CHAPTER 7

RESULTS

SPECULATIONS ON THE DYNAMICS OF THE MOPANEVELD

This chapter represents a discussion on the particularly interesting results regarding vegetation dynamics, which arouse from the synthesis. These results stimulated interest on the role phytosociological data could play in explaining vegetation dynamics within the Mopaneveld. Since speculations on Mopaneveld dynamics do not fulfil one of the major objectives of the study, no in-depth dynamics study was undertaken, although such a future long-term study is urged.

The structure and outlay of this chapter is slightly different since sufficient background information needs to be included for best expression of the findings. The outlay includes a general study background, methodology, results, discussion and conclusions as to follow the common outlay of a scientific paper for the purpose of possible publication.

7.1 Introduction

African ecosystems have been studied with the assumption that they are potentially stable (equilibrial) systems which become destabilised by human disturbances, such as sustained heavy stocking and grazing, or clearing for agricultural purposes (Chesson & Case 1986; DeAngelis & Waterhouse 1987; Dodd 1994; Ellis & Swift 1988; Sprugel 1991; Laycock 1991; Westoby *et al.* 1989; Rothauge 2000). Stability of equilibrial ecosystems implicates that historical effects, chance factors, and occasional environmental perturbations play a small role. In natural systems, however, the environment is continually changing and species in many communities do not appear to have the attributes for stable equilibria. (Chesson & Case 1986; Sprugel 1991). Stability in ecosystems also involves the orderly and directional process of succession where one association or community of plant species replaces another (Stoddart *et al.* 1975; Milton *et al.* 1994). This implies that, after disturbance, the original climax state will be reached through a predictable sequence of intermediate vegetation stages (Figure 22a). The idea of an area maintained in a dynamic equilibrium by a balance between disturbance and recovery is attractive, because it provides some sense of stability even in the presence of constant change (Sprugel 1991). This view of African savannas has been reviewed (DeAngelis & Waterhouse 1987; Ellis & Swift 1988; Westoby *et al.* 1989; Friedel, 1991; Laycock 1991; Sprugel 1991; Palmer & Van Staden 1992; Behnke & Scoons 1993; Dodd 1994; Milton *et al.* 1994; Illius & O'Connor 1999; Rothauge 2000) and resulted in dynamic, rather than purely static models to explain vegetation change over time. This new tendency retains the idea of species composition change after severe disturbance, but questions the classic process of recovery.

The southern African Mopaneveld prevails under semi-arid conditions, making this extensive vegetation type susceptible to dynamic shifts in plant species composition due to the unpredictability of rainfall in most of its distribution range. This study therefore aims to present possible explanation on the vegetation dynamics of the southern African Mopaneveld according to results obtained during a phytosociological synthesis of the Mopaneveld.

7.2 The study

The Mopaneveld is one of the most distinctive vegetation types in the savanna biome, however, until recently, little was known about its ecology. In southern Africa *Colophospermum mopane* vegetation types cover approximately 555 000 km^2 (Mapaure 1994). In recent history an increase in *Colophospermum mopane* trees and shrub density and a decrease of herbaceous plants are perceived (Smit 1994). Economical implications of such a shift in the vegetation composition emphasised the need to understand the dynamics of Mopaneveld vegetation. Population dynamics of *Colophospermum mopane* have been studied exclusively (Thompson 1960; Scholes 1990; O'Connor 1992; Smit 1994; Smit & Rethman 1998b), but little attention is given to the dynamics of associated herbaceous species.

A phytosociological synthesis on Mopaneveld vegetation in southern Africa is being conducted at the University of Pretoria. Although the synthesis did not aim to give explanations on the dynamics of the Mopaneveld, multivariate analysis revealed useful information on the temporal shifts in plant species composition.

7.3 Methods

Phytosociological data on Mopaneveld vegetation, consisting of 2 298 relevés and 1 465 species selected from vegetation studies undertaken in South Africa, Zimbabwe and Namibia, were incorporated into a TURBOVEG (Hennekens 1996a) database. The first approximation of a vegetation classification, based on the total floristic data set was obtained by the application of Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979) at a single division level on default cutlevels. This first step of classification procedure separated azonal and intrazonal vegetation from the zonal Mopaneveld data set. This single division classification was repeated until a cluster of purely zonal vegetation resulted. Relevés from azonal and intrazonal types were excluded and stored in a separate database for future analysis. A total of 2 246 relevés representing zonal Mopaneveld were used for further vegetation analysis. A single division application of TWINSPAN to the zonal vegetation was expected to express two major units within the Mopaneveld, maybe indicating the co-existence of two different major higher syntaxa (subclasses or orders) within the Mopaneveld class. The results of this first step in the

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classification procedures are presented in a synoptic two-way table to facilitate exploration (Table 9). Species of less than 10% presence in both synrelevés were excluded in refinement procedures to produce a clear explanation of species composition.

7.4 Results

Contrary to the expectation, TWINSPAN results did not distinctly separate two different major vegetation units within the Mopaneveld. A vegetation unit representing *Combretum apiculatum* dominance was expected to be separated from *Colophospermum mopane* dominated vegetation. Although *Combretum apiculatum* is more frequently found in cluster 1 (species group A, Table 9), *Colophospermum mopane* (speices group C), occurs in equal percentages in clusters 1 and 2.

The second possible interpretation of the TWINSPAN division is that of a geographical separation between the Western Mopaneveld (Namibian Mopaneveld) and the Eastern Mopaneveld. Parallel to this division is the moisture difference between the more mesic Eastern Mopaneveld, largely represented by species group A, Table 9 and the arid Western Mopaneveld, largely represented by species group B. Although the above interpretation could be related to the location of the majority of sample plots, several sample plots however, did not correspond to this interpretation. These plots were classified into the semi-arid to arid cluster 2, rather than to the cluster representing mesic Mopaneveld (cluster 1), where they indeed belong to. Investigations into the species composition differences between the two clusters revealed that this separation was caused by differences in the herbaceous vegetation, especially in the grass species, rather than in the woody species (Table 9). Table 10 represents a summary on the arrangement of annual grass species and climax grass species along the two major clusters. The definition of annual and climax grass species conform to that of Van Oudtshoorn (1999).

Table 9 Synoptic presentation of the major division of the data set

Cluster number	1	2
Number of relevés	1895	379

Species Group A

	1	2
Combretum apiculatum	61	18
Digitaria eriantha	47	2
Acacia nigrescens	37	1
Urochloa mosambicensis	47	0.5
Tragus berteronianus	47	19
Abutilon austro-africanum	15	0.3
Achyranthes aspera	11	6
Aristida congesta s. barbicollis	35	0.8
Blepharis integrifolia	10	0.5
Bothriochloa radicans	16	5
Chloris virgata	10	9
Commelina benghalensis	22	0.3
Euclea divinorum	15	3
Indigofera rhytidocarpa	12	.
Ipomoea crassipes	10	.
Lantana rugosa	14	1
Oropetium capense	13	5
Panicum maximum	60	5
Panicum coloratum	13	6
Pupalia lappacea	12	4
Seddera capensis	21	0.5
Solanum panduriforme	21	4
Sporobolus nitens	10	.
Tragia dioica	12	.
Phyllanthus species	16	0.3
Acacia tortilis	12	6
Albizia harveyi	18	.
Chamaecrista mimosoides	14	.
Commelina africana	15	3
Cymbopogon plurinodis	15	0.3
Eragrostis superba	21	2
Evolvulus alsinoides	31	8
Hermbstaedtia odorata	10	4
Ipomoea obscura	11	5
Lannea schweinfurthii	20	0.8
Ormocarpum trichocarpum	11	.
Pavonia burchellii	14	4
Ruellia patula	18	.
Sclerocarya birrea	29	3
Themeda triandra	17	.
Vernonia fastigiata	10	.
Cissus cornifolia	39	.
Hibiscus micranthus	40	6
Maerua parvifolia	24	0.3
Mariscus rehmannianus	12	.

Cluster number	1	2
Number of relevés	1895	379
Talinum caffrum	10	0.8
Cyperus rupestris	11	.
Flueggea virosa	15	4
Heliotropium steudneri	24	0.5
Kyllinga alba	10	2
Kyphocarpa angustifolia	39	5
Leucas glabrata	17	.
Asparagus setaceus	15	0.3
Dalbergia melanoxylon	20	.
Lonchocarpus capassa	16	0.8
Tephrosia polystachya	35	0.3
Ziziphus mucronata	13	5
Dicoma tomentosa	24	6
Gisekia africana	11	7
Acacia exuvialis	18	.
Aptosimum lineare	17	8
Clerodendrum ternatum	20	6
Combretum imberbe	14	7
Corchorus asplenifolius	25	0.8
Heteropogon contortus	24	9
Rhynchosia totta	23	5
Tricholaena monachne	19	2
Eragrostis rigidior	30	0.8
Pogonarthria squarrosa	25	2
Acalypha indica	15	1
Limeum fenestratum	18	1
Combretum hereroense	18	5
Kohautia virgata	11	.
Grewia monticola	15	0.8
Bulbostylis hispidula	13	5
Chamaecrista absus	13	1
Melhania rehmannii	13	6
Maytenus heterophylla	11	0.3
Ceratotheca triloba	12	0.3
Waltheria indica	21	0.8
Melhania forbesii	21	2
Aristida congesta s. congesta	24	3
Enneapogon scoparius	12	7
Ipomoea magnusiana	14	0.5
Combretum mossambicense	11	3
Hermannia boraginiflor	21	0.3
Commiphora mollis	18	2
Sesamum alatum	11	.
Bothriochloa insculpta	12	.
Indigofera vicioides	16	.
Phyllanthus maderaspatensis	16	5
Brachiaria deflexa	30	4
Aristida congesta	17	7

	1	2
Cluster number	1	2
Number of relevés	1895	379
Endostemon tereticauli	11	.
Species Group B		
Boscia albitrunca	9	29
Aristida meridionalis	3	12
Monechma divaricatum	2	21
Acacia nilotica	3	14
Chascanum pinnatifidum	0.7	10
Stipagrostis uniplumis	7	43
Otoptera burchellii	0.3	18
Commiphora pyracanthoides	5	20
Croton gratissimus	0.9	21
Asparagus species	1	17
Boscia foetida	0.6	12
Geigeria ornativa	3	12
Terminalia sericea	9	13
Urochloa brachyura	3	13
Tribulus terrestris	10	12
Grewia flava	7	17
Eragrostis trichophora	8	28
Hermannia modesta	1	10
Eragrostis nindensis	0.3	17
Catophractes alexandri	0.1	22
Grewia retinervis	.	14
Acacia mellifera	.	11
Acacia erioloba	0.1	10
Rhigozum brevispinosum	0.1	19
Heliotropium ovalifolium	0.3	10
Enneapogon desvauxii	.	16
Eragrostis echinochloidea	0.1	14
Leucosphaera bainesii	.	24
Anthephora schinzii	0.1	16
Acacia reficiens	.	17
Acacia fleckii	.	11
Anthephora pubescens	.	22
Helinus integrifolius	.	11
Montinia caryophyllaceae	.	14
Schmidtia kalihariensis	.	16
Pechuel-Loeschea leubnitziae	.	11
Pogonarthria fleckii	.	15
Species Group C		
Colophospermum mopane	59	59
Melinis repens	27	29
Grewia flavescens	14	11
Terminalia prunioides	22	36
Schmidtia pappophoroides	40	23
Enneapogon cenchroides	50	46
Dichrostachys cinerea	48	36
Grewia bicolor	52	31

Cluster number	1	2
Number of relevés	1895	379
Commiphora africana	18	10
Aristida adscensionis	27	38
Eragrostis lehmanniana	12	24
Cenchrus ciliaris	11	22

Table 10 Arrangement of diagnostic annual grass species and climax grass species between the two major clusters within Mopaneveld

	Cluster 1	Cluster 2
Total number of diagnostic grass species	19	11
Total number of annual grass species	4	5
Percentage annual grass species	21 %	45 %
Total number of climax grass species	6	2
Percentage climax grass species	31 %	18 %

From the above it is evident that, despite indications of a geographical or moisture induced division in the data set, the major groups (Cluster 1 and Cluster 2) were separated according to the frequency of climax, perennial grass species and the pioneer, annual grass species.

Although the discussion will mainly follow the results obtained from the single division in TWINSPAN, the identification of major vegetation types according to the application of TWINSPAN on default levels of division (6) strongly supported speculations on the dynamics of Mopaneveld vegetation. The *Enneapogon scoparius – Colophospermum mopane* major vegetation type is regarded as a transition community between the semi-arid to arid Western Mopaneveld and the more mesic conditions of the South African Lowveld Mopaneveld and the Save River Valley Mopaneveld (Chapter 5). The transition character of the *Enneapogon scoparius – Colophospermum mopane* major vegetation type can be supported by its location on the scatter diagram representing major vegetation types along a gradient of decreasing moisture (Figure 19, Chapter 5).

7.5 Discussion

This section focuses on answers related to the following key questions:

1. Considering the Mopaneveld as semi-arid, could non-equilibrial models for vegetation change testify these results?

2. Can phytosociological studies predict aspects of vegetation dynamics?

3. Does the woody component in a system necessarily follow the same model for dynamics as the herbaceous layer?

1. Non-equilibrial models to testify the results

Prior to the discussion of the applicability of non-equilibrial models to Mopaneveld, a few important notes are listed below.

- For the purpose of this discussion, **non-equilibrium / disequilibrium** refers to any situation where species composition and densities do not remain constant over time at each spatial location.

- Most parts of the Mopaneveld can be considered semi-arid since annual rainfall usually ranges below 500 mm. Although some areas in Mopaneveld (e.g. Zambia) receive well over 500 mm rainfall annually, it is still regarded semi-arid since soil moisture availability is limited due to high rainfall intensity (Chapter 3).

- With reference to the synthesis of the Mopaneveld, sample plots that did not correspond to speculations of a geographical separation by TWINSPAN, will be referred to as *odd relevés*. These relevés are all situated in cluster 2 of Table 9.

- These *odd relevés* are mixed in locality. Personal communication with the authors of these relevés revealed that vegetation surveying was undertaken under extreme drought conditions.

Literature review

Plant succession can be defined as the orderly and directional process whereby one plant community replaces another (Stoddart *et al.* 1975). The classical equilibrial theory (Clements 1916) assumes that a single, persistent and characteristic plant community, the climax, would dominate a particular site (Behnke & Scoones 1993; Milton *et al.* 1994). Furthermore the theory is based on predictable, unidirectional, community-orientated vegetation change after a disturbance to eventually reach the climax state again (Westoby *et al.* 1989; Milton *et al.* 1994; Cook 1996; Rothauge 2000) (Figure 22a).

In semi-arid areas of unpredictable and erratic rainfall patterns or often sustained drought conditions, abiotic, rather than biotic events tend to drive system dynamics (O'Connor 1985;

Ellis & Swift 1988; Milton *et al.* 1994; Illius & O'Connor 1999). These stochastic events, usually being associated with soil moisture availability, determine vegetation composition of especially the herbaceous component (O'Connor 1985; Mentis *et al.* 1989; Skarpe 1992; Milton *et al.* 1994). Fluctuations in the herbaceous species composition as a response to episodic events are not consistent with simple successional pathways (Mentis *et al.* 1989; Behnke & Scoones 1993; O'Connor 1999). In the interest of range scientists, it is important to note vegetation change of, especially the herbaceous component. The study of plant species composition as a result of stochastic events evoked interest in the dynamics of semi-arid savanna systems.

One of the first attempts to explain vegetation change in a model, was the range and succession model which was purely based on principles adapted from Clementsian concepts of plant ecology (Rothauge 2000). The equilibrial theory of Clements (1916) was thought to give a clear explanation of vegetation change until recently. From several studies where the spatio-temporal variation in the herbaceous plant species composition was studied, it became clear that Clementsian concepts of single equilibrium communities and deterministic succession pathways are no longer as dominant in ecology as when it was applied in range management (DeAngelis & Waterhouse 1987; Skarpe 1992; Rothauge 2000). Emphasis moved to ecological theories based on alternative stable states, discontinuous and irreversible transitions, non-equilibrial communities and stochastic events in succession (Westoby *et al.* 1989; Skarpe 1992; Milton *et al.* 1994) (Figure 22b & 22c).

A few non-equilibrial models for vegetaton change were selected to discuss their possible applicability to the situation in the Mopaneveld.

conditions, other species become more abundant. It is therefore evident that species composition in plant communities of areas exposed to low ecological potential (especially exposure to dry conditions) resembles species composition of highly degraded systems in areas where ecological potential is usually moderate to high (such as the Eastern Mopaneveld).

Climate, soil moisture availability and vegetation dynamics

The availability of moisture for plant growth is determined by total rainfall levels and distribution, soil physical properties (particularly infiltration rates) and topography (Behnke & Scoons 1993). Nutrient availability, as influenced by parent geology as well as by nutrient transport from weathering and water movement, in combinations with soil moisture availability, is proposed to create major vegetation types (Behnke & Scoons 1998). Vegetation change is therefore imperceptible of climate variability, especially variability in rainfall events. The unpredictability and variability of rainfall events in semi-arid areas inevitably supports non-predictable response to rainfall events. Annual rainfall is however not directly proportional to vegetation change since soil moisture and soil nutrients availability has a more pronounce influence on plant species composition (Behnke & Scoons 1993). Plant communities within significant annual rainfall measures often do not reflect high moisture availability. Species composition in such areas often reflects conditions of low ecological potential. Igneous basic rocks, such as gabbro and basalt, produces heavy, clayey soils with low infiltration rates. Soil moisture retention in combination with low infiltration produces conditions of low soil moisture availability for plant growth, although clayey soils are often associated with high levels of nutrients. A significant part of Mopaneveld vegetation occurs on these substrates, especially in the Eastern Mopaneveld (e.g. shrubmopaneveld of the Kruger National Park). Vegetation composition shifts towards affinity to arid environments (in terms of annual rainfall) could therefore be predicted after sustained drought conditions.

Another controversial concept of vegetation shifts, involves areas of significantly high annual rainfall measures (e.g. 1 000 mm per annum) which present plant species composition in accordance with semi-arid areas (e.g. maximum 500 mm rainfall per annum). Although 1 000mm rainfall is measured in some parts of Zambian Mopaneveld (Chapter 3), species composition do not reflect mesic conditions. Taking into account that the majority of precipitation falls during two months of the wet season (Figure 10), high run-off rates prevent

soil moisture accumulation. These severe rainfall events are usually followed by eight months of hot, dry conditions (Figure 10). The herbaceous species composition therefore does not necessarily represent stable conditions as being expected in mesic environments. The herbaceous sward of the Mopaneveld in this type seems to be driven by alternating rainfall and drought events.

It is therefore evident that rainfall variability should not be excluded from vegetation dynamic models in the Mopaneveld of southern Africa.

a)

Perennials dominant:
Digitaria eriantha,
Panicum maximum,
Urochloa mossambicense

x_1

Higher abundance of
Stipagrostis uniplumis and
Eragrostis lehmanniana

Perennials dominant:
Stipagrostis uniplumis,
Eragrostis lehmanniana

y_1

"stable state" in
Western Mopaneveld

Event
(prolonged drought)

Perennials dominant:
Stipagrostis uniplumis,
Eragrostis lehmanniana

x_2

Lesser dominance of D.eriantha, P.
maximum, Themeda triandra, U.
mossambicense

Affinity to Western Mopaneveld
in terms of species composition

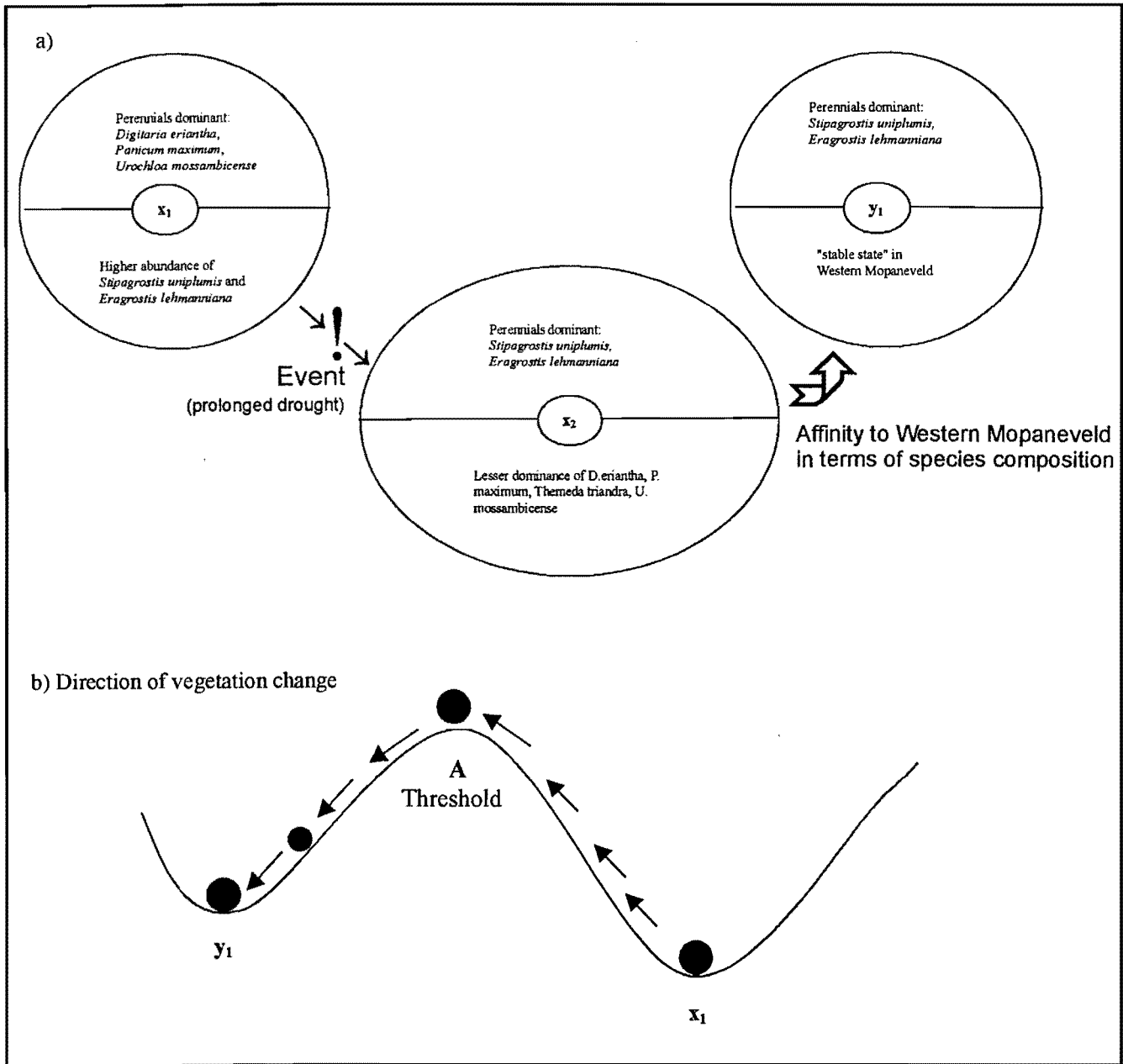b) Direction of vegetation change

A
Threshold

y_1

x_1

Figure 24 Simplified illustration to explain affinities of the *odd relevés* to the Western Mopaneveld.

2. Can phytosociological studies predict aspects of vegetation dynamics?

The major objectives of phytosociological studies will never be to study vegetation dynamics. Phytosociological results of a study such as the entire Mopaneveld were expected to be more exact than it was due to its distribution over environmental extremes, especially rainfall extremes. The strange results evoked deeper examination into the state of the data, which contributed to the results. Most phytosociological studies are undertaken on a much more local scale, preventing disorganisation of the classification output.

From the synthesis of the Mopaneveld it is evident that aspects on vegetation dynamics can be speculated upon. Long-term vegetation surveying is however inevitable for a clear explanation of the dynamics of an ecosystem. Phytosociological sytheses can only lighten speculations on vegetation dynamics. It will not replace studies on vegetation dynamics.

This study is however not the first to use the tools of phytosociology to predict vegetation change. Palmer & Van Staden (1992) also used the concept of floristic relevés to compare the state of vegetation with previous records.

2. Does the woody component in a system necessarily follow the same model for dynamics as the herbaceous layer?

The discussion on the dynamics of the woody component in relation to the herbaceous component in the Mopaneveld is based purely on speculations.

Savanna ecosystems show co-dominance of trees and grasses, but the mechanisms involved in their co-existence remain unresolved (Knoop & Walker 1985; Jeltsch et al. 1996; Jeltsch et al. 1998). It is inevitably true that woody species have a pronounce influence on herbaceous vegetation (Knoop 1985; Smit 1994; Smit & Swart 1994; Jeltsch et al. 1996; Jeltsch et al. 1998; Smit & Rethman 1998b), but do they necessarily follow the same dynamic pathway towards the same stable state?

Competition

The dominant woody species in Mopaneveld, namely *Colophospermum mopane*, exerts a pronounce influence on the growth of grasses through competition for soil moisture (Smit 1994). Drought invariably results in a decline in the abundance of perennial grasses in Mopaneveld (Donaldson *et al.* (1984) in O'Connor (1999)), as a result of competition with woody species (Knoop & Walker 1985). Considering grasses as the superior competitors for water in the topsoil and woody plants being it for the subsoil, it can be expected that drought conditions would have a more pronounce effect on the herbaceous layer than on the woody layer (Knoop & Walker 1985; Skarpe 1992).

Considering density-dependent and density independent competition in a typical semi-arid savanna system: when moisture is limited for a small period, there will still be sufficient moisture available to compete for in the sub-soil. Competition in the woody layer will therefore be density dependent, almost through any state of vegetation change. Under the exact same environmental conditions (limited moisture), the herbaceous component of the Mopaneveld system is speculated to be density-independent since moisture in the topsoil is limited to such an extent that, regardless the density of the herbaceous layer, individuals will die off as a result of limited soil moisture. It is rather abiotic events that control the co-existence of herbaceous species in semi-arid systems such as the Mopaneveld. Density dependent competition can however prevail under conditions of high soil moisture availability in a transition state (high percentage cover as a result of a rainfall event after a prolonged drought event).

It is therefore presumed that woody species in the Mopaneveld prevail under density dependent competition under dry conditions whereas herbaceous species rapidly emerge after a rainfall event, compete for the top-soil moisture under density dependent conditions, but after prolonged drought conditions, density independent mortality crashes the temporal stable state.

Trees and the herbaceous layer: parallel or non-parallel dynamic shifts?
O'Connor (1999) depicted changes, not only in the herbaceous vegetation, but also in the woody vegetation after a sustained drought in the semi-arid Mopaneveld. Almost complete mortality was observed for some trees and shrubs after the sustained drought conditions. Although *Colophospermum mopane* was also negatively influenced by the drought, it showed a greater

tolerance to these dry conditions. Complete mortality or substantial topkill of several shrub species had occurred owing to the drought (O'Connor 1999). From these results it is apparent that the woody layer experienced a shift in species composition. *C. mopane* would probably fill the open spaces created by the dieback of other woody species. The succession pathway of the woody component is however speculated to be slower than for the herbaceous layer. Due to its rapid response to rainfall events, the herbaceous layer would alternate between different stable states or transition states, whereas the response of the woody component to an event is not as rapid, nor will the outcome of the event be evident over a short period.

The above speculations propose that in semi-arid savannas, the herbaceous vegetation and the woody vegetation are neither consistent in competition nor in dynamics. Competition in the woody layer, especially when dominated by *Colophospermum mopane*, seems to be density dependent. Suggesting non-equilibrial models to explain vegetation change in the herbaceous component of the Mopaneveld, abiotic events tend to drive system dynamics to rapidly changing species composition, which does not tend to regain the initial species composition. The same woody species composition over a given time can therefore comprise several states of the herbaceous component as a consequence of response to several events.

Since these speculations are purely philosophical thoughts, it is suggested that a clear view on these dynamic aspects of the Mopaneveld need to receive attention in the nearby future.

7.6 Conclusions

The study of Mopaneveld vegetation beyond the superior plant community evoked special interest in the dynamics of the vegetation of the Mopaneveld. The idea of Mopaneveld being a non-equilibrial system which follows stochastic events, were produced totally independent from results obtained from long-term dynamics studies (e.g. O'Connor 1999; Oelofse *et al.* 2000). The question evolved whether the observations in ecosystem dynamics could be explained simply by looking at vegetation composition. Comparison with long-term studies on Mopaneveld vegetation dynamics revealed significant support on speculations based upon a phytosociological synthesis. A great deal of derivations on vegetation dynamics can therefore be made from phytosociological data, but more comprehensive long-term studies are needed to

support speculations. Phytosociological studies could not replace vegetation dynamic monitoring. They can however depict temporal species composition change after historical data to motivate further investigation.

Plant communities are not static representations of species composition. They are constantly adjusting to new conditions, but never completes the adjustments before conditions change again. Equilibrium concepts are highly scale-dependent. On a sufficiently small scale, in space or in time, all ecosystems are unstable and transient. Small scale – short-term disequilibrium may promote large scale – long term dynamic equilibrium persistence. The present community therefore cannot be clearly explained simply by studying it today!