Ber. d. Reinh.-Tüxen-Ges. 18, 69-82. Hannover 2006

Vegetation type and dynamics in African savannas

- G.J. Bredenkamp and L.R. Brown -

Abstract

Various savanna types occur in southern Africa, generally with moister savannas in the eastern and dry savanna in the western part of the region. The main functional distinction is between fine-leaved (thorny) savannas in arid nutrient-rich environments and broad-leaved savannas in moist, nutrient-poor environments. The broad-scale distribution on a regional basis is highly predictable from water and nutrient availability in the environment, though both functional savanna types may occur in a mosaic distribution pattern in slightly undulating landscapes, with broad-leaved savanna on sandy, leached crests and fine-leaved savannas on clayey, nutrient-rich valley bottoms.

The management of savanna ecosystems in southern Africa has for a long time been based on the assumption that the dynamics of these ecosystems are by conventional succession, thus, that these systems are stable and in equilibrium. Ecosystems are considered to be of the equilibrium type when plant growing conditions are relatively favourable and stable over time, with low inter-annual variation in rainfall and predictability in timing and magnitude of rainfall. These systems fluctuate around one or more points of equilibrium, to which they return after recovery from a disturbance.

Another way of thinking is that stable equilibria cannot be achieved in many arid or semi-arid ecosystems, though long term persistence might be achievable. Here ecosystem dynamics are controlled by external control mechanisms (abiotic factors), which are not subject to feed-back control from within the ecosystem. These ecosystems are event-driven and non-equilibrial and reactions are not as predictable as in the case of equilibrium systems. The system's dynamics is not dependent on the density of grazing animals, but rather on abiotic factors, often events of drought. A sharp distinction is therefore made between dependent (biotic) factors and independent environmental constraints influencing the system.

From semi-arid to arid southern African savannas examples of vegetation are now described that represent different positions on an equilibrium – non-equilibrium vegetation dynamics gradient. The main determining factor for savanna dynamics is rainfall, which provides plant-available soil moisture. The equilibrium – non-equilibrium gradient is essentially the response of the vegetation along a rainfall gradient, with the moister savanna towards the equilibrium side of the gradient, and arid savanna towards the arid side. Soil texture modifies the position of the different savanna types on the gradient, where the droughty fine-textured soils tend to push the dynamic process towards the non-equilibrium side of the gradient. It is also shown that the woody and herbaceous layers of a particular savanna can occupy different positions on the gradient, implying that, in spite of a very specific tree-grass interaction, these layers may have different dynamic processes. The interplay of soil moisture, soil nutrients, herbivory and fire in savanna dynamics is discussed.

1. Introduction

The management of savanna ecosystems in southern Africa has for a long time been based on the assumption that the dynamics of these ecosystems are by conventional succession, thus, that these systems are stable and in equilibrium (TAINTON & HARDY 1999). This means that natural savanna systems exist in a homeostatic state which is maintained by interactions among its biotic components. If the ecosystems are essentially in equilibrium, controlled mainly by strong biotic interactions, then destabilization and degradation are primarily caused by overstocking, negative feed-back from livestock to plants. In these ecosystems degradation of the herbaceous (grass) layer was considered to be due to disturbances caused by poor land management e.g. overstocking, or fire (BOSCH 1989, BOSCH & JANSE VAN RENSBURG 1987, NEL et al. 1993, VAN ROOYEN et al. 1991), and management aimed at restoring the equilibrium by giving the vegetation the opportunity to recover naturally by reducing grazing animal numbers and managing the fire regime. Management would imply stabilising procedures to reduce consumer density relative to vegetation resources. Classical succession, although an inadequate model to explain all vegetation change, represents this view, and this model is currently still dominating perceptions of ecosystem dynamics (ELLIS & SWIFT 1988).

Another way of thinking is that stable equilibria cannot be achieved in many arid or semi-arid ecosystems, though long term persistence might be achievable. Here ecosystem dynamics are controlled by external control mechanisms (abiotic factors), which are not subject to feed-back control from within the ecosystem (ELLIS & SWIFT 1988). These ecosystems are event-driven and non-equilibrial (WESTOBY 1979, DE ANGELIS & WATERHOUSE 1987, WESTOBY et al. 1989, MENTIS et al. 1989, LAYCOCK 1991, BEHNKE & SCOONES 1993, DODD 1994), and reactions are not so predictable as in the case of equilibrium systems. This means that the system's dynamics is not dependent on the density of grazing animals, but rather on abiotic factors, often events of drought (NOY-MEIR 1975, WIENS 1984). A sharp distinction is therefore made between dependent (biotic) factors and independent environmental constraints influencing the system (ACKER 1990).

ILLIUS & O'CONNOR (1999) argue that savanna ecosystems are spatially and temporally heterogeneous in the strength of the forces tending to equilibrium, which implies that conditions may exist, spatially or temporally, where different processes of dynamics may occur. WIENS (1977), working on bird populations in arid to semi-arid environments, proposed that savanna ecosystems exist along a gradient from equilibrium conditions where biotic interactions structure communities to non-equilibrium conditions where abiotic controls determine system structure and dynamics.

Various savanna types occur in southern Africa, generally with moister savannas in the eastern and dry savanna in the western part of the region (BREDENKAMP 1999, TAINTON 1999, VAN ROOYEN 1999a & 1999b). The main functional distinction is between fine-leaved (thorny) savannas in arid nutrient-rich environments and broad-leaved savannas in moist, nutrient-poor environments (HUNTLEY 1982, SCHOLES 1990). The broad-scale distribution on a regional basis is highly predictable from water and nutrient availability in the environment, though both functional savanna types may occur in a mosaic distribution pattern within tens to hundreds of meters in slightly undulating landscapes, with broad-leaved savanna on sandy, leached crests and fine-leaved savannas on clayey, nutrient-rich valley bottoms.

The degree of herbivory differs markedly between fine-leaved and broad-leaved savannas (SCHOLES 1993). The grass (often Chloridoideae) in microphyllous savanna has NAD or PCK photosynthesis (EHLERINGER et al. 1997) and has a forage protein content sufficient for grazer maintenance throughout the year. This is preferred by grazers, and is named "sweet veld" in South Africa. These grasses have a high rate of litter decomposition and less accumulation of flammable litter (BOND et al. 2003) and therefore experience a smaller frequency of fire. These grasses remain viable without becoming moribund in the absence of fire (TAINTON & MENTIS 1984). On the contrary, the grass component (mostly Andropogoneae) in broad-leaved savanna "sour veld" has NADP-me photosynthesis resulting in high production of material that has a low nutritional value and it becomes extremely fibrous, with tannins (ELLIS 1990), during the dry winter season when it is avoided by grazing animals (SCHOLES 1990, O'CONNOR & BREDENKAMP 1997, BREDENKAMP 1999, BOND et al. 2003). The low nutritional value and tannin content reduce decomposition rates, resulting in accumulation of litter which is highly flammable and consequently fires of high intensity occur frequently in these systems.

Thorny, fine-leaved trees, (mostly Mimosoideae) are also nutrient (protein)-rich and are preferred by browsers (COOPER & OWEN-SMITH 1986), where-as broad-leaved species (Proteaceae Combretaceae, Caesalpinoideae,) are hardly browsed, due to high concentrations of digestion-retarding substances, particularly tannins (SCHOLES 1997). This means that differences in herbivory of the herbaceous and woody components might play a differential role in the dynamics of different southern African savanna ecosystems.

Fire frequencies and intensities differs greatly between fine-leaved and broad-leaved savannas and this is also considered to have marked effects on the dynamics of savanna ecosystems (SKARPE 1992, BOND 1997, TROLLOPE 1999).

Complex spatial and/or temporal variation at various scales, in plant available soil moisture, plant available soil nutrients, herbivores and fire are found in any savanna system (WALKER 1987, SKARPE 1992, BEHNKE & SCOONES 1993, JELTSCH et al. 1999). This leads to a great variety of plant community types (syntaxa), each with a specific plant species composition and structure, with differences in nutritional value to grazers and browsers, differences in accumilation of flammable material, and differences in dynamics.

The aim of this paper is to indicate the variation in dynamic processes within different southern African savanna types.

2. Methods

Vegetation data from various literature sources on different southern African savannas were used to interpret savanna dynamics in different savanna communities over a spectrum of environmental conditions.

3. Results

3.1 Moist Broad-leaved savanna on sandy, nutrient poor soils

This Sour Mountain Bushveld occurs in areas of >600 mm rain on nutrient poor soils derived from sandstone or quartzite.

Examples: Various described plant communities dominated by one or more of the woody *Protea caffra, Faurea saligna* (Proteaceae), *Englerophytum magalismontanum* (Sapotaceae), *Diplorrhynchus condylocarpon* (Apocynaceae), *Croton gratissimus*, *Pseudolachnostylis maprounaeifolia* (Euphorbiaceae) (COETZEE, 1974 & 1975, BREDENKAMP & THERON 1978, BEZUIDENHOUT et al. 1994, WESTFALL et al. 1985, COETZEE et al. 1995, GROBLER et al. 2002, HENNING 2002, VAN STADEN 2002).

The dominant grasses in these systems are often one, or a combination of *Trachypogon spicatus, Tristachya leucothrix, Loudetia simplex, Panicum natalense, Schizachyrium sanguineum, Harpochloa falx, Diheteropogon amplectens* and *Aristida transvaalensis*. These are all “sour” grasses (NADP-me photosynthesis) with low nutrient content, inpalatable and high accumilation of flammable material. They are classified as Increaser 1 species (TROLLOPE et al. 1990, VAN OUDTSHOORN 1991), which increase in abundance when the vegetation is under-utilised by grazers.

In these systems (summer) rainfall during the growing season is relatively high and rather predictable. Adequate soil water is available to plants during the growing season. Both trees and grasses flourish, especially during the early growing season. A dense grass layer develops quickly due to rainfall during early summer. The soils are very low in nutrients and these are quickly utilised by plants and are furthermore also quickly leached from the very coarse sandy soils. During the late summer season nutrient translocation to grass roots occurs and the sour grass becomes unpalatable and is avoided by grazers resulting in a low grazing pressure. This results in a high biomass causing a high fire frequency and intensity. In the next summer season there is again a quick response of the herbaceous layer, especially after a fire.

The system is stable and predictable without much change caused by droughts or grazing. This system is considered to be close to an equilibrium system, though severe drought conditions and manmade drought (caused by overgrazing) may suggest elements of non-equilibrium systems.

3.2 Moist Microphyllous savanna on clayey, nutrient rich soils

This savanna thornveld type occurs in areas of >600 mm rain on nutrient rich soils derived from dolerite or other igneous rocks.

Examples: Sweet *Acacia nigrescens* veld on dolerite within Sour Mountain Bushveld (BREDENKAMP et al. 1989, WINTERBACH 1998), valley or plains Thornveld, dominated by *Acacia karroo* (BREDENKAMP & THERON 1980, FRIEDEL 1987, BREDENKAMP & BEZUIDENHOUT 1990, BEZUIDENHOUT & BREDENKAMP 1991, DU PREEZ & BREDENKAMP 1991).

These systems occur within Sour Mountain Bushveld and likewise receive relatively high, fairly predictable rainfall during the growing season. The soils are however derived from dolerite or other igneous rocks, therefore usually with a high clay content, and are relatively rich in nutrients.

Acacia karroo-dominated systems are often associated with clayey, nutrient-rich alluvial or colluvial soils associated with river banks or the foot of hills within the grassland biome (BEZUIDENHOUT & BREDENKAMP 1991). Woody species associated with this vegetation are *Asparagus suaveolens, A. laricinus, Rhus pyroides, R. lancea, Ziziphus mucronata, Diospyros lycioides* and *Celtis africana.*

Due to the relatively high rainfall, adequate water is normally available to plants, trees and grasses flourish, and a dense grass layer develops. However, due to the clay soils the water retention is relatively high and the soils are therefore physiologically drier than the adjacent sandy soils.

The dominant grass species are often *Panicum maximum* or *P. coloratum* and *Digitaria eriantha*, but being a physiologically dry system, many of the species present may be short-lived. The grass layer has a high production, is nutritious and palatable throughout the year and is preferred by grazing animals, resulting in a high grazing pressure and trampling throughout the year. Consequently the biomass is reduced, which in turn results in a low fire frequency and intensity.

During drought conditions the grass layer is reduced. Even during brief drought periods the top soil layers are desiccated by the hot summer conditions. Continued high grazing pressure may completely diminish the herbaceous layer, which may change to dominance of *Urochloa mosambicensis*, *Chloris virgata*, *Bothriochloa insculpta* or other species, or only bare soil may remain after certain stochastics events. This usually favours trees, who extract water from deeper soil layers. The reduced herbaceous layer provides open spaces for tree seedlings to establish as soon as water becomes available, resulting in bush increase. Though, there is normally a quick recovery of the herbaceous layer after the following rainfall event. This recovery is even faster if the grazing pressure on the vegetation is released. Although there may be changes in species composition and especially dominance, most herbaceous species that were present may establish again, not only certain pioneer species.

It seems that this is a mixed system, the herbaceous layer being quite unstable, driven by rainfall, drought and (heavy) grazing events, while fire is less important. The tree layer seems to be more stable, though may be favoured by a less vigorous herbaceous layer.

This system is therefore considered to be mainly a non-equilibrium system, especially for the herbaceous layer. The amount of rainfall can periodically be close to the threshold of a dry system and during these periods the clay soils cause physiological drought unfavourable for the maintanance of the herbaceous layer, though with less effect on the woody layer. The dynamics of the woody layer may therefore represent an equilibrium system.

3.3 Dry Broad-leaved savanna on sandy, nutrient poor soils

This savanna type occurs in areas of 300-600 mm rain on nutrient poor soils derived from granite, sandstone or quartzite.

Examples: *Combretum apiculatum* or *C. zeyheri* dominated Bushveld on granite, communities dominated by *Terminalia sericea*, *Burkea africana* or *Ochna pulchra* and Miombo on sandy substrates (VAN DER MEULEN 1979, VAN ROOYEN et al. 1981a, COETZEE 1983, BREDENKAMP 1987, BREDENKAMP & THERON 1990, BROWN et al. 1996, 1997, WINTERBACH 1998)

The rains are unpredictable, usually in the form of thunder storms, intense and of short duration, and in spite of the sandy soils, water runoff can be high, reducing the effectivity of the rainfall. Droughts are often experienced.

When the seasonal summer rainfall period commences, there is a high water penetration into the sandy soils, which have a low water retention and water is freely available to the plants. The herbaceous layer has a quick response to rain, even little rainfall showers, which provide water to the sandy top soil layers. With more rain the nutrients are easily leached into lower soil layers, favouring tree growth.

The herbaceous layer is mostly open (not dense), with many annual plant species (or individuals). The grass component mainly contains sour grasses, e.g. *Eragrostis pallens*, *E. rigidior*, *Perotis patens*, *Schizachyrium jeffreysii*, *Aristida diffusa*, *A. meridionalis*, which becomes unpalatable, with a low nutritional value, during the winter. Sweet grasses may also be present, e.g. *Panicum maximum*, *Digitaria eriantha*, *Anthephora pubescens*, *Schmidtia pappophoroides*, *Themeda triandra*, *Heteropogon contortus*, giving rise to "mixed bushveld" (ACOCKS 1988). Animals may graze this vegetation to the presence of some sweet grasses, though grazing pressure may be only medium, due to the dominance of sour grasses.

The biomass production is medium, due to lack of water and nutrients, and consequently the fire frequency and intensity is also medium.

The herbaceous layer seems to change between equilibrium (dominant?) and non-equilibrium systems, depending on rainfall events and the intensity and length of drought periods, the woody layer is more stable and seems to represent an equilibrium system.

3.4 Dry Microphyllous savanna on clayey, nutrient rich soils

These *Acacia*-dominated systems occur in areas of 300-600 mm rain on clay soils in granite bottomlands or on very clayey montmorillonite soils derived from basalt or other igneous rocks. These soils are considered to be high in nutrients.

Examples: *Acacia nigrescens, A. tortilis* and *A. nilotica*-dominated communities on granite bottomlands and basalt plains (COETZEE et al. 1976, VAN DER MEULEN 1979, COETZEE 1983, BREDENKAMP & THERON 1991, BROWN et al. 1995, 1996 & 1997, WINTERBACH 1998).

Dominant woody species include *Acacia tortilis A.karroo, A. robusta, A. nilotica, A. mellifera, Combretum hereroense, Euclea crispa, Euclea undulata, Gymnosporia buxifolia* and *Grewia flava.* Prominent grass species are *Panicum coloratum, Themeda triandra, Urochloa mosambicensis.*

The rainfall is relatively low and unpredictable during the summer growing season, whereas the dry season may be long and droughts are often experienced. The drought conditions are enhanced by the slow percolation and high water retention of the clay soils.

Due to the relatively low rainfall, little water penetration and high water retention inadequate water is often available to plants. Little rainfall will wet only the top soil, favouring the grass layer, trees are often dwarfed and widely scattered. The grass is sweet, nutritious and palatable throughout the year, with a relatively high production during the rainy season. Consequently there is high grazing pressure throughout year, resulting in reduced biomass, though in higher rainfall years the biomass may still be high.

Fire frequency and intensity are high with higher rainfall periods, though drop considerably after very dry years due to the lack of fuel.

This vegetation has a quick response to rain and drought events, and the system is considered to be highly fragile, unstable and event driven, with the non-equilibrium system dominant, though it may react as an equilibrium system during higher rainfall periods.

3.5 Arid Microphyllous savanna on very dry, nutrient rich, sandy soils

This type of savanna occurs in areas of <300 mm rain on nutrient poor aeolian sands.

Kalahari Thornveld on Aeolian sand with communities dominated by one or more of *Acacia erioloba, A. haematoxylon* and *A. mellifera* (VAN ROOYEN et al. 1991, LUBBINGE 1999, SMIT 2000).

Contrary to the other microphyllous savannas normally found on fertile, though relatively dry clay soils (due to water retention of the soil), the sandy soils where this vegetation occurs are for long periods so extremely dry that it can support only microphyllous savanna. Due to the very low rainfall these soils are not leached.

The development of both tree and grass is limited by the low rainfall. During dry periods the herbaceous layer is diminished totally and only bare soil is seen. In the rare vent of rain the herbaceous layer responds very quickly, the grass is sweet, palatable and nutritious throughout the year, causing high grazing pressure which rapidly reduces the biomass. Annuals constitute a large proportion of the vegetation in these systems.

Due to very low biomass fire is normally excluded from these systems, though extraordinary rainfall events may result in a denser herbaceous layer which may be prone to rare but devastating fire during its very dry (winter) stage. Fire also cause much damage to the trees in this system as these woody plants are not adapted to fire, as in other more fire-prone savanna ecosystems.

The dynamics of this ecosystem is totally dependant on rainfall and the intensities and duration of drought periods, and is considered to be an event driven, non-equilibrium system.

3.6 Arid Broad-leaved savanna on arid, nutrient rich, clay soils

This savanna type occurs in areas of <300 mm rain on nutrient rich soils mostly derived from basalt or other igneous rock.

Example: *Colophospermum mopane* vegetation (LOUW 1970, WERGER & COETZEE 1978, VAN ROOYEN et al. 1981b, GERTENBACH 1987, O'CONNOR 1992, DEKKER & VAN ROOYEN 1995, DU PLESSIS 2001, STRAUB 2002, SIEBERT et al. 2003).

The vegetation is totally dominated by *Colophospermum mopane*. The reason why this special type of vegetation that occur on dry clay soils is broad-leaved, is still speculative (BOND et al. 2003), and it is difficult to assign this vegetation to a specific soil type (SCHOLES 1990).

Colophospermum mopane is associated with woody species such as *Sclerocarya birrea, Acacia nigrescens, Combretum apiculatum, Kirkia acuminata, Terminalia prunoides*, *Adansonia digitata* and several species of *Grewia* and *Commiphora*. The open grassy undergrowth is mainly made up of annuals such as *Enneapogon cenchroides* and *Aristida* species with a few scattered perennials like *Schmidtia pappophoroides* and *Cenchrus ciliaris*.

In South Africa this savanna type occurs under very dry conditions, mostly on heavy clays where there is little water penetration and high water retention. Both the tree and grass components have to survive arid conditions, though the tree density is usually very high, leaving little space for the herbaceous layer. The herbaceous layer contains many perennial and annual species, but may become totally diminished with only bare soil remaining.

SMIT et al. (1999) calculated that *Colophospermum mopane* will return after 30 years after the woody layer was removed (SMIT & RETHMAN 1998). However, this tree was totally replaced by *Acacia tortilis* on a ploughed field, and no *Colophospermum mopane* seedlings appeared after more than 30 years of vegetation development (STRAUB 2002). The woody layer is under normal arid conditions quite stable, however if harshly impacted on *Colophospermum mopane* is replaced by *Acacia* species.

After a rainfall event the herbaceous layer responds quickly, the grass is sweet and palatable, though there is normally only a low production due to the low rainfall. This leads to low grazing pressure and also low fire frequency and intensity.

This herbaceous layer has a quick response to both rain or drought events, the system is highly fragile (SMIT & RETHMAN 1998, OELOFSE et al. 2000), unstable and event driven, representing a non-equilibrium system.

4. Discussion and Conclusions

The structure and characteristics of savanna systems are the result of interplay between soil water and nutrient availability with fire and herbivores as modifiers in the dynamics of these systems (WALKER 1987, SKARPE 1992, BEHNKE & SCOONES 1993).

Climate (rainfall) is the main driving force for savanna dynamics, determining the overall soil moisture availability to savanna vegetation. The dramatic response of plant biomass production to rainfall or drought clearly indicates the pervasive role of climate on the vegetation dynamics in the arid parts of southern Africa (PAULSEN & ARES 1961, ELLIS & SWIFT 1988). Water availability strongly affects the relative importance of event-driven, independent and inter-active, dependent processes in arid Savannas (NOY-MEIR 1982, WALKER & NOY-MEIR 1982, KNOOP & WALKER 1985, WALKER 1989) as opposed to the "normal" equilibrium dynamic processes in moist savannas.

Differences in the processes of savanna dynamics occur spatially on a regional basis, differentiating between different floristic, structural or functional kinds of savanna on the spatial rainfall gradient (there is also a gradient between the different floristic or structural kinds of savanna). Gradients therefore exist between equilibrium dynamics in wet savannas (close to forest) and non-equilibrium dynamics in very dry savannas (close to desert), as also suggested for birds by WIENS (1984). Principal types of savanna dynamics are points in a continuous spectrum (DE ANGELIS & WATERHOUSE 1987). This implies that different processes of dynamics may occur at any particular site within a particular savanna community, the degree (ratio) of non-equilibrium versus equilibrium processes determines the position of the particular site on the gradient. This ratio may change at a temporal scale, depending on (erratic) rainfall conditions, implying that the position on the gradient of this particular site my change from time to time. Another site within the same community, but at a different spatial area where the rainfall at the time is different, may occupy a different position on the gradient, as the ratio between non-equilibrium and equilibrium processes may differ, due to local differences in water availability.

Disturbances caused by external abiotic factors and biotic interactive mechanisms with feed-back controls both affect and determine the degree and direction of change in savanna ecosystems. Any factor that may affect the effectivity of the rainfall and/or the availability of water to the plants and/or the plant's ability to utilise the water may influence (or contribute to) the position of a particular savanna type, within a specific time period, on the savanna dynamics gradient. These factors include, *inter alia,* soil texture (water holding capacity, water retention), soil chemistry (sodic soils, water retention), soil depth (water volume), topographical position (runoff), temperature (evapotranspiration), animals (grazing, browsing, trampling, excretions), fire and human disturbances.

Plant-available soil nutrients, (often linked with soil texture, which is in turn linked with lithology or sometimes with topographical position in the landscape) are more important in determining savanna types on a spatial gradient than a temporal scale (BREDENKAMP 1986, BREDENKAMP & THERON 1988, SCHOLES 1990). Changes do occur on the temporal scale, but these are normally quite slow, except on the very local scale e.g. animal middens. Although plant-available soil nutrients (are supposed to) favour the woody component (MEDINA 1978, MEDINA & SILVA 1990, SKARPE 1992), it is often observed, even with relatively high rainfall, that fine-textured soils with higher nutrient contents, support less trees (are more open) though has a well developed, dense, herbaceous layer (VAN ROOYEN et al. 1981a, BREDENKAMP 1986, BREDENKAMP & THERON 1988 & 1990, BROWN et al. 1995, 1996 & 1997). Heavy clays seem to retard development of the woody layer in spite of a relatively high nutrient content. This might be due to the water retention in the fine-textured soils, where grasses out-compete the woody plants. It may also be due to poorer root development by the woody plants or root fracturing due to swelling and shrinking in the heavy, vertic clays (GERTENBACH 1978, BREDENKAMP & DEUTSCHLANDER 1994, BREDENKAMP 1999). On the contrary, deep sandy soils with a relatively low nutrient content but less water retention often support a dense woody layer and a more open, weakly developed herbaceous layer (COETZEE 1983, BREDENKAMP & THERON 1988 & 1990, VAN ROOYEN et al. 1981a). At higher rainfall (700-900 mm per annum) nutrient deficiency may become a limiting factor to plant growth (DESHMUKH 1984, SCHOLES 1990).

Fire is on most scales a highly interactive factor in the savanna ecosystem (SKARPE 1992). Natural fires from lightning and man-made fires are common in savannas, with high frequency and intensity in wet savannas where the herbaceous production is high, not so intensively grazed due to unpalatability, and subsequent high accumulation of dry biomass during the dry season (TROLLOPE 1980, 1982, BREDENKAMP 1999, BOND et al. 2003). Drier savannas have a lower production, the grass is mostly palatable and intensely grazed, therefore dry matter accumulation is low and fire occurrence is infrequent and with low intensity (SKARPE 1992, HIGGENS et al. 2000, BOND et al. 2003). After-burn drought, not uncommon in dry savanna systems, may cause the resprouting grass to wilt and die back due to lack of water and/or due to defoliation by grazers, which often prefer to graze on the new grass growth that appear after a fire. Frequent fires under these circumstances may cause changes in plant species composition (OELOFSE et al. 2000), decreases in perennials and increases in annuals and even increases in woody vegetation due to decreased competition from the herbaceous layer (FROST & ROBERTSON 1987, SKARPE 1992).

In spite of the interactions between the woody layer (trees and shrubs) and the herbaceous layer in a particular savanna ecosystem, these two layers may react differently to the factors affecting the system, and may occupy different positions on the savanna dynamics gradient. Although the woody layer is often more stable over shorter temporal scales than the herbaceous layer, and therefore may occupy a position closer to the equilibrium side on the gradient than the herbaceous layer, the tree layer may also react to events which may e.g. cause increase in germination, establishment and survival of woody individuals (e.g. bush encroachment or clumping) or (extra-ordinary) mortality of woody individuals, changing the structure of the savanna.

Although non-equilibrium dynamic systems are considered to lack strong biotic interactions and feed-back controls (NOY-MEIR 1975, 1980, WIENS 1984), meaning that the system's dynamics is not dependent on the density of grazing animals, but rather on abiotic factors, often events of drought, and degradation of the herbaceous layer in these systems are mostly a result of major variations in growing conditions, (e.g. rainfall), forced grazing by domestic livestock (wild animals will either migrate or have high mortality) will still have adverse effects on the vegetation (WESTOBY 1980, MILTON et al. 1994, ILLIUS & O'CONNOR 1999), as this will enhance the drought conditions (man-made drought). Grazed species may loose their competitiveness and decrease while less grazed species increase (BOSCH & VAN RENSBURG 1987, SKARPE 1990, VAN ROOYEN et al. 1991, NEL et al. 1993), or where grazing-tolerant species become dominant in regularly grazed patches (MCNAUGHTON 1979, STUART-HILL & TAINTON, 1989, JELTSCH et al. 1997a). Heavy grazing may result in a change from palatable perennial grasses to unpalatable dicotyledonous forbs or dwarf shrubs, or annuals (ACOCKS 1988, WERGER 1977, BOSCH & VAN RENSBURG 1987, OELOFSE et al. 2000). This is supported by WESTOBY (1979) as he included grazing as an event in the original State and Transition model.

Any particular savanna ecosystem can therefore change its position on the dynamics gradient on the temporal scale, depending on the time spacing of events. These events include both external control mechanisms (abiotic factors), and feed-back control mechanisms (biotic factors) from within the ecosystem. This is more obvious on the dry and less stable (non-equilibrium) side of the gradient.

References

ACOCKS, J.P.H. (1988): Veld types of South Africa. 3rd ed. – Memoirs of the botanical survey of South Africa **57**: 1-146.

ACKER, S.A. (1990): Vegetation as a component of a non-nested hierarchy: a conceptual model. – Journal of Vegetation Science **1**: 683-690.

BEHNKE, R.H. & SCOONES, I. (1993): Rethinking range ecology: implications for rangeland management in Africa. – In: R.H. BEHNKE, I. SCOONES & C. KERVEN (eds.), Range ecology at disequilibrium, pp 1-30. Overseas Development Institute, Londen.

BEZUIDENHOUT, H. & BREDENKAMP, G.J. (1991): The vegetation of the Bc Land Type in the western Transvaal grassland, South Africa. – Phytocoenologia **19** (4): 497-518.

BEZUIDENHOUT, H., BREDENKAMP, G.J. & THERON, G.K. (1994): Syntaxonomy of the vegetation of the Fb land type in the western Transvaal grassland, South Africa. – South African Journal of Botany **60** (1): 72-80.

BOND, W.J. (1997): Fire. – In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.). Vegetation of southern Africa, pp 421-446. Cambridge University Press, Cambridge.

BOND, W.J., MIDGLEY, G.F. & WOODWARD, F.I. (2003): What controls South African vegetation – climate or fire? – South African Journal of Botany **69** (1): 79-91.

BOSCH, O.J.H. (1989): Degradation of the semi-arid grasslands of southern Africa. – Journal of Arid Environments **16**: 165-175.

BOSCH, O.J.H. & JANSE VAN RENSBURG, F.P. (1987): Ecological status of species on grazing gradients on shallow soils of the western grassland biome in South Africa. – Journal of the Grassland Society of southern Africa **4**: 143-147.

BREDENKAMP, G.J. (1986): Ecological Profiles of potential bush encroacher species in the Manyeleti Game Reserve. – South African Journal of Botany **52** (1): 53-59.

BREDENKAMP, G.J. (1987): An overview of the major plant communities of the Manyeleti Game Reserve, Gazankulu, South Africa. – Coenose*s* **2** (1): 29-38.

BREDENKAMP, G.J. (1999): Bushveld. – In: KNOBEL, JOHAN, The Magnificent Natural Heritage of South Africa. Pp 26-33. Sunbird Publishing, Llandudno, South Africa.

BREDENKAMP, G.J. & BEZUIDENHOUT, H. (1990): The vegetation of the Faan Meintjes nature reserve, western Transvaal. – South African Journal of Botany **56** (1): 54-64.

BREDENKAMP, G.J. & DEUTSCHLÄNDER, M.S. (1994): The *Themedo triandrae-Setarietum incrassatae,* a new association from gabbro in the Manyeleti Game Reserve, Gazankulu, South Africa. – Koedoe **37** (2): 43-57.

BREDENKAMP, G.J. & THERON, G.K. (1978): A synecological account of the Suikerbosrand Nature

Reserve, Part I: The phytosociology of the Witwatersrand geological system. – Bothalia **12** (3): 513-529.

BREDENKAMP, G.J. & THERON, G.K. (1980): A synecological account of the Suikerbosrand Nature Reserve, Part II: The phytosociology of the Ventersdorp geological system. – Bothalia **13** (1&2): 199-216.

BREDENKAMP, G.J. & THERON, G.K. (1988): Relations between soil chemistry and plant species distribution in the Manyeleti Game Reserve, Gazankulu, South Africa. – South African Journal of Science **84** (5): 423-427.

BREDENKAMP, G.J. & THERON G.K. (1990) The vegetation of the fersiallitic soils of the Manyeleti Game Reserve. – Coenoses **5** (3): 167-175.

BREDENKAMP, G.J. & THERON, G.K. (1991): The *Eucleo divinori-Acacietum nigricentis*, a new association from the calcareous bottomland clays of the Manyeleti Game Reserve, Eastern Transvaal Lowveld, Gazankulu, South Africa. – Vegetatio **93**: 119-130.

BREDENKAMP, G.J., VAN ROOYEN, N. & DU TOIT, J. (1989): A vegetation and game management plan for Lapalala Game Farms. Veldplan, Pretoria.

BROWN, L.R, BREDENKAMP, G.J. & VAN ROOYEN, N. (1995): The phytosociology of the western section of Borakalalo Nature Reserve, South Africa. – Koedoe **38** (2): 49-64.

BROWN, L.R, BREDENKAMP, G.J. & VAN ROOYEN, N. (1996): Phytosociology of the northern section of the Borakalalo Nature Reserve. – Koedoe **39** (1): 9-24.

BROWN, L.R, BREDENKAMP, G.J. & VAN ROOYEN, N. (1997): Phytosociological synthesis of the vegetation of the Borakalalo Nature Reserve, North-West Province. – South African Journal of Botany **63** (5): 242-253.

COETZEE, B.J. (1974): A phytosociological classification of the vegetation of the Jack Scott Nature Reserve. – Bothalia **11**: 329-347

Coetzee, B.J. (1975): A phytosocological classification of the Rustenburg Nature Reserve. – Bothalia **12**: 561-580

COETZEE, B.J. (1983) Phytosociology, vegetation structure and landscapes of the central district, Kruger National Park, South Africa. – Dissertationes Botanicae **69**: 1-456.

COETZEE, B.J., VAN DER MEULEN, F., ZWANZIGER, S., GONSALVES, P. & WEISSER, P. (1976): A phytosociological classification of the Nylsvley Nature Reserve. – Bothalia **12**: 137-160.

COETZEE, J.P., BREDENKAMP, G.J. & VAN ROOYEN, N. (1995): Plant communities of the Subhumid Cool Temperate Mountain Bushveld in the Pretoria Witbank Heidelberg area. – South African Journal of Botany **61**: 114-122

COOPER, S.M. & OWEN-SMITH, R.N. (1986): Effects of plant spinescence on large mammalian herbivores. – Oecologia **67**: 142-146.

DE ANGELIS, D.L. & WATERHOUSE, J.C. (1987): Equilibrium and non-equilibrium concepts in ecological models. – Ecological Monographs **57** (1): 1-21.

DEKKER, B. & VAN ROOYEN, N. (1995): The physical environment and plant communities of the Messina Experimental Farm. – South African Journal of Botany **61** (3): 158-167.

DESHMUKH, I.K. (1984): A common relationship between precipitation and grassland peak biomass for East and southern Africa. – African Journal of Ecology **22**: 181-186.

DODD, J.L. (1994): Desertification and degradation in Sub-Saharan Africa. – Bioscience **44** (1): 28-34.

DU PLESSIS, F. (2001): A phytosociological synthesis of Mopaniveld. – M.Sc. thesis, University of Pretoria, Pretoria.

DU PREEZ, P.J. & BREDENKAMP, G.J. (1991): Vegetation classes of the south-eastern Orange Free State (Republic of South Africa) and the highlands of Lesotho. – Navorsinge van die Bloemfontein Museum **7** (10): 477-526.

EHLERINGER J.R., CERLING, T.E. & HELLIKER, B.R. (1997): C4 photosynthesis, atmospheric CO_2, and climate. – Oecologia **112**: 285-299.

ELLIS, J.E. & SWIFT, D.M. (1988): Stability of African pastoral ecosystems: Alternate paradigms and implications for development. – Journal of Range Management **41** (6): 450-459.

ELLIS R.P. (1990): Tannin-like substances in grass leaves. – Memmoirs of the Botanical Survey of South Africa **59**: 59-77.

FRIEDEL, M.H. **(**1987): A preliminary investigation of woody plant increase in the western Transvaal and implications for veld assessment. – Journal of the Grassland Society of Southern Africa **4**: 25-30.

FROST, P.G.H. & ROBERTSON, F. (1987): The ecological effects of fire in savannas. – In: WALKER, B.H. (ed.) Determinants of tropical savannas, pp 93-140. ICSU Press, Miami.

GERTENBACH, W.P.D. (1978): Plantgemeenskappe van die gabbro-kompleks in die noordweste van die sentrale distrik van die Nasionale Krugerwildtuin. – M.Sc. thesis, Potchefstoom University for CHE, Potchefstromm.

GERTENBACH, W.P.D. (1987): An Ekologiese studie van die suidelikste Mopanieveld in die Nasionale Krugerwildtuin. – Ph.D. thesis, University of Pretoria, Pretoria.

GROBLER, C.H., BREDENKAMP, G.J. & BROWN, L.R. (2002): Natural woodland vegetation and plant species richness of the urban open spaces in Gauteng, South Africa. – Koedoe **45**: 19-34.

HENNING, B.J. (2002): The ecosystems of the Waterberg Biosphere Reserve and its relevance to ecotourism. – Ph.D. thesis, University of Pretoria, Pretoria.

HIGGENS, S.I., BOND, W.J. & TROLLOPE, W.S.W. (2000): Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. – Journal of Ecology **88**: 213-229.

HUNTLEY, B.J. (1982): Southern African Savannas. – In: B.J. HUNTLEY & B.H. WALKER (eds.) Ecology of tropical savannas. Ecological Studies **41**:101-119. Springer-Verlag, Berlin.

ILLIUS, A.W. & O'CONNOR, T.G. (1999): On the relevance of non-equilibrium concepts to arid and semi-arid grazing systems. – Ecological Applications **9** (3): 798-813.

JELTSCH, F., MILTON, S.J. DEAN, W.R. & VAN ROOYEN, N. (1997a): Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. – Journal of Vegetation Science **8**: 177-188.

JELTSCH, F., MILTON, S.J. DEAN, W.R. & VAN ROOYEN, N. (1997b): Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. – Journal of Applied Ecology **34**: 1497-1508.

JELTSCH, F., MOLONEY, K. & MILTON, S.J. (1999): Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. – Oikos **85**: 451-466.

KNOOP, W.T. & WALKER, B.H. (1985): Interactions of woody and herbaceous vegetation in a southern African savanna. – Journal of Ecology **73**: 235-253.

LAYCOCK, W.A. (1991): Stable states and thresholds of range condition on North American rangelands: A viewpoint. – Journal of Range Management **44** (5): 427-433.

LOUW, A.J. (1970): ‚n Ekologiese studie van Mopane-veld noord van die Soutpansberg. – D.Sc. Agric thesis, University of Pretoria, Pretoria.

LUBBINGE, J.W. (1999): 'n Fitososiologiese studie van die suidelike Kalahari duineveld. – M.Sc. thesis, University of Pretoria, Pretoria.

MCNAUGHTON, S.J. (1979): Grazing as an optimising process: grass-ungulate relationships in the Serengeti. – American Naturalist **113**: 691-703.

MEDINA, E. (1978): Requirements, conservation and cycles of nutrients in the herbaceous layer. – In: WALKER, B.H. (ed.) Determinants of tropical savannas, pp 39-36. ICSU Press, Miami.

MEDINA, E. & SILVA, J.F. (1990): Savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. – Journal of Biogeography **17**: 403-413.

MENTIS, M.T., GROSSMAN, D., HARDY, M.B. O'CONNOR, T.G. & O'REAGAIN, P.J. (1989): Paradigm shifts in South African range science, management and administration. – South African Journal of Science **85**: 684-687.

MILTON, S.J., DEAN, W.R.J., DU PLESSIS, M.A. & SIEGFRIED W.R. (1994): A conceptual model of arid rangeland degradation. – Bioscience **44**: 70-76.

NEL, P.J., BREDENKAMP, G.J. & VAN ROOYEN, N. (1993): Ecological status of grass species in the red turfveld of the Springbok Flats Turf Thornveld, Transvaal. – South African Journal of Botany **59** (1): 45-49.

NOY-MEIR, I. (1979): Structure and function of desert ecosystems. –Israel Journal of Botany **28**: 1-19.

NOY-MEIR, I. (1980): Structure and function of desert ecosystems. – Israel Journal of Botany **28**: 1-19.

NOY-MEIR, I. (1982): Stability of plant-herbivore models and possible application to savanna. – In: B.J. HUNTLEY & B.H. WALKER (eds.), Ecology of tropical savannas, pp 591-609. Springer-Verlag, Berlin.

O'CONNOR, T.G. (1992): Woody vegetation-environment relations in a semi-arid savanna in the northern Transvaal. – South African Journal of Botany **58** (4): 268-274.

O'CONNOR, T.G. & BREDENKAMP, G.J. (1997): Grassland. – In*:* COWLING, R.M., RICHARDSON, D.M. & PIERCE, S.M. (eds) Vegetation of Southern Africa, pp 215-257. Cambridge University Press, Cambridge.

OEFOLSE, J., BROCKETT, B.H., BIGGS, H.C. & EBERSOHN, C. (2000): The effect of drought and post fire grazing on the herbaceous layer of shrub mopane veld on basalt in the Kruger National Park, South Africa. – Vith International Rangeland Congress Proceedings Vol. I: 505-507.

PAULSEN, H.A. & ARES, F.N. (1961): Trends in carrying capacity and vegetation on arid southwestern range. – Journal of Range Management **14**: 78-83.

SCHOLES, R.J. (1990): The influence of soil fertility on the ecology of southern African savannas. – Journal of Biogeography **17**: 417-419.

SCHOLES, R.J. (1993): Nutrient cycling in arid grasslands and savannas: its influence on pattern, productivity and stability. – Proceedings of the 17th International Grasslands Congress. International Grassland Society, Palmerston North.

SCHOLES, R.J. (1997): Savanna. – In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.), Vegetation of southern Africa, pp 258-277. Cambridge University Press, Cambridge.

SIEBERT, F., BREDENKAMP, G.J. & SIEBERT, S.J. (2003): A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. – Bothalia **33** (1): 121-134.

SKARPE, C. (1990): Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. – Journal of Applied Ecology **27**: 873-885.

SKARPE, C. (1992): Dynamics of savanna ecosystems. – Journal of Vegetation Science **3**: 293-300.

SMIT, G.N. & RETHMAN, N.F.G. (1998): The influence of tree thinning on the reproduction dynamics of *Colophospermum mopane*. – South African Journal of Botany **64** (1): 25-29.

SMIT, G.N., RICHTER, C.G.F. & AUCAMP, A.J. (1999): Bush encroachment: an approach to understanding and managing the problem. – In: N.M. TAINTON (ed.), Veld management in South Afri-

ca, pp 246-260. University of Natal Press, Pietermaritzburg.
SMIT, J.H.L. (2000): Fitososiologie en veldbestuur van die oostelike Kalahari doringveld. – M.Sc. thesis, University of Pretoria, Pretoria.
STRAUB, A.F. (2002): Vegetation study of Breslau Game Farm in Northern Province, South Africa. – M.Sc. thesis, University of Pretoria, Pretoria.
STUART-HILL, G.C. & TAINTON, N.M. (1989): The competitave interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. – Journal of Applied Ecology **26**: 285-298.
TAINTON, N.M. (1999): The ecology of the main grazing lands of South Africa. – In: N.M. TAINTON (ed.), Veld management in South Africa, pp 23-50. University of Natal Press, Pietermaritzburg.
TAINTON, N.M. & HARDY, B.M. (1999): Introduction to the concepts of development of vegetation. – In: N.M. TAINTON (ed.), Veld management in South Africa, pp 1-21. University of Natal Press, Pietermaritzburg.
TAINTON, N.M. & MENTIS M.T. (1984): Fire in grassland. – In: BOOYSEN, P. DE V. & TAINTON, N.M. (eds.). Ecological effects of fire in South African Ecosystems. Springer-Verlag, Berlin, pp 115-148.
TROLLOPE, W.S.W. (1980): Controlling bush encroachment with fire in the savanna area of South Africa. – Proceedings of the Grassland Society of South Africa **15**: 173-177.
TROLLOPE, W.S.W. (1982): Ecological effects of fire in South African savannas. – In: HUNTLEY, B.J. & WALKER, B,H. (eds.), Ecology of tropical savannas, pp 292-306. Springer-Verlag, Berlin.
TROLLOPE, W.S.W. (1999): Fire behaviour. – In: N.M. TAINTON (ed.), Veld management in South Africa, pp 218-245. University of Natal Press, Pietermaritzburg.
TROLLOPE W.S.W., TROLLOPE, L.A. & BOSCH, O.J.H. (1990): Veld and pasture management terminology in southern Africa. – Journal of the Grassland Society of southern Africa **7**: 52-61.
VAN DER MEULEN, F. (1979): Plant sociology of the western Transvaal Bushveld, South Africa: A syntaxonomic and synecological study. – Dissertationes Botanicae **49**: 192.
VAN OUDTSHOORN, F. (1991): Guide to the grasses of South Africa. – Briza Publications, Pretoria.
VAN ROOYEN, N. (1999a): Kalahari. – In: KNOBEL, JOHAN, The Magnificent Natural Heritage of South Africa, pp 10-25. Sunbird Publishing, Llandudno, South Africa.
VAN ROOYEN, N. (1999b): Lowveld. – In: KNOBEL, JOHAN, The Magnificent Natural Heritage of South Africa, pp 34-51. Sunbird Publishing, Llandudno, South Africa.
VAN ROOYEN, N., BREDENKAMP, G.J. & THERON, G.K. (1991): Kalahari vegetation: veld condition trends and ecological status of species. – Koedoe **34** (1): 61-72.
VAN ROOYEN, N., THERON, G.K. & BREDENKAMP, G.J. (1991): Long-term vegetation dynamics in the semi-arid Kalahari. – Koedoe **34** (1): 91-92.
VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. (1981a): A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa. 2. The Sandveld communities. – Journal of South African Botany **47** (3): 405-449.
VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. (1981b): A floristic description and structural analysis of the plant communities of the Punda Milia-Pafuri-Wambiya area in the Kruger National Park, Republic of South Africa. 3. The *Colophospermum mopane* communities. – Journal of South African Botany **47** (4): 585-626.
VAN STADEN, P. (2002): The vegetation of the Marekele National Park. – M.Sc. thesis, University of Pretoria, Pretoria.
WALKER, B.H. (1987): A general model of savanna structure and function. – In: WALKER, B.H. (ed.), Determinants of tropical savannas, pp 1-12. ICSU Press, Miami.
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.
WERGER, M.J.A. (1977): Environmental destruction in southern Africa: the role of overgrazing and trampling. – In: A. MIYAWAKI & R. TÜXEN (eds.), Vegetation Science and environmental protection. pp 301-305. Maruzen, Tokyo.
WERGER, M.J.A. & COETZEE, B.J. (1978) The Sudano-Zambezian Region. – In: WERGER, M.J.A. Biogeography and ecology of Southern Africa. Dr W. Junk Publishers, The Hague. p352-354.
WESTFALL, R.H., VAN ROOYEN, N. & THERON, G.K. (1985): The plant ecology of the farm Groothoek Thabazimbi District II: Classification. – Bothalia **15**: 655-688.
WESTOBY, M. (1979): Elements of a theory of vegetation dynamics in arid rangelands. – Israel Journal of Botany **28**: 169-194.
WESTOBY, M., WALKER, B. & NOY-MEIR, I. (1989): Range management on the basis of a model which does not seek to establish equilibrium. – Journal of Arid Environments **17**: 235-239.
WIENS, J.A. (1977): On competition and variable environments. – American Scientific **65**: 590-597.
WIENS, J.A. (1984): On understanding a non-equilibrium world: myth and reality in community patterns and processes. – In: D.R. STRONG, JR., D. SIMBERLOFF, L.G. ABELE, A.B. THISTLE (eds.), Ecological communities: Conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey.
WINTERBACH, R. (1998): A phytosociological synthesis of *Acacia tortilis* communities in the northwestern savanna of South Africa. – M.Sc. thesis, University of Pretoria, Pretoria.

Adress of the autors:
Prof. Dr. George J. Bredenkamp, African Vegetation and Plant Diversity Research Centre, Department of Botany, University of Pretoria, 0002 Pretoria, South Africa

Dr. L. R. Brown, Applied Behavioural Ecology and Ecosystem Research Unit, College for Agriculture and Environmental Sciences, Unisa, Private Bag X6, Florida, 1710, South Africa

Zeitschrift/Journal: Berichte der Reinhold-Tüxen-Gesellschaft

Jahr/Year: 2006

Band/Volume: 18

Autor(en)/Author(s): Bredenkamp George J., Brown L. R.

Artikel/Article: Vegetation type and dynamics in African savannas 69-82