

# ECOLOGICAL DYNAMICS OF CENTRAL NAMIBIA'S SAVANNAS: PART 1 – GRASS ECOLOGY

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## ABSTRACT

The ecological processes of the three dominant savannas found in central Namibia, namely the Highland, Thornbush and Camelthorn savannas, are explained with a state-and-transition model that incorporates aspects of Clementsian succession as well as Walter's two-layer theories. A savanna can persist either in a grassy or in a woody (bushy, bush-encroached) state. Within each, climax and pioneer states with higher and lesser production potential exist. The first part of this article describes the grassy states. Transitional forces and events that shift savannas between and within states are described in detail, as well as the opportunities and risks these changes bear for the land manager. A transition that should be avoided at all cost is that from pioneer grassy state to desertification, because desertification is believed to be irreversible in practice. A critical state occurs when the grassy is changed to a bushy state, but this is discussed in greater detail in Part 2 of this article.

## INTRODUCTION

A savanna is a tropical or near-tropical rangeland that consists of a continuous herbaceous layer and an open, discontinuous woody layer. It is subject to pronounced seasonal fluctuations in terms of productivity and nutritive value (Skarpe, 1991). The balance between the herbaceous and the woody layer is determined by ecological processes such as climate (mainly rainfall and temperature), soil fertility, incidence of naturally-ignited fires, animal activity, etc., as well as by human factors such as anthropological fires, fire exclusion, selective defoliation of the various plant components, etc. When the grass – bush balance is disrupted, and there is an excessive densification of the woody component at the expense of the grasses, bush encroachment has occurred (Smit, Richter & Aucamp, 1999). Bush encroachment drastically reduces the grass-based carrying capacity of a rangeland (Adams & Werner, 1990). It has affected most of the savannas and dry woodlands (Bester, 1998) that cover 84 % of Namibia's land area (Mendelsohn, Jarvis, Roberts & Robertson, 2009). It is a problem of national significance and has severe economic implications, causing beef producers an estimated loss of N\$ 700 million per year in foregone income because of the drastically reduced production potential of cattle ranches (De Klerk, 2004). Bush encroachment has always existed in Namibia on a small scale, e.g. around oft-frequented

water holes (Vedder, 1934), but the inundation of whole landscapes by bush is a relatively recent phenomenon. Accordingly, a lot of research has yet to be done as our current knowledge of savanna ecological dynamics is far from complete (Ward, 2005). It is believed that these ecological processes are very similar in the three dominant savanna types found in central Namibia, i.e. the Highland, Thornbush and Camelthorn savannas (Giess, 1971).

When Westoby, Walker and Noy-Meir (1989) devised the state-and-transition model to better explain ecological dynamics in an environment in constant disequilibrium, it caused a paradigm shift in the perception of how semi-arid southern African savannas work and function (e.g. Milton & Hoffman, 1994; Rothauge, 2000; Smit, 2003). The state-and-transition theory includes elements of Clements' (1928) dated classical vegetation succession theory and Walter's (1971) two-layer model of competition between herbaceous and woody components of savanna vegetation. The proposed ecological model of central Namibia's savannas is based mainly on these theories and models, applying in principle to the Highland savanna, the Thornbush savanna to its north and the Camelthorn savanna to its east. This series of papers investigates the ecological processes of central Namibia's savannas (Joubert, Rothauge & Smit, 2008), firstly the ecology of grassy states and then that of woody states, so that the major problem of landscape-level bush encroachment can be better understood and dealt with.

## ECOLOGICAL CHARACTERISTICS OF THE HIGHLAND SAVANNA OF CENTRAL NAMIBIA

Most of the research for this paper was performed on the farms Neudamm and Krumhuk in the Highland savanna of central Namibia, which will be briefly characterised below. It is one of the smaller vegetation types, occupying only 45 000 km<sup>2</sup> or 5,5 % of Namibia's land area (calculated from Coetzee, 1998). It is probably the vegetation type that has the longest been exposed to commercial ranching; since the late nineteenth century (Rawlinson, 1994). Highland savanna occurs at altitudes of 1 350 m to 2 200 m above sea level and with some extremely steep slopes of more than 30°. The terrain is highly broken and undulating. Typical mountain soils are lithic leptosols, overlying base material of sandstone and metamorphic schists. They are shallow, contain a lot of gravel, extremely low in organic matter content, leached (pH = 5,5), relatively infertile (e.g.

phosphorus content < 25 ppm) and erodible because of their low clay content (< 8 %). A surface layer of quartzitic pebbles that reaches a cover of almost 100 % on steep slopes is a notable feature and influences vegetation dynamics by serving as a mulch that improves soil moisture content (Joubert, 1997).

Typically for this sub-tropical area, precipitation is seasonal and 80 % or more of the total annual rainfall of 373 ± 158,6 mm occurs from January to March (Rothauge, 2008). Rainfall is highly variable with a coefficient of variation of more than 40 % and decreases from north-east to south-west. Due to the high evaporation rate, the annual water deficit exceeds 2 000 mm (Mendelsohn *et al.*, 2009). In summer, average maximum temperatures (about 29 °C) are cooler than in lower-lying neighbouring savannas, while winters are fairly cold (average minimum temperature is 3 °C, but -9 °C is recorded regularly) and frost occurs about 20 nights per year (Mendelsohn *et al.*, 2009). The early onset of low night-time temperatures results in a very short vegetative growing period of 40 to 60 days (Coetzee, 1998).

Giess (1971) described the Highland savanna as characterised by woody species including *Acacia hereroensis*, *Acacia hebeclada*, *Acacia reficiens*, *Albizia anthelmintheca*, *Dombeya rotundifolia*, *Euclea undulata*, *Ozoroa crassinervia*, *Rhus marlothii* and *Tarchonanthus camphoratus*. Notably, *Acacia mellifera* is missing from this list of characteristic species, despite it being the dominant woody species in large parts of the Highland savanna today, and recognised as the major species involved in bush thickening (Bester, Van Eck, Kölling, Van Rooyen & Prinsloo, 2002). Climax grass species include *Antheophora pubescens*, *Brachiaria nigropedata*, *Cymbopogon* spp., *Digitaria eriantha* and *Heteropogon contortus*. Sub-climax grasses such as *Eragrostis nindensis* and *Schmidtia pappophoroides* are usually the most abundant (e.g. Kellner, 1986; Joubert, 1997). Kellner (1986) described the Highland savanna as mostly an *Acacia hereroensis* – *Eragrostis nindensis* alliance but, due to the topographical diversity, it is quite heterogeneous.

The Highland savanna has a high degree of animal and plant biodiversity and endemism in comparison to other regions of Namibia (Barnard, 1998). The higher altitude biomes (e.g. the Auas mountains) support a number of reptile, insect and plant species with a severely restricted range. Despite this, only 0,2 % of the Highland savanna is managed as government-protected conservation areas (Barnard, 1998). Due to the undulating terrain and the proximity of mountain refuges, large ungulate herbivores (e.g. kudu, gemsbok, hartebeest, warthog) and their associated predators (e.g. jackal, caracal, cheetah, leopard) have always been common and occur freely. Their movement is little impeded by obstructions associated with human utilisation of the range, such as fences.

The predominant land use in the Highland savanna is ranching for profitable beef production on privately owned farmland. Livestock is free-ranging within large camps,

dependent on natural vegetation and receives only small inputs of nutritional supplements, labour and management (Pagot, 1992). Commercial farms are typically 5 000 hectares to 10 000 hectares in extent and sub-divided into camps to facilitate planned rotational grazing and livestock management. According to the International Development Consultancy (IDC; 2005), commercial ranchers maintain a fairly static stocking rate of about 15 ha per Large Stock Unit (LSU). Communally farmed areas constitute less than 15 % of the Highland savanna and are less sub-divided. While also focussing on beef production, much more use is made of sheep and goats. These domestic livestock species are stocked at a combined rate of about 4,5 ha/LSU (IDC, 2005). Communal production is predominantly for subsistence.

Irrespective of land ownership, livestock ranching activities have not been successful in maintaining the Highland savanna rangeland in a productive state. Degradation of soil and rangeland is widespread (Bester *et al.*, 2002). This, together with a decline in the comparative profitability of meat production and the high income potential of tourism and ecotourism (Elkan, Van der Linde & Sherbourne, 1993), prompted a switch to game ranching on privately-owned guest and hunting farms. It was initially thought that conservancies, in which groups of ranches are partially managed together to enhance the sustainable utilisation of game animals, would reduce the negative impact of game ranching on the vegetation, but there is growing concern that this is not the case.

#### ECOLOGICAL STATES AND TRANSITIONS BETWEEN STATES: THE BASIC MODEL

Typically, central Namibian savannas occur in two basic states that can be sub-divided further according to the advancement of degradation (Figure 1). A savanna can either be in a grassy state or in a bush-encroached (woody, bushy) state. In the grassy state, the continuous herbaceous and the discontinuous woody layer of the savanna are still in balance, giving the impression of an open rangeland in which the woody component occurs at “natural density”. In the bushy state, the density of the woody component has increased far beyond its probable “natural density” and is more continuous while the herbaceous layer is breaking up and discontinuous.

In-between these two basic states is a transitional state, not shown in Figure 1, that of bush seedling establishment. In savannas in the transitional state, the invasive woody species (in this case *Acacia mellifera*) proliferates and starts to invade the landscape. This is a crucial phase in the ecology of the savanna as intervention at this stage can nip bush encroachment in the bud.

Various degradation forces and events shift the condition of the savanna from climax to pioneer condition and within the woody state from vigorous to the fully mature, senescent condition. These transitions pose a threat to the land user, as they diminish the potential of the rangeland to

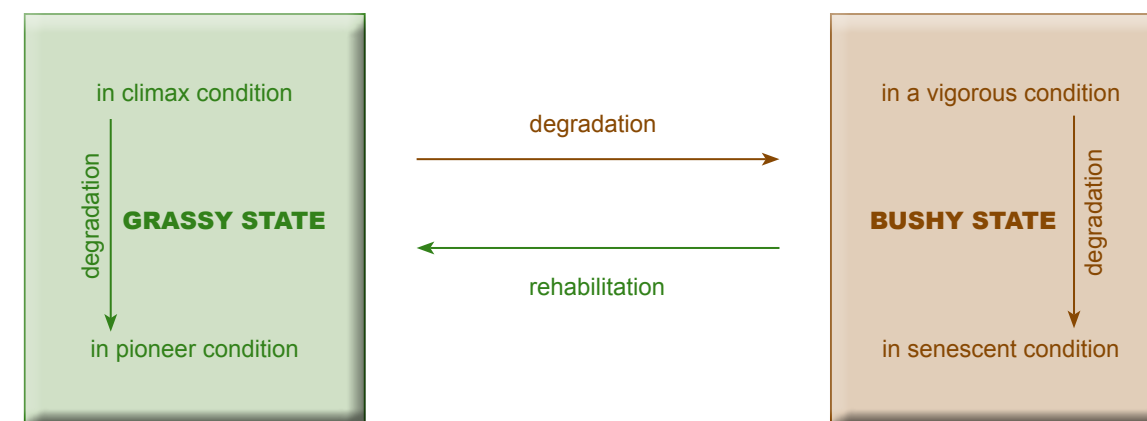


Figure 1. The two basic states of a semi-arid savanna in central Namibia.

sustain animal production. Rehabilitative transitions work in the opposite direction to improve the condition of the savanna. They present opportunities for the land user to restore the rangeland’s production potential. Eventually, a full, comprehensive model emerges (Figure 2) that offers land managers a multitude of opportunities to manipulate the savanna to suit their objectives, within the constraints

of local ecological conditions. On a single ranch, or within a community’s core grazing area, the savanna can be in different states in different places and different forces may be at work pushing the savanna in different directions; thus creating a mosaic of heterogeneous patches and a plethora of conditions and transitions within the rangeland.

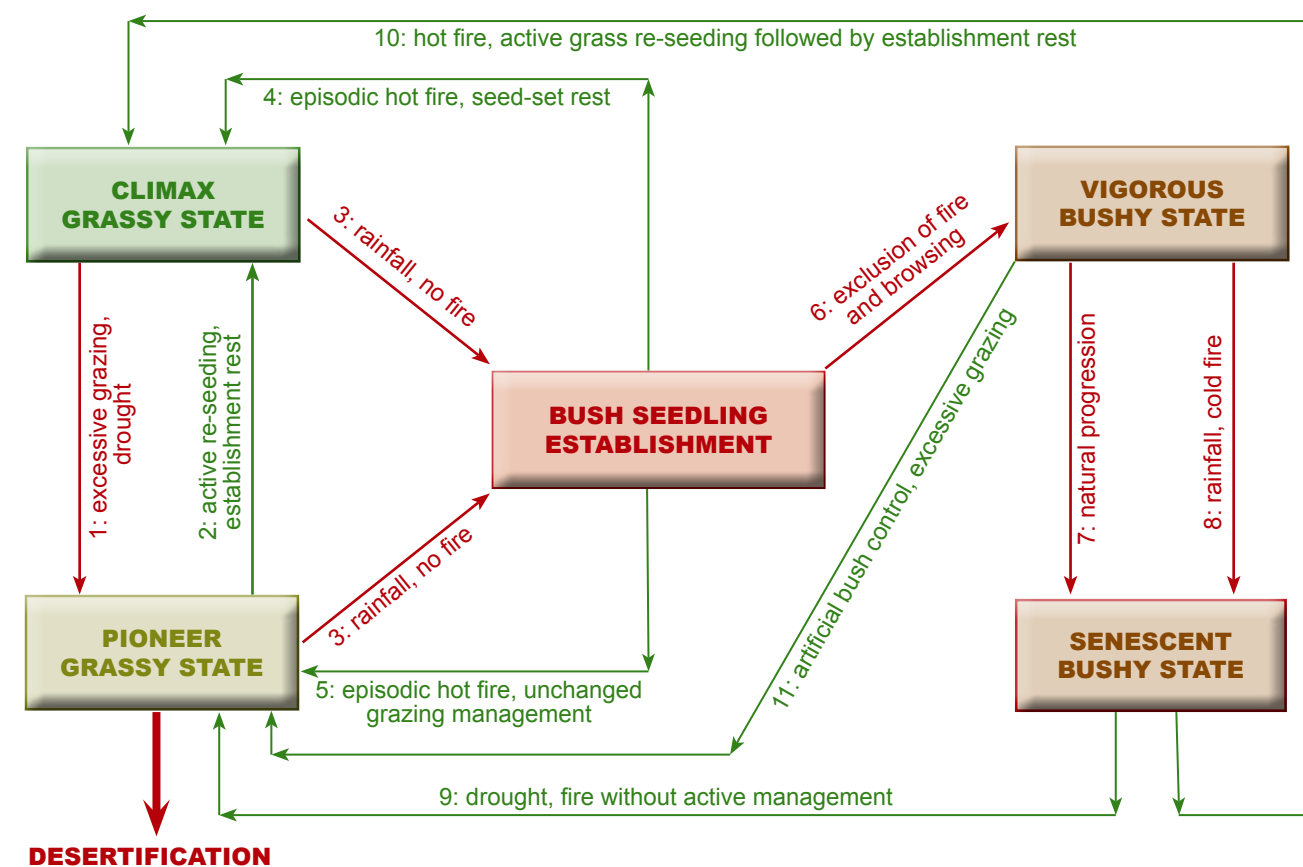


Figure 2. Complete schematic presentation of the five states of the Highland savanna and the eleven transitions between states (red = degradation and green = rehabilitation transitions).

## THE DETAILED ECOLOGICAL MODEL

### 1. The climax grassy state

The grassy state in good condition is dominated by mesophytic climax perennial grasses that can achieve a long-term average canopy cover in excess of 75% (Rothauge, 2007) or a basal cover of up to 12% (Joubert, 1997). More than 70 species of perennial grasses occur, of which about half are climax or sub-climax species (Van Eck, 2007). Depending on the topographical unit, the typically dominant grasses include *Schmidtia pappophoroides*, *Eragrostis nindensis*, and *Antheophora pubescens* (Joubert, 1997; Rothauge, 2007). In dry years, annual grasses are almost absent, but in wet years, palatable annual grasses such as *Melinis repens* subsp. *grandiflora* and *Enneapogon cenchroides* form a significant part of the sward due to favourable conditions for germination (Rothauge, 2007). The grass-based carrying capacity varies with rainfall, ranging between 5 to 20 ha/LSU (Rothauge, 2007), although the average over the last 20 years was around 13 ha/LSU (Mendelsohn *et al.*, 2009). Such a grass sward of palatable, perennial grasses is able to support highly productive beef cattle production systems.

A wide variety of forbs may contribute up to 15% of the herbaceous layer (Rothauge, 2007). These include many leguminous species and perennials with fleshy roots of the *Aizoon*, *Aptosimum*, *Chascanum*, *Indigofera* and *Lotononis* genera. Their value to domestic livestock lies mainly in the contribution of small amounts of highly nutritious feed at critical times of the year, especially during the hot-dry season (Rothauge, 2006a).

Woody vegetation in the climax grassy state seldom exceeds a canopy cover of 10% and is dominated by 2 m to 3 m high single-stemmed *Acacia hereroensis* (Joubert, 1997; Rothauge, 2007). This species appears to have a greater ability than other *Acacia* species to survive fire, regenerate through coppicing and tolerate harsh frost (Rothauge, 2006b). Woody species co-dominating the climax state are *Rhus marlothii* and *Tarchonanthus camphoratus*, which are also fire-tolerant (Rothauge, 2006b). Other species such as *Boscia albitrunca* and *Albizia anthelmintheca* form a small, but consistent component of this state on stony soil while *Acacia erioloba* is common only in the deep loamy soils of river valleys (Rothauge, 2007). *Acacia mellifera* is typically rare in the climax state on a landscape scale because its immature cohort is susceptible to frost, fire and competition by the vigorous, perennial grass sward.

Natural fires maintain the Highland savanna in a climax grassy state. Early-season dry thunderstorms often ignite fires naturally in high-lying areas,

because lightning has a propensity to strike mountain tops. Mountain fires are difficult to contain due to the rugged terrain. If natural fires follow on wet years, they are very hot (fierce) because of the accumulation of grass fuel and often ravage extensive areas. They either destroy woody plants outright, or burn off their above-ground parts (top-kill), forcing them to coppice again. Coppiced bushes are weakened and revert to an immature state in which they do not produce seeds. Their canopy is now within easy reach of browsers. Many coppiced bushes eventually succumb to the after-effects of the fire within 2 to 5 years (Rothauge, 2006b), or are killed off by next season's fire.

Perennial grasses are not seriously affected by hot, early-season fires that follow on wet years. Copious or late rains during the preceding season result in surplus soil moisture carried over to the next season. This moisture induces an early-season, reserve-driven growth flush of perennial grasses that makes the tuft base green, moist and more tolerant of an early-season fire. Mountainous areas of the Highland savanna are thus more often in State 1 (climax state) than hilly or flat terrain, with appreciably less woody cover and an excellent sward of perennial grasses, and represent vegetation in a fire climax state.

### 2. Transition 1 towards a pioneer grassy state

When the climax grassy state degrades to the pioneer state, it does so along a continuum of changes in especially the herbaceous component (Joubert, 1997). It mirrors a classical retrogressive Clementsian succession. Transformation of the species composition of the grass sward towards less desirable perennial species and later, annual grass species is the first sign of deterioration of the rangeland. In the adjacent semi-arid camelthorn savanna to the east, this transformation occurs when long-term stocking rates exceed 30 ha/LSU or 15 kg cow mass per hectare (Figure 3) (Rothauge, 2006a). Transition towards a pioneer grassy state decreases the sustainability of ranching

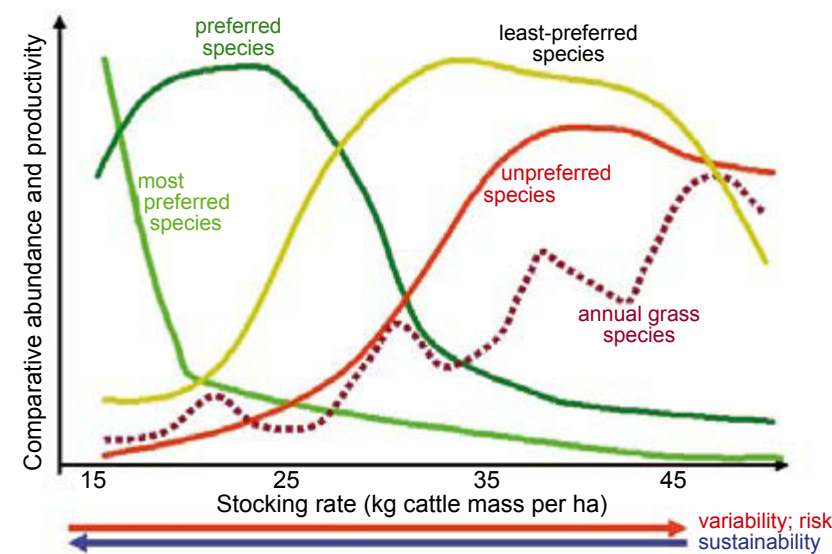


Figure 3. Transformation of the grass sward of the Camelthorn savanna due to increasing the long-term stocking rate of beef cattle (Rothauge, 2006a).

enterprises and increases farming risk and environmental variability. Mesophytic climax grasses decline in vigour and abundance while xerophytic perennial species fill the void. Valuable climax grasses that are most preferred by grazing herbivores such as *Brachiaria nigropedata* and *Antheophora pubescens* decline dramatically in response to increased grazing pressure. Preferred species such as *Schmidtia pappophoroides* and *Melinis repens repens* decline more gradually (Joubert, 1997; Rothauge, 2006a). Their place in the grass sward is taken by less preferred sub-climax perennial species such as *Stipagrostis uniplumis* and *Eragrostis rigidior*, followed later by unpalatable perennials such as *Aristida stipitata* and annual pioneer grasses such as *Enneapogon cenchroides*, *Eragrostis cylindriflora* and *Chloris virgata*. Such grazing pressure may arise when ranchers overstock parts of their farm to compensate for other parts that are already in a bush-thickened state with a low grazing capacity, or that have suffered an unplanned setback to their herbage production caused by a wild-fire, drought, locust or termite activity or poor grazing planning.

Typical most-preferred perennial grass species in central Namibia are *Antheophora pubescens*, *Brachiaria nigropedata*, various perennial *Panicum* and *Digitaria* species and, in north-central Namibia, *Urochloa oligotricha*. Typical preferred grass species are *Schmidtia pappophoroides*, *Melinis repens repens*, *Eragrostis lehmanniana* and, south-central Namibia, *Centropaudia glauca* and *Stipagrostis obtusa*. Typical least preferred grass species are *Cenchrus ciliaris*, *Stipagrostis uniplumis*, *Eragrostis rigidior* and *Fingerhutia africana*. Unpreferred species typically include the perennial *Aristida* species and many *Eragrostis* species, e.g. *Eragrostis pallens*.

### 3. The pioneer grassy state

In the grassy pioneer state, the savanna remains grassy and open, but is now dominated by annual pioneer grasses such

as *Aristida stipoides*, *Enneapogon cenchroides*, *Eragrostis cylindriflora*, *Eragrostis porosa*, *Pogonarthria fleckii* and *Tragus racemosus*. Small and low-yielding xeric perennial grasses such as *Aristida congesta*, *Michrochloa caffra*, *Monelytrum luederitzianum* and some resilient, grazing-tolerant, high-yielding bulky sub-climax species like *Stipagrostis uniplumis* are also still present (Joubert, 1997; Rothauge, 2007). Palatable annuals such as *Melinis repens* subsp. *grandiflora* may occur opportunistically in good rainy seasons, but do not dominate. While productivity in exceptional rainfall years may rival that of the grassy climax state, productivity in dry years is extremely low since few annual grasses germinate and grow, eventually leading to smaller cattle size and declining fertility (Figure 4). Grass basal cover can be as low as 0.5% (Joubert, 1997). Poor cover results in capping of the soil surface by the harsh impact of raindrops during thunderstorms and sheet erosion, caused by the overland flow of rainwater rather than its infiltration (Rothauge, 2007).

Woody species still form a relatively small component of the degraded savanna with *Acacia mellifera* perhaps forming a larger proportion than before, since transitions towards encroachment may have occurred at microsite level. However, the abundance of dwarf xerophytic karroid shrubs like *Eriocephalus luederitzianum*, *Leucosphaera bainesii*, *Salsola* spp. and *Monachne* spp. increases noticeably to about 15% (Rothauge, 2007). These small shrubs indicate aridification of the ecosystem. High browsing pressure may prevent further degradation towards a bushy state, despite excellent rains.

The degraded pioneer grassy state represents a hazardous situation for rangeland managers since in years of exceptional rainfall, bush colonisation is initiated and the transition towards landscape-level bush encroachment may easily occur. Even worse is the likelihood of further degradation towards desertification if this state remains self-perpetuating due to the export of rainwater and soil

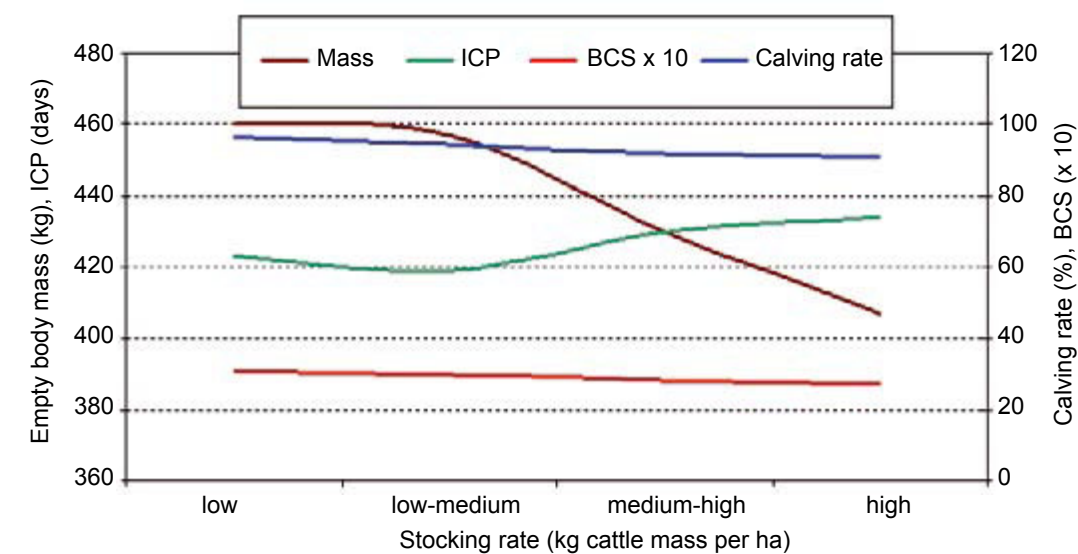


Figure 4. Response of individual cattle to an increase in the long-term stocking rate of the camelthorn savanna (Rothauge, 2006a). ICP: inter-calving period, BCS: body condition score.



nutrients, thus preventing succession towards a climax grassy state, even in years of high rainfall. If large areas have become degraded, seeds of large-seeded climax grasses such as *Brachiaria nigropedata*, *Antheophora pubescens* and *Schmidtia pappophoroides* are likely to be absent since these species are more prone to local extinction than small-seeded species such as *Stipagrostis uniplumis*, *Eragrostis rigidior* and the annual grasses (Owen-Smith & Danckwerts, 1997); further reducing the likelihood of a succession towards the climax grassy state. Such desertification is much more difficult to address than degradation.

#### 4. Continued degradation towards desertification

Continued degradation of the pioneer grassy state due to severe grazing combined with a drought may severely affect basic ecological processes and cause desertification (Skarpe, 1991). Desertification results in the export of nutrients and moisture from the landscape and loss of ecosystem services. The ground water table is lowered due to reduced infiltration of rainwater into the soil due to poor permeability caused by soil capping, overland flow of rainwater and soil erosion (both sheet and gully erosion). The landscape aridifies despite normal rainfall; the so-called “man-made drought” is brought about. Increased exposure of the soil surface to the elements, especially the hard impact of raindrops and the sterilising effect of solar radiation, cause the top layer of soil to heat up. High soil temperature destroys soil microflora and plant seeds, which can no longer germinate in these hostile conditions. Weakened grasses attract grass-eating harvester termites, which compete with herbivorous ungulates for growing grasses. The landscape rapidly slides towards a state that cannot easily be restored and may well result in a permanent reduction of the production potential of the land.

Desertification is considered by Hoffman & Ashwell (2001) to be a serious problem in southern Africa. It represents degradation on a higher level. It is much more difficult in terms of time, knowledge and means to rectify than transformation of the grass sward or bush encroachment; and may not be reversible at all.

#### 5. Transition 2 back towards the climax grassy state

The transition from the degraded pioneer grassy state back to the climax state is no fait accompli brought about by resting and de-stocking only. It requires active management such as overseeding with desired climax grass species followed by establishment rest from grazing, breaking the soil cap (e.g. by using animal impact or a pit plough/“kapploeg”) and slowing the overland flow of rainwater (e.g. by erecting brush barriers or ripping on the contour) in addition to destocking grazing herbivores. However, exclusion of livestock from Namibian farmland is not economically feasible, thus potentially preventing this favourable transition. If the pioneer state occurs on pebble mulch, the transition towards a climax state may be facilitated since the mulch improves infiltration and

reduces evaporation (Joubert, 1997); improving overall soil moisture conditions for mesophytic climax grasses to establish. However, this transition has not been researched and therefore it is difficult to determine whether this transition occurs, if at all. Indications from a similar savanna in Texas are that recovery from a pioneer towards a climax grassy state is reversible, intermittent and may take as long as 25 years (Fuhlendorf, Briske & Smeins, 2001).

Hypothetically, a fire with subsequent lenient grazing may initiate the transition towards the climax state by mineralisation of plant nutrients and clearing the seed bank of the dominant annual grasses and herbs. This allows the few perennial grass tufts that may still be present to expand and set seed. Long and efficient rest periods between grazing events aimed at seed production and subsequent seedling establishment of the mesophytic climax grasses would be essential for these grasses to establish, aided (obviously) by good rainfall. If these perennial grasses are locally extinct, active reseeding is required. The re-introduced grass seeds would have to be protected from insect and bird predation by encasing them in, for example, dung slurry or cakes. The emerging, highly palatable grasses would also have to be protected from over-utilisation by packed thorn branches, ring-fencing, etc. Bare ground offers opportunistic alien invasive plants such as various cacti and the grass *Pennisetum setaceum*, already present in the Highland savanna (Joubert & Cunningham, 2002), a foothold to invade degraded rangelands and are another factor that may prevent recovery towards the climax grassy state.

#### 6. Transition 3 towards the establishment of bush seedlings

This transition towards establishment of *Acacia mellifera* seedlings is easily overlooked in the field because the establishing woody seedlings are unobtrusive and hidden within the grass sward. It represents a crucial ecological turning point that will be discussed in detail in the next part of this article.

#### IN SUMMARY

In summary, central Namibian savannas that are in the climax grassy state have great potential for beef cattle and game ranching. The biggest danger is that these climax states may degrade to a much less productive pioneer state because of excessive grazing and drought, or a combination thereof. A critical contributing factor may be the reduction of the cover of the topsoil, inducing aridification through sheet wash. Once in the pioneer grassy state, perpetuation of over-utilisation may induce desertification; an apparently permanent and highly unproductive condition. Rehabilitation of a degraded grassy savanna may require much more than mere resting and de-stocking, e.g. re-seeding with perennial grasses, breaking the soil cap, treating the symptoms of erosion, etc.

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