift, 1988; Behnke, 1993; Sullivan, 1996, 1999) have argued that many of the degradation processes and patterns attributed to people and domestic stock in arid environments, instead can be attributed to natural variations in climate, particularly rainfall.

The objectives of this study were to examine the variations in the annual and seasonal abundance of vegetation in the Hoanib River catchment in response to rainfall during the 1999 and 2000 wet seasons and during the 2000 dry season. In addition, the spatial and temporal distribution of vegetation and the implications of a non-equilibrium system on domestic stock and wildlife in an arid environment were assessed.

#### *Study site*

The location of the Hoanib River catchment and vegetation transect lines are shown in Fig. 1.

Vegetation checklists for the Hoanib River catchment area have been compiled by Maggs *et al.*, (1994, 1998) and the ethnobotany of the region has also been reported (Malan & Owen-Smith, 1974; Sullivan, 1998). In addition, the vegetation has been previously mapped by Giess (1971), Viljoen (1980) and Becker & Jurgens (2000). Becker & Jurgens (2000) reported a vegetation gradient from east to west in Kaokoland with mixed *Colophospermum mopane* vegetation type dominating the area that corresponds to the 100–350 mm rainfall zone. The drier areas (50–100 mm



**Figure 1.** Map of Hoanib River catchment area showing the location of transect, north-western Namibia.

rainfall zone) are dominated by larger stands of *Stipagrostis uniplumis* forming permanent grasslands.

Sullivan (1999) reported that the floristic communities, diversity, density, cover and population structure of woody vegetation in the Sesfontein, Warmquelle and Khowarib areas were not degraded by local herders except on a local scale close to settlements. The Sesfontein area has long been regarded by researchers as 'degraded' (e.g. Van Warmelo, 1962; Loxton Hunting & Associates, 1974; Nærua *et al.*, 1993) as a result of overuse by local herdsmen. Sullivan (1999) suggests that these previous studies may have been flawed in that researchers failed to take into account spatial and temporal scale interpretations of ecological data, the importance of abiotic factors, and the belief that traditional communal farming practices are environmentally degrading.

In the arid north-west, rainfall is spatially and temporally variable. Seasonal rainfalls are highly variable and the average rainfall does not necessarily serve as good indicators of the amount of rainfall that can be expected in any given season (Jacobson *et al.*, 1995). For example, Sesfontein has an average rainfall of 107 mm, but in 1995 the area received 335 mm of rain while in 1981, 0 mm of rain was recorded (Leggett *et al.*, 2001). Both of these rainfall figures fell within the natural variability range for rainfall in the area. The rainfall in the catchment for the 1999 and 2000 wet seasons are discussed in detail in Leggett *et al.* (2002a). During the 1999 wet season, the catchment received approximately 70% of the long-term mean rainfall. However, during the 2000 wet season, the eastern section of the catchment received approximately 170% (above-average rains) of the long-term mean and the western catchment received 100% (average rainfall).

For the purposes of this study, annual grasses and forbs were defined as species that grow and seed seasonally, but usually do not survive the dry season. In contrast, perennial grasses generally form tufts and retain their leaf throughout the year. Growth, flowering and seeding in both the annual and perennial grasses occurs primarily during the wet season.

### Method

A detailed description of field sampling technique (Zurich–Montpellier method) is given in Leggett *et al.* (2002a).

#### *Vegetation transects*

Vegetation transect lines were established in eight focal areas of the catchment. The point of origin for the transects was chosen as the major permanent water source (either borehole, wetland or spring) in seven of the focal areas, with the only exception being the Serengeti transects where point of origin was the Hoanib riverbed. Only one southern transect was undertaken at Kaross due to the large number of water sources in the northern section of the park. The direction of each transect was deliberately chosen to exclude the influence of any other water point. At nine plots (geology and geography permitting), data were recorded at 0 m (water source), 500 m, 1, 2, 3, 4, 5, 6 and 7 km along each of the transect lines. Plots were assessed for vegetation species and abundance by the Zurich–Montpellier method (Braun-Banquet, 1932; Mueller-Dombois & Ellenberg, 1974; Werger, 1974; Bonham, 1989; McAuliffe, 1990). Trees, shrubs, grasses and forbs were identified by National Botanic Research Institute (NBRI) of Namibia.

Three surveys (one dry and two wet seasons) were undertaken at each of the plots along the transect lines. The wet season in the Hoanib River catchment can begin as early as October and finish as late as April the following year. For the purposes of this study, the wet season is named in the year that the last rains fell. For example, if the rains began in the October 1999 and ended in April 2000, this period is referred to as the 2000 wet season. The dry season is the period between April (after the last falls of rain) and the end of October (or the start of the first rains).

The same plots were used for vegetation studies during both wet and dry season surveys. Only those species of tree and shrub that were carrying leaf were identified and analysed. Those trees and shrub species that are normally deciduous and become dormant during the dry season were not taken into account during the surveys. However, even species known to be deciduous were counted if they were carrying any leaf at the time of the surveys.

#### *Veld condition*

An evaluation method for veld condition developed by du Plessis *et al.* (1998a, b) was used to assess the veld. The method involves the classification of grass species into either 'Decreasers' or 'Increasers' (Trollope, 1990) depending on how the species respond to grazing pressure. Species were categorized as follows:

*Category 1:* Species dominant in underutilised veld ('Increaser 1' species),

*Category 2:* Species abundant in lightly grazed veld, decreasing with under- or overutilized veld ('Decreasers'),

*Category 3:* Species with low abundance in underutilized or lightly grazed veld which tends to increase in abundance when vegetation is moderately grazed ('Increaser 2a'),

Category 4: Species that are more abundant in moderately overutilized veld ('Increaser 2b'),

Category 5: Species becoming dominant in severely overutilized veld ('Increaser 2c').

The grass species (annuals and perennials) present in each plot were recorded in the same manner as described for cover abundance (Leggett *et al.*, 2002a).

### Statistical analysis

As physical condition varied from season to season, parametric statistics could not be applied to the data. Non-parametric statistics in the form of the Kruskal–Wallis ANOVA/Median test was used to test the significance of the data sets of the observed transects. The Mann–Whitney *U*-test was used to compare data around water sources and non-linear regression analysis was used on the 'dead grass' data.

## Results

### Vegetation abundance

The average catchment-wide abundance of ground cover, bare ground, tree and shrub canopy cover, 'dead' grass, annual grass, perennial grass and forbs are presented in Figs. 2–8.

There was a significant difference in average ground cover (tree, shrub, grass and forb) abundance between the 1999 and 2000 wet seasons ( $\chi^2 = 26.536$ ,  $p < 0.001$ ). There was also a seasonal difference in average ground cover between the 2000 wet and dry seasons ( $\chi^2 = 24.424$ ,  $p < 0.001$ ). While there was a decrease in the ground cover abundance near water points (0 km), this was not statistically significant ( $U = 161.5$ ,  $p = 0.216$ ).

The abundance of bare ground varied across the catchment seasonally and annually. A significant decrease in bare earth was observed from the 1999 to 2000 wet seasons ( $\chi^2 = 9.647$ ,  $p = 0.0019$ ). In addition, a significant decrease was observed in bare earth between the 2000 wet and dry seasons ( $\chi^2 = 39.76$ ,  $p < 0.001$ ); however, little difference was observed in bare earth between the 1999 wet season and the 2000 dry season.

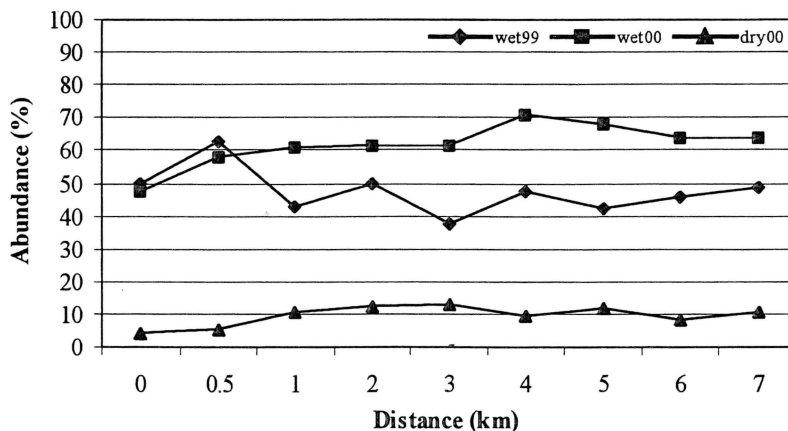
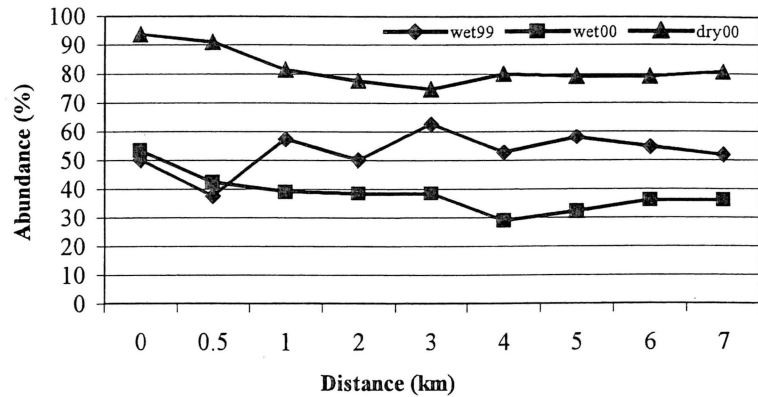
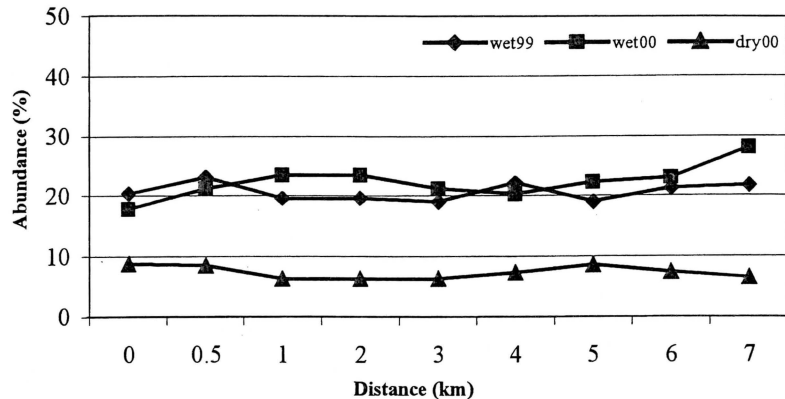


Figure 2. Average wet and dry season ground cover abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.



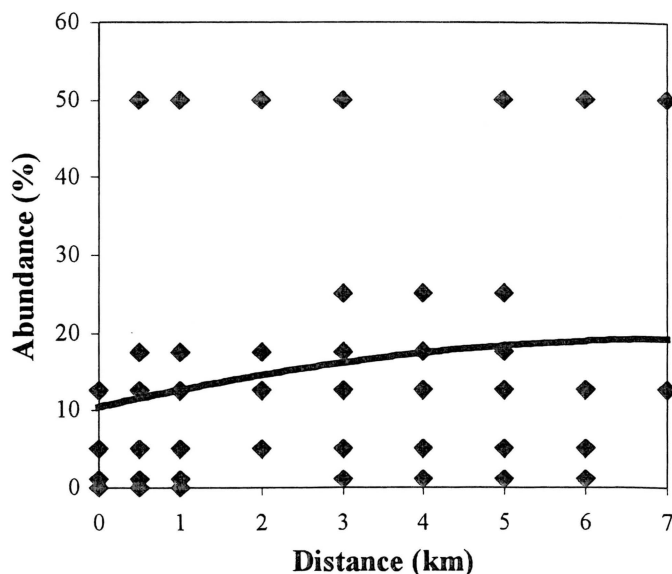
**Figure 3.** Average wet and dry season bare ground abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.



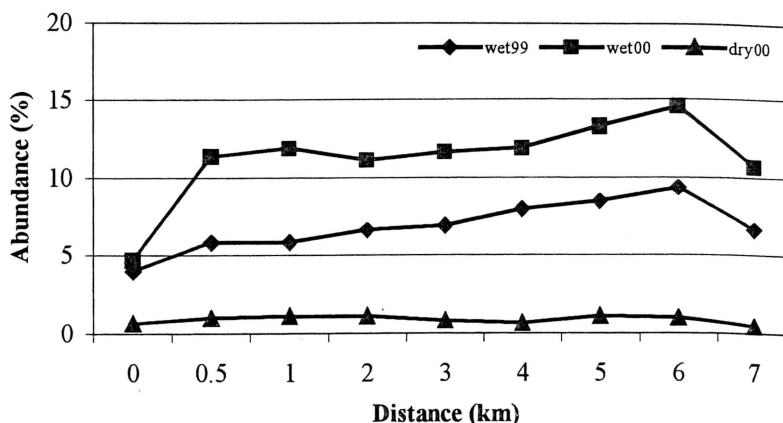
**Figure 4.** Average wet and dry season tree and shrub canopy cover abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.

There appeared to be a significant seasonal variation in the canopy cover of trees and shrubs between the 1999 and 2000 wet seasons across the catchment ( $\chi^2 = 10.277$ ,  $p = 0.001$ ). The 2000 dry season canopy cover was significantly lower than both the 1999 and 2000 wet seasons ( $\chi^2 = 7.439$ ,  $p = 0.006$  and  $\chi^2 = 36.085$ ,  $p < 0.001$ , respectively). The standing 'dead grass' (dried stalks of annual and perennial grasses) abundance was surveyed during the 2000 dry season. The average standing 'dead grass' abundance across the catchment varied from between 0.5–12.5%. The minimum standing 'dead grass' abundance was observed closest to water points (0 km) and maintained a relatively constant abundance after 2 km distance from the water point ( $r = 0.8901$ , variance = 79.23%).

The abundance of the annual grasses varied both annually and seasonally. The 2000 wet season had a significantly greater annual grass abundance than the 1999 wet season ( $\chi^2 = 3.878$ ,  $p = 0.049$ ). Both wet seasons annual grass abundance was significantly greater than that of the dry season ( $\chi^2 = 61.073$ ,  $p < 0.001$  for 1999 and  $\chi^2 = 127.895$ ,  $p < 0.001$  for 2000). While there was a decrease in annual grasses abundance within 1.0 km of a water point, this was not significant ( $U = 31.5$ ,  $p = 0.065$ ).



**Figure 5.** Average dry season dead grass abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.



**Figure 6.** Average wet and dry season annual grass abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.

There appeared to be no significant annual difference in perennial grass abundance across the catchment ( $\chi^2 = 0.388$ ,  $p = 0.534$ ). Overall, the abundance of perennial grasses was relatively low; however, local abundance was observed (e.g. Serengeti plains, Khowarib and Sesfontein). There was also little seasonal difference in perennial grasses between the 1999 and 2000 wet and 2000 dry seasons ( $\chi^2 = 1.523$ ,  $p = 0.217$  for 1999 and  $\chi^2 = 0.663$ ,  $p = 0.416$ ).

There appeared to be little annual difference in forb abundance between the 1999 and 2000 wet seasons ( $\chi^2 = 0.130$ ,  $p = 0.789$ ). However, there was a significant seasonal difference in forb abundance with both wet seasons having a greater abundance than the dry season ( $\chi^2 = 5.628$ ,  $p = 0.018$  for 1999 and  $\chi^2 = 7.895$ ,  $p = 0.005$  for 2000). There was an increase in average abundance of annual forbs within 1.0 km of a water point but it was not significant ( $U = 184$ ,  $p = 0.507$ ).

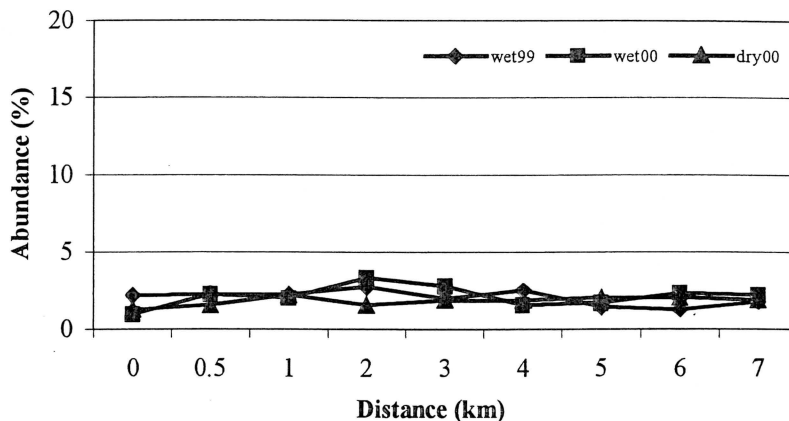


Figure 7. Average wet and dry season perennial grass abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.

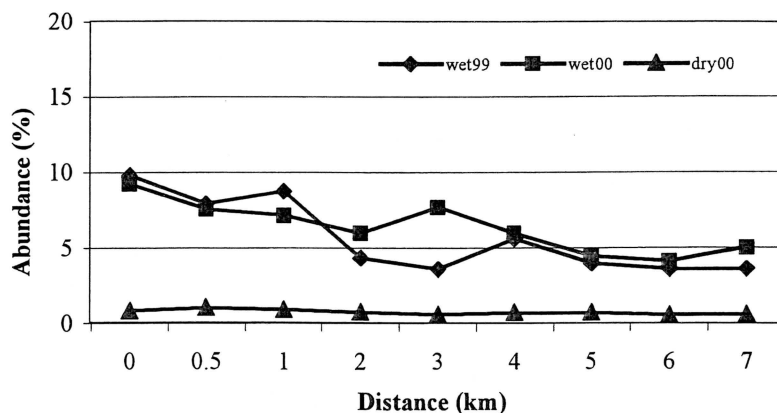


Figure 8. Average wet and dry season annual forb abundance during 1999 and 2000 in the Hoanib River catchment, north-western Namibia.

#### Vegetation phenology

A summary of the number of species of trees and shrubs, grasses and forbs found in the transect plots is presented in Table 1.

Seventy-five species of woody trees and shrubs were identified in the Hoanib River catchment transects during the 1999 and 2000 wet seasons. The most dominant tree and shrub species throughout the catchment was *C. mopane*. In the higher rainfall sections of the eastern catchment, *C. mopane*, *Terminalia prunioides* and *Combretum apiculatum* were dominant. As the rainfall decreased, *C. mopane* formed stands with *T. prunioides*. In the drier areas, *C. mopane* formed stands with both *T. prunioides* and *Acacia tortilis*. The dwarf shrub species of *Leucosphaera bainesii* (bitter bush), *Monechma salsola* and *Petalidium englerianum* were common throughout the catchment. The only species found to carry leaf during the dry season were *A. erioloba*, *Boscia albitrunca*, *B. foetida*, *Faidherbia albida*, *Maerua parvifolia*, *M. schinzii* and *Salvadora persica*.

Of the 49 grass species observed across the catchment, 46 are annual species and of these *Antheophora schinzii*, *Eragrostis porosa*, *Kaokochloa nigrirostris*, and



**Table 1.** A summary of the number of species of trees and shrubs, grasses and forbs found during the 1999 and 2000 wet seasons and the 2000 dry season in transect plots in the Hoanib River catchment, north-western Namibia

	No. of species of trees and shrubs		No. of species of grasses		No. of species of forbs	
	Wet season	Dry season*	Wet season	Dry season	Wet season	Dry season
Otjokavare	36	18	24	3	76	10
Hobatere	30	19	27	6	70	32
Kaross	28	21	24	2	37	15
Palmfontein	21	17	14	4	35	29
Omuramba	21	12	32	2	39	13
Serengeti plains	17	13	24	5	36	12
Khowarib	15	13	15	1	37	6
Sesfontein	20	15	18	3	32	8
Mean and	23.5	16.0	22.3	3.3	45.3	15.6
S.D. (in brackets)	(±7.2)	(±3.3)	(±6.2)	(±1.7)	(17.3)	(±9.6)

\*Only those species that were carrying leaf at the time of the survey were included in the analysis.

*Stipagrostis hirtigluma* were the most abundant. During the dry season very few annual grass species were observed. The four annual grass species listed above had greater abundance in order of magnitude than other observed annual species. The abundance of annual grass species also appeared to change with the amount of rainfall. For example, during the 1999 wet season (rainfall ca. 100 mm), the dominant annual grass on the Serengeti plain was *K. nigrirostis* (avg. abundance 50–75%) with lesser abundance of *S. hirtigluma* (avg. abundance 12.5–25%). However, in the same plots during the 1999–2000 wet season (rainfall ca. 300 mm), *K. nigrirostis* and *S. hirtigluma* had a similar average abundance (25–50%).

The only perennial grasses observed in the catchment were *S. hochstetteriana*, *S. namaquensis*, and *S. uniplumis*. The abundance of perennial grasses was lowest in the eastern section of the catchment, while they formed a significant proportion of the grass abundance on the Serengeti, Khowarib and Sesfontein plains.

Ninety-seven different annual forb species were collected from the transect plots during this study. Of these only 41 species were identified by the NBRI, while the remaining 56 species remain unidentified. Annual forbs were found to be abundant in all plots during the wet season; however, they were most abundant in diversity and number in plots around water points and in highly disturbed area (human settlements and areas of intensive agricultural activity). *Tribulus zeyheri* and *Zygophyllum* spp. were found to be the most abundant of the annual forb species and were encountered in nearly all transect plots. A large reductions in the number of species and abundance of forbs was observed during the dry season.

## Discussion

### *Annual and seasonal variation in vegetation*

There appeared to be a strong catchment-wide correlation between abiotic factors (mainly rainfall) and vegetation growth. In particular, the abundance of annual grasses and annual forbs seemed to be dependent on seasonal rainfall. The abundance of

perennial grasses and cover abundance of trees and shrubs appeared less dependent on seasonal variability, although increased growth and flowering in all species was observed after higher rainfall events. The increased growth of annual grasses provided a significant standing 'dead layer' of grasses that was observed during the following 2000 dry season. This 'dead layer' was not observed during the 1999 dry season as the growth of annuals was significantly less. Most of the observed dead layer was thought to be *S. hirtigluma* which was observed to have formed large stands of grasses during the 2000 wet season.

There appeared to be little difference in the abundance of perennial grasses over much of the catchment, while in most areas and across the seasons, the abundance appeared to be relatively low. However, a relatively high abundance of perennial grasses (*S. uniplumis* and *S. hochstetteriana*) was observed on the Serengeti, Khowarib and Sesfontein plains after the above average rains of the 2000 wet season. These two species are regarded as 'decreasers' (Category 2) (du Plessis *et al.*, 1998*a, b*), that is they are only found in underused or slightly used veld. It is possible to describe the Serengeti plains as an underused veld as there are few water points and it is only grazed seasonally by domestic stock and wildlife. However, the Khowarib and Sesfontein plains have long been regarded as an overused and degraded area (Van Warmelo, 1962; Loxton, Hunting & Associates, 1974; Nærva *et al.*, 1993; MAWRD, 1997) and the presence of and abundance of 'decreaser' species indicated a disparity with previous researchers. A possible explanation for this disparity could be the growth behaviour of the perennial grasses in this arid environment. In the western section of the Hoanib River catchment, where below-average rains are regularly recorded for several consecutive seasons, perennial grasses are thought to exhibit a similar growth form to annual grasses. They 'die back' soon after seeding, if insufficient moisture is available to maintain growth throughout the dry season. During the 1999 wet season, a small percentage of perennial grasses on the Khowarib and Sesfontein plains were observed to sprout new leaf (in comparison to the 2000 season). Few of those that sprouted leaf were observed to carry this leaf through to the following wet season. Therefore, when the rains fell, both perennial and annual grasses grew at approximately the same rate. However, if the wet season provided above-average rains, as was the case during the 2000 wet season, the perennial grasses retained leaf (i.e. did not die back to a tuft) throughout the dry season.

The seasonal variation in vegetation was marked. The abundance of bare ground increased dramatically during the dry season to be the most abundant parameter. The abundance of all vegetation species decreased to their lowest at this time. Many tree and shrub species lost their leaves and in many of the areas only *Boscia* spp. and *Maerua* spp. remained with leaf. The same was true for annual grasses and forbs with low abundance observed for both vegetation types. Similar results were reported by Skarpe (1986) in the central Kalahari Desert, Botswana. Only perennial grasses retained leaf into the dry season, but again this only occurred due to the above-average rainfalls of the 2000 season.

The seasonal dependence of vegetation growth on variable rainfall supports the non-equilibrium argument that has been proposed by a number of authors in arid lands (e.g. Ellis & Swift (1988) and specifically Sullivan (1996, 1999).

#### *Spatial and temporal distribution of vegetation*

The distribution of vegetation communities in the Hoanib River catchment is similar to those reported by Becker & Jurgens (2000) for an area 200 km to the north of the focus area. The vegetation communities in the Hoanib River catchment could be divided into the following groups and approximate rainfall zones. The *C. mopane*, *T. prunioides* and *Com. apiculatum* communities in the eastern section of the catchment

correspond approximately to the 250–350 mm rainfall zone (Otjokavare, Hobatere, Kaross and Palmfontein). *C. mopane* and *T. prunioides* communities correspond approximately to the 150–250 mm rainfall zone (Serengeti plains and Omuramba). *C. mopane*, *T. prunioides* and *A. tortilis* communities and grasslands dominated by *S. hirtigluma*, *S. uniplumis* and *S. hochstetteriana* that correspond approximately to the 100–150 mm rainfall zone (Khowarib, Warmquelle and Sesfontein). In the very western section of the catchment, the more permanent grasslands dominated by *S. uniplumis* corresponding approximately to the 50–100 mm rainfall zone (west of Sesfontein).

The area around the water sources, up to a radius of 2 km, was found to have a low species diversity and abundance (with the exception of forbs). This area was affected by the disturbance caused by constant animal movement in both the wet and dry seasons and has been termed by a number of authors (Perkins & Thomas, 1993; Ringrose *et al.*, 1997) as a 'sacrifice zone' or 'high-impact zone'. This zone tended to be larger during the dry season and contracted during the wet season; however, over the study period the zone existed in all areas, regardless of rainfall. Annual forbs dominated this zone, mainly due to the fact that forbs could establish themselves rapidly and were not particularly palatable to domestic stock. Only annual grass species that could cope with disturbed environments occurred here *E. porosa*, and *Monelytrum luederitzianum*). Very few perennial grasses, shrubs and trees were found in the immediate area around the water source. Large trees (> 10 m height) were found in this zone as they were large enough not to be knocked over by domestic stock nor have their foliage browsed significantly, though distinct browse lines were observed. These results were similar to those observed by Perkins & Thomas (1993) in Botswana.

Outside the 'high-impact zone', there appeared to be little change in vegetation abundance and number of species. There tended to be a decrease in the abundance of annual forbs and an increase in annual grass abundance. Perennial grasses, shrub and tree abundance appeared to remain relatively constant for the remainder of the distance plots. The term 'overgrazed' has often been used to describe the communal areas of north-western Namibia (Van Warmelo, 1962; Loxton, Hunting & Associates, 1974; Nærva *et al.*, 1993; MAWRD, 1997), and the most abundant species of grasses occurring in the Hoanib River catchment are symptomatic of moderately-to-severely overused veld. Perennial grasses that are generally associated with 'lightly' grazed veld (du Plessis, 1998a, b), exist in areas normally associated with overgrazing (Khowarib and Sesfontein). A possible explanation for the relative stability of grass species and abundance is probably because all the grass species (annual and perennial) behave similarly in a below-average or average rainfall year. That is, they germinate or sprout quickly at the onset of rain, have a short growing season, seed and then 'die-off' when the land dries out. It is only in the exceptional, above-average rainfall years that the perennials retain some leaf growth throughout the dry season. This could be a special adaptation of certain perennial grasses to survive in low and erratic rainfall regimes.

The almost constant abundance and number of species of both annual and perennial grasses across the study area would support Sullivan (1996, 1999) and cast doubt on the theory, especially in non-equilibrium conditions, that traditional pastoralism leads to a decrease in species within a climatic zone (Du Toit & Cumming, 1999).

#### *Implications of a non-equilibrium system on animal populations*

The long dry season in semi-arid and arid areas of the world can produce long intervals of nutritional deprivation for ungulates (Mosi *et al.*, 1976; Pratt & Gwynne, 1977; Coppock *et al.*, 1986). Studies conducted in North America under similar

environmental constraints to arid areas of Africa showed that livestock could endure up to 6 months on 'sub-maintenance' grazing (Schwartz & Ellis, 1981). This was also observed for African arid areas by Coppock *et al.* (1986), who reported that in the Turkana region of Kenya, domestic stock were able to survive during the dry season for up to 6 months on below the minimum standards of nutrition. Cattle, donkeys, sheep and goats were reported to survive on 70%, 80%, 83% and 95%, respectively, of the minimum nutritional requirements recommended by National Research Council (Coppock *et al.*, 1986).

During the dry season in the Hoanib River catchment, areas that contained higher concentrations of domestic stock (Otjokavare and Omuramba) tended to have very little available grazing and browsing. At this time of the year, both domestic stock and wildlife were observed grazing on dead *C. mopane* leaves and seedpods of the *F. albida* trees. In particular, wildlife was observed to congregate in the riverbed during the dry season, primarily feeding on the seedpods and leaves of *F. albida*. Elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*) and gemsbok (*Oryx gazella*) were observed eating the bark and pods of *F. albida* and *C. mopane* trees (Leggett *et al.*, 2002b). Domestic stock, particularly goats, were observed to browse extensively on the *F. albida* trees as well as numerous shrub species (for example, *Grewia* spp.). However, in most areas along the Hoanib River, the browse heights of *F. albida* were too high for goats to browse extensively. In areas of the catchment, where the dried stalks from the previous seasons annual grasses were available, domestic stock were observed eating the bark and pods of *F. albida* and *C. mopane* trees (Leggett *et al.*, 2002b). Domestic stock, particularly goats, were observed to graze extensively. Coppock *et al.* (1986) reported a similar behaviour. The food habit of livestock from here ranged from grass-dominated (96%) for cattle, to browse-dominated (95%) for camels, while goats, sheep and donkeys tended to be mixed feeders on herbaceous and non-herbaceous vegetation. Livestock were thought to obtain their crude protein and bulk feed from dry grass with supplementary protein from browsing. Sheep and goats increased their nitrogen intakes by eating the seedpods of *A. tortilis* (Coppock *et al.*, 1986).

Immediately before and just after the first rains of the wet season, numerous tree species (*C. mopane*, *Grewia* spp., *T. prunioides*, *Com. apiculatum* and some *Commiphora* spp.) sprouted leaves that were readily browsed by both domestic stock and wildlife. This new vegetation was usually available before the annual and perennial grasses had germinated or sprouted leaf. Wildlife was observed to leave the riverbeds and trek many kilometres into the hills to browse on other more palatable species (*Commiphora* spp.), immediately after the onset of the first rains (Leggett *et al.*, 2002b). Similar observations to these were reported by Skarpe (1986) for Kalahari Desert, Botswana, where some species of trees and shrubs (*B. albitrunca*, *Lycium namaquensis*, *Grewia flava* and *Rhus tenuinervis*) had the habit of sprouting in advance of the wet season to take advantage of any early rains. This was dependent on the 'carry over' moisture from the previous seasons.

During a drought in the Hoanib River catchment where below-average rains fell for several consecutive years, very little grazing was available for animals; however, some of the animals survived for long periods. In the 1980–82 drought, the whole of north-west Namibia received three consecutive years of low rainfall (in the 1981 season, no rain fell in Sesfontein). During this period, 90% of the domestic stock and 80% of some wildlife species died (Viljoen, 1982). Many of the animals did not die in the first season of the drought but survived well into the second year feeding entirely on available browse (Leggett *et al.*, 2002b). Trees and shrubs normally sprout leaves, even during below-average rainfall years, and provide browsing even when there is little available grazing, this would be sufficient to sustain animal populations. However, during the second year of the drought very few of the trees sprouted new buds, depriving animals of nutrition and hence, the large mortality (R. Loutit pers. comm.). The natural resistance and resilience of this ecosystem to droughts and disturbance

has been discussed in Leggett *et al.* (2002a). However, it would appear as though the abundance and availability of browse during below-average rainfall years and drought is what sustains animals for long periods. Grazing appears to be the 'bonus' to the system in that it may only be available irregularly for short periods of time, but when available supports both domestic stock and wildlife populations.

### Summary

The Zurich–Montpellier method of vegetation assessment was used to assess the vegetation in the Hoanib River catchment during the 1999 and 2000 wet seasons and the 2000 dry season. The 2000 wet season had above-average rainfall across all areas of the catchment, which induced copious vegetation growth. The annual and seasonal abundance of ground cover, bare earth, canopy cover, annual grass, perennial grass and annual forbs were measured in eight focus-study areas located across the catchment. The abundance and distribution of vegetation varied both annually and seasonally and was dependent on seasonal rainfall. The amount of dry season grazing was also dependent on the previous seasons rainfall, with 'dead grass' and perennial grass being only available after 'above-average' rainfall season.

The vegetation in the Hoanib River catchment appeared to be in a non-equilibrium state responding to annual rainfall rather than land use.

The spatial and temporal distribution of vegetation was also investigated. There appeared to be four different vegetation communities that corresponded roughly to annual rainfall. Mixed *C. mopane* woodlands dominated from 350 to 100 mm rainfall zone, while perennial grasses (predominantly *S. uniplumis*) dominated the 50–100 mm rainfall zone. Around water sources, there was a reduction in the vegetation diversity and abundance with the area dominated by annual forbs. This 'high-impact zone' appears to vary seasonally but rarely extends beyond a 2 km radius even in the dry season. Outside this zone, there appeared to be very little disturbance to the vegetation.

The long dry season causes particular problems for domestic stock and wildlife and during these periods, animals were observed to eat dried stalks of grass, fallen leaves, bark and buds of trees from the previous seasons growth and when available, seed pods of the *F. albida*. In a variable rainfall zone such as the Hoanib River catchment, the degree to which grazing and browsing supports domestic stock and wildlife varies from one season to the next. It is not uncommon to have several years in succession with below-average rainfall and limited grazing and browsing. Under these conditions, it appears that browsing assumes a greater role in maintaining animal populations. During a drought when no grazing is available, the domestic stock and wildlife rely on the browsing. When there is insufficient rain to stimulate the shrubs and trees to bud, large mortalities were observed in animal populations.

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### References

- Becker, T. & Jurgens, N. (2000). Vegetation along climate gradients in Kaokoland, North-West Namibia. *Phytocoenologia*, **30**: 543–565.

- Behnke, R. (1993). Natural resource management in pastoral Africa. *Paper presented to the UNEP Workshop on Listening to the People: Social Aspects of Dry land Management*, Nairobi, Kenya.
- Behnke R. & Scoones I. (1993). Rethinking range ecology: implications for rangeland management in Africa. In: Behnke R., Scoones I. & Kerven C. (Eds), *Range Ecology at Disequilibrium: New Models of Natural Variability & Pastoral adaptation in African Savannas*, pp. 1–30. London, U.K.: IIED/ODI/Commonwealth Secretariat. 210 pp.
- Behnke R.H., Scoones, I. & Kerven, C. (Eds) (1993). *Range Ecology at Disequilibrium: New Models of Natural Variability & Pastoral Adaptation in African Savannas*. London: U.K. ODI/IIED/Commonwealth Secretariat. 248 pp.
- Bonham, C.D. (1989). *Measurement for Terrestrial Vegetation*. New York: Wiley. 338 pp.
- Braun-Blanquet, J. (Ed.) (1932). *Plant Sociology: The study of Plant Communities*. [Translated from German by G.D. Fuller and H.S. Conrad.] New York: McGraw-Hill. 439 pp.
- Coppock, D.L., Swift, D.M. & Ellis, J.E. (1986). Seasonal nutritional characteristic of livestock diets in a nomadic pastoral ecosystem. *Journal of Applied Ecology*, **23**: 585–595.
- Dankwerts, J.E. & Stuart-Hill, G.C. (1988). The effect of severe drought and management after drought on the mortality and recovery of semi-arid grassveld. *Journal of the Grasslands Society of South Africa*, **5**: 218–222.
- Dean, W.R.J. & Macdonald, I.A.W. (1994). Historical changes in stocking rates of domestic stock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. *Journal of Arid Environments*, **26**: 281–298.
- Dodd, J.L. (1994). Desertification and degradation in Sub-Saharan Africa: the role of livestock. *BioScience*, **44**: 28–34.
- Downing, B.H. (1978). Environmental consequences of agricultural expansion in South Africa since 1850. *South African Journal of Science*, **74**: 147–152.
- DRFN (2001). *NAPCOD—An Overview from 1994–2001. Overview*. Windhoek, Namibia: Desert Research Foundation of Namibia. 18 pp.
- du Plessis, W.P., Bredenkamp, G.J. & Trollope, W.S.W. (1998a). Response of herbaceous species to a degradation gradient in the western region of Etosha National Park, Namibia. *Koedoe*, **41**: 9–18.
- du Plessis, W.P., Bredenkamp, G.J. & Trollope, W.S.W. (1998b). Development of a technique for assessing veld condition in Etosha National Park, Namibia, using key herbaceous species. *Koedoe*, **41**: 19–29.
- Du Toit, J.T. & Cumming, D.H.M. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, **8**: 1643–1661.
- Ellis, J.E. & Swift, D.M. (1988). Stability of African pastoral ecosystems: alternative paradigms and implications for development. *Journal of Rangeland Management*, **41**: 450–459.
- Ellison, L. (1960). Influence of grazing on plant succession of rangelands. *Botanical Review*, **26**: 1–78.
- Giess, W. (1971). A preliminary vegetation map of South West Africa. *Dinteria*, (Windhoek, Namibia) **4**.
- Jacobson, P.J., Jacobson, K.M. & Seely, M.K. (1995). *Ephemeral Rivers and Their Catchments: Sustaining People and Development in Western Namibia*. Windhoek, Namibia: Desert Research Foundation of Namibia. 160 pp.
- Leggett, K.E.A., Fennessy, J. & Schneider, S. (2001). *Rainfall, Water Sources and Water Use in the Hoanib River Catchment, Northwest Namibia*, Vol. 15, pp. 37–75. DRFN Occasional Paper. 85 pp.
- Leggett, K.E.A., Fennessy, J. & Schneider, S. (2002a). Does land use matter in an arid environment? A case study from the Hoanib River catchment, Northwestern Namibia. *Journal of Arid Environments*, in press.
- Leggett, K.E.A., Fennessy, J. & Schneider, S. (2002b). A study of animal movement in the Hoanib River catchment, Northwestern Namibia. *Journal of African Zoology*, in review.
- Loxton, R.F., Hunting & Associates (1974). *The Natural Resources of Damaraland*. Unpublished report undertaken for the Department of Bantu Administration and Development, Pretoria.
- Maggs, G.L., Kolberg, H.H. & Hines, C.J.H. (1994). Botanical diversity in Namibia — an overview. *Strelitzia*, **1**: 93–104.
- Maggs, G.L., Craven, P. & Kolberg, H.H. (1998). Plant species richness, endemism and genetic resources in Namibia. *Biodiversity and Conservation*, **7**: 435–446.

- Malan, J.S. & Owen-Smith, G.L. (1974). The ethnobotany of Kaokoland. *Cimbebasia*, 2: 131–178.
- McAuliffe, J.R. (1990). A rapid survey method for estimation of density and cover in desert plant communities. *Journal of Vegetation Science*, 1: 653–656.
- Ministry of Agriculture, Water & Rural Development (MAWRD) (1997). *Detailed Land Use Plan for the Sesfontein Constituency*. Windhoek, Namibia: TRP Associates. 172 pp.
- Mosi, A.K., Tessema, S. & Temple, R.S. (1976). Livestock nutrition in the dry tropics of Africa. In: Fomesbeck, P.V., Harris, L.E. & Kearn, L.C. (Eds). *Proceedings of the First International Symposium on Feed Composition, Animal Nutrient Requirements and Computerisation of Diets*, pp. 392–400. Logan: Utah Agricultural Experiment Station, Utah State University.
- Mueller-Dombois, D. & Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. New York: Wiley. 315 pp.
- Muller, M.A.N. (1984). *Grasses of South West Africa/Namibia*. Windhoek, Namibia: John Meinert Publishers. 278 pp.
- Mwalyosi, R.B.B. (1992). Influence of livestock grazing on range condition in south-west Masailand, Northern Tanzania. *Journal of Applied Ecology*, 29: 581–588.
- Nærua, T., Devereux, S., Frayne, B. & Harnett, P. (1993). *Coping with Drought in Namibia: Informal Social Security Systems in Caprivi and Erongo, 1992*. NISER Research Report. Windhoek, Namibia: 12 Multidisciplinary Research Centre, University of Namibia. 119 pp.
- Perkins, J.J. & Thomas, D.S.G. (1993). Spreading deserts or spatially confined environmental impacts? Land degradation and cattle ranching in the Kalahari desert of Botswana. *Land Degradation and Rehabilitation*, 4: 179–194.
- Pratt, D.J. & Gwynne, M.D. (Eds) (1977). *Rangeland Management and Ecology in East Africa*. London: Hodder and Stoughton. 310 pp.
- Ringrose, S., Vanderpost, C. & Matheson, W. (1997). The use of image processors and GIS techniques to determine the extent and possible causes of land management/fencing induced degradation problems in the Okavango area, Northern Botswana. *International Journal of Remote Sensing*, 18: 2337–2364.
- Sandford, S. (1983). *Management of Pastoral Development in the Third World*. Chichester, UK: John Wiley & Sons. 316 pp.
- Schwartz, C.C. & Ellis, J.E. (1981). Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology*, 18: 343–353.
- 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.
- Sullivan, S. (1996). Towards a non-equilibrium ecology: perspectives from an arid land. *Journal of Biogeography*, 23: 1–5.
- Sullivan, S. (1998). People, plants and practice in drylands: socio-political and ecological dimensions of resource use by Damaraland farmers in north-west Namibia Ph.D. thesis, University College, London. 448 pp.
- Sullivan, S. (1999). The impacts of people and livestock on topographically diverse open wood- and shrub-lands in arid north-west Namibia. *Global Ecology and Biogeography Letters, Special Issue on Degradation in Open Woodlands*, 8: 257–277.
- Trollope, W.S.W. (1990). Development of a technique for assessing veld condition in Kruger National Park using key grass species. *Journal of the Grassland Society of South Africa*, 7: 46–51.
- Van Warmelo, N.J. (1962). Notes on the Kaokoveld (South West Africa and its people). *Ethnological Publications*, Vol. 26. Pretoria: Department of Bantu Administration.
- Viljoen, P.J. (1980). Veldtypes, Verspreiding van die groter Soogdiere, en enkele Aspekte van die Ekologie van Kaokoland. M.Sc. thesis, Pretoria, South Africa (unpublished).
- Viljoen, P.J. (1982). The distribution and population status of the larger mammals in Kaokoland, South West Africa/Namibia. *Cimbebasia*, 7: 5–33.
- Wenger, M.J.A. (1974). On concepts and techniques applied in the Zürich–Montpellier methods of vegetation survey. *Bothalia*, 11: 309–323.