



**THE EFFECTS OF BURNING AND MOWING ON MICROCLIMATE AND SOIL
RESOURCES AND IMPLICATIONS FOR SPECIES CHANGE IN THE SOUTHERN
TALL GRASSVELD OF KWAZULU-NATAL**

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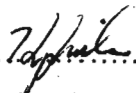
2004

DECLARATION

This thesis is the result of the author's original work except where acknowledged. I hereby certify that this research work has never been submitted for any degree or examination at any University or similar academic institutions.

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ABSTRACT

Promotion of a predictive understanding of plant community response to various forms, frequencies and seasons of disturbance, either through the direct physical effect on biota and/or indirect effect on plants, through modification of microclimate and soil attributes is currently a major goal in plant ecology. In particular, the effect of disturbance on altering the ratio between available light and nutrients and their resultant effect on growth, shoot/root allocation, and thus community composition has gained considerable recognition in connection with the mechanisms of plant succession under a popular heading “the resource ratio hypothesis of plant succession”. Contemporary and long-term (>50 years) burning and mowing experiments in KwaZulu-Natal (KZN) provide important sites for investigation that in the mesic grasslands of KZN, community composition changes in response to the frequency, time and type of disturbances such as burning, mowing and veld fertilization. However, the relationship between disturbance-resource-plant traits and their interactive role in species change is virtually unknown. This study sought to improve understanding of mesic grassland dynamics in KZN, using short-term pot and plot experiments. The principal objectives were: 1) by subjecting plants to different levels of resources viz. light, nutrients, water and cutting to determine the relative above and below-ground growth performances (biomass allocation) of species from contrasting habitat preference in KZN, which implies their relative competitive ability for limiting resources and tolerance to cutting, 2) by using a short-term (one-season period) burning and mowing experiment to determine the effect of different veld management practices on microclimate and availability of soil resources and their subsequent effect on plant growth performances, 3) testing the relative shade tolerance of representative species from contrasting habitat preferences, 4) by combining the outcomes from these experiments, to provide a general synthesis concerning species’ response to disturbance/resource which further signifies species change.

The hypothesis that competitive ability as a function of biomass allocation is fertility dependent was supported by a pot experiment. In low nutrient treatments short grass species that predominate infertile soils in KZN viz. *Aristida junciformis* and *Themeda triandra* attained double the shoot biomass, more than double root biomass, initiated more tillers and

re-grew better (after cutting) than those inherently tall species that predominate fertile sites viz. *Eragrostis curvula* and *Hyparrhenia hirta*. In contrast, in high nutrient treatments, tall species attained far higher shoot biomass and grew taller in height. Interestingly, short species had a smaller shoot: root ratio than tall species, consistent with the prediction of the resource ratio hypothesis. However, no evidence was obtained suggesting that tall species were more shade tolerant than short species. A field-based shade experiment rather showed that, those species that initiate tillers below-ground viz. *Aristida junciformis*, *Eragrostis curvula* and *Tristachya leucothrix* were more shade tolerant than those species that initiate tillers above-ground viz. *Hyparrhenia hirta* and *Themeda triandra*.

On the other hand, the effect of disturbance/resource relationship in influencing the growth (biomass production, growth rate, and basal circumference) of contrasting species was examined by conducting a short-term (one season) burning and mowing experiment. The effect of disturbance, its form and frequency through its effect on light and soil moisture was able to account for a substantial difference in species vigour, which can potentially impact community composition. Short species (*Themeda triandra* and *Tristachya leucothrix*) showed their highest biomass production and higher basal circumference enlargement in burnt summer mown sites, whereas medium to tall species (*Aristida junciformis*, *Eragrostis curvula* and *Hyparrhenia hirta*) were less tolerant to summer mowing. *Aristida junciformis* and *Eragrostis curvula* appeared to be more vigorous (both in terms of above-ground biomass production and growth rate) in burnt but not mown and control treatment respectively. High biomass and litter accumulation on sites protected from disturbance appeared to have a large influence on species vigour. Species such as *Aristida junciformis*, *Eragrostis curvula* and *Tristachya leucothrix* had high tolerance to litter accumulation while in contrast *Hyparrhenia hirta* and *Themeda triandra* were more vulnerable. In total this study has revealed that the association of some short species e.g. *Themeda triandra* with the recurrence of disturbance is mainly due to increases in light availability and lowered dominance from tall species in frequently disturbed sites rather than nutrient related. However, this study has revealed that there are some indications whereby the notion that the inverse relationship between available light and nitrogen are important driving variables in species change is an important working theory in the mesic grassveld of KZN.

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CHAPTER ONE

An overview

1.1 INTRODUCTION

The humid fire climax (mesic) grassveld occupies a large part of the higher-lying eastern region of South Africa, and the total land area covers up to 13 million hectares (Acocks 1988). In KwaZulu-Natal (KZN), these grasslands constitute approximately 48% of the total area of the region (Phillips 1973). A large proportion (approx. 53.5%) of these humid fire climax grasslands is utilized for livestock production on natural veld (Fotheringham 1981). These grasslands carry a considerable population of livestock under both commercial and communal tenure systems. Many of South Africa's most important water catchments fall within these mesic grasslands. Ecologically and economically therefore, the mesic grasslands are one of the most important vegetation types in South Africa, and thus the stability of these grasslands is of paramount importance (Tainton 1999). However, while the humid grasslands are considered to be more stable than the arid and semi-arid grasslands (Mentis and Huntley 1982), they are more vulnerable to degradation¹ (Bayer 1955, Acocks 1988, Marriott 1997, Tainton 1999).

Recent reports (2003) from the Department of Agriculture of the region show that the province has second highest veld degradation index in the country with the rate indicated as increasing. Degradation happens both in terms of species composition or soil erosion, which in turn results in the invasion of relatively unpalatable species (Marriott 1997, O'Connor *et al.* 2003). This degradation in most cases involves the removal of valuable grass species such as *Themeda triandra* from the sward, leaving strongly tufted and less palatable species of grasses such as *Aristida*, *Eragrostis*, *Sporobolus*, *Panicum* and others (Bayer 1955, Tainton 1972, 1999). Degradation may, or may not, be reversible and not along a single or linear pathway

¹ For the purpose of this study, degradation is related to the compositional change, which further decreases the ability of the sward to produce palatable grass species to maintain livestock (Tainton 1999).

(Morris and Tainton 1993). Surprisingly, in the mid 1840s when the Voortrkkers (first white settlers in the country) moved up to Natal (the present day KZN), *Themeda triandra* was the dominant grass species over the greater part of the region (Bayer 1955). By contrast, recent reports show that in many areas of the southern Tall Grassveld in KZN, the originally *Themeda triandra* dominated veld is now encroached by *Aristida junciformis* (Venter 1968, Edwards *et al.* 1979, Van Zyl 1998, Tainton 1999), *Eragrostis curvula* and *Eragrostis plana* (Tainton 1999, Kirkman and Morris 2003) and the rate of infestation appears to be increasing. The regeneration ability of this fire climax species (*Themeda triandra*) once destroyed is generally slow or unlikely. Attempts made to replace severely *Aristida junciformis* infested areas by *Themeda triandra* have met with limited success. Thus, viewed from a livestock production perspective, such a replacement of valuable grasslands by relatively less palatable species is problematic and the case can be regarded as a serious problem with substantial ecological and economic consequences (Edward 1968, Van Zyl 1998, Tainton 1999, Kirkman and Morris 2003). Indeed, Acocks (1988) warned that, unless positive steps were taken to halt this degradation, the sustainability of these grasslands as valuable resources will cease by the year 2050. Despite the seriousness of the problem however, research efforts focussed on the mechanisms of invasion and the ways of curbing the potential risk are apparently limited.

Compositional changes are intrinsic characteristics of grasslands (Vogl 1979, O'Connor *et al.* 2003) and may be caused by many factors which can be grouped into three main categories viz. vegetation itself via succession, climate of the area and man-induced (anthropogenic) changes (Acocks 1988). Anthropogenic changes include all the changes caused by veld management practices e.g. burning, grazing, mowing, resting etc. O'Connor *et al.* (2003) who recently revisited Acocks' veld types to determine the extent of grassland change after fifty years, have reported striking management-induced compositional changes in the mesic grassvelds of KZN. Therefore, vegetation may inevitably change via succession (Clements 1916), which begins by individual species replacement and goes up to higher-level alteration of ecosystems as a result of different forces of nature and human interventions.

Predictive understanding of such changes at an individual and community scales are of great ecological and economic importance, as these predictions can be used for the formation of local, national as well as global policies (McIntosh 1981, Bazzaz 1996). It might be relatively simple to measure the pattern of botanical change of a community however; such information documents only the occurrence of change and provides no reasons as to how and why changes (succession) occurred. Why does succession happen? What are the responsible mechanisms governing it? Why do species appear in a hierarchy along a successional pathway? What can cause one species or a group of species to be displaced by another or others? These are some of the basic questions that a grassland manager needs to ask. Plant ecologists and resource managers should provide a description, an understanding and a prediction of the complex pattern of vegetation change that results from management actions as well as natural processes as long as the central goal of ecology and ecologists is to understand the causes and mechanisms of changes we observe in nature. Globally, predicting the future of individuals, communities and populations is currently a major goal in ecology. The scientific community is being challenged to answer many questions regarding the future of major ecosystems under various global change scenarios (Bazzaz 1996). Similarly, in KZN currently there is an ardent interest in predicting the real mechanisms governing the dynamics of species in the mesic grasslands. The desire for predictions is being enhanced by the pressing need to appropriately manage ecosystems, which inevitably requires a good understanding of the ecological mechanisms causing changes. Moreover, knowledge of the major processes operating on natural resources and their subsequent effects on the rate and direction of the change is vital to determine whether the management practices such as veld burning, mowing and veld fertilization are successful tools or not.

The project under discussion was established on one of the humid fire climax vegetation types in KZN, viz. the southern Tall Grassveld (Acocks 1988) (Map of the southern Tall Grassveld is given Fig. 3.2. Chapter 3). The southern Tall Grassveld of KZN, is a grassland where fire, mowing and defoliation by herbivory play a major role in determining species dynamics (Tainton *et al.* 1978, Heard *et al.* 1986). The influence of fire, grazing, mowing and other forms of disturbances on compositional change are not independent of the physical and chemical properties of the environment. For instance, activities of grazers,

biomass consumption and trampling may result in greater resource availability to plants than in ungrazed grassland (Grime 1979). Furthermore, due to disturbances by fire and defoliation (by mowing), light availability (Savage and Vermeulen 1983, Fynn *et al.* 2003), nutrient availability (Blair 1997, Fynn *et al.* 2003) and soil water content (I'Ons 1960, Hulbert 1969) may be modified. These factors are some of the major factors, which determine the structure, dynamics, and function of grasslands (Bazzaz 1979, 1996, Tilman 1985, 1988). Their influence may further determine the fate of individual species contained within the community (O'Connor and Everson 1999, Tilman 1985, 1988). Apart from the natural factors, degree and timing of the impact and the combination of disturbances in a specific sequence may influence the pathway of compositional changes in these mesic grasslands (Westoby *et al.* 1989). An ability to predict the rate and direction of botanical change under specific impacts of disturbances is a useful tool for managing grasslands in the desired fashion. However, in these mesic grasslands the ecological mechanisms governing species and cover change are not fully understood yet. Consequently, our ability and our confidence in predicting the effects of various forms of disturbance and management practices on specific compositional change is still lacking.

Thus, the aim of this study was to obtain greater insight into the ecological mechanisms governing succession under the impacts of fire, defoliation (mowing) and veld fertilization as well as their interactive effects. While designing this project, considerable attention was given to the role of disturbances of fire and mowing on resource availability i.e. light, mineral nutrients and water, from a resource ratio hypothesis perspective (Tilman 1985) to determine the consequential effect of disturbance on the competitive response of grasses species of contrasting traits and habitat preferences in KwaZulu-Natal. This study forms part of the comprehensive research initiative taken by the Discipline of Grassland Science (Kirkman² K.P. Pers.Comm.). It constituted three independent but theoretically integrated experiments, which will be described as Study I, II and III. These are:

Study I. Pot Experiment (PE) aimed at testing the effects of resource ratios on above and below-ground allocation and thus determining the competitive abilities of species of

grasses of contrasting habitats, strategies and successional stages by subjecting them to different combinations of resources and cutting levels.

Study II. Burning and Mowing Experiment (BME) aimed at investigating the impacts of management practices i.e. burning and mowing on modification of the physical and chemical properties of the Tall Grassveld and its subsequent effect on the growth performance of five naturally occurring grassland species of contrasting habitats and traits.

Study III. Shade Cloth Experiment (SCE) aimed at testing species' tolerance to conditions of light-stress and understanding the role of shade in species replacements.

1.2 BACKGROUND AND MOTIVATION

The idea, which gave rise to this experiment, was basically born from the previous and ongoing long-term burning and mowing trial (BMT) and veld fertilization trial (VFT) running on the plateau of Ukulinga (Research farm of the University of KwaZulu-Natal) near Pietermaritzburg. The burning and mowing trial (BMT) and veld fertilization trial (VFT) were initiated by J.D Scott in 1950 and are still running. These experiments are amongst the longest running field experiments in Africa (Swift *et al.* 1994). Treatments have continued uninterrupted, providing insight into the ecology of the Tall Grassveld. The original objectives of BMT and VFT were primarily agricultural. Treatments were designed to examine the influence of mowing the Tall Grassveld at different times in summer, and removing the aftermath in winter by burning or mowing, on the yield and quality of hay, whereas the VFT was designed to examine the possible ways of increasing yield of the veld by fertilizing with various elements. In these studies regular records of herbage yields and botanical analysis data, studies on the effects of various treatments on microclimate factors (e.g. soil temperature and soil moisture content) have been carried out from time to time. The effects of veld burning, mowing and veld fertilization on botanical composition, nutritive value, flowering, seed production and nitrogen dynamics of the mesic grassveld of KZN have been studied by many authors (e.g. I'Ons 1960, Edwards 1968, Tainton *et al.* 1977, Mentis and Tainton 1984, Morris *et al.* 1992, Fynn *et al.* 2003) and research outcomes are well documented.

Today (2004), results of the burning and mowing trial (BMT) and veld fertilization trial (VFT) have clearly revealed that the exclusion of fire from the Tall Grassveld for five decades has resulted in the invasion of indigenous and exotic *Acacia* and broad leaved trees in the no burn plots (Titshall 2001). The second transformation of the Tall Grassveld resulted from defoliation (by mowing) during the growing season, which markedly increased the relative abundance of *Themeda triandra* (Tainton and Mentis 1984). In less frequently burnt plots, the original species *Themeda triandra* and *Tristachya leucothrix* were replaced by *Diheteropogon filifolius*, *Aristida junciformis*, *Eragrostis curvula* and *Cymbopogon validus*. By contrast, treatments that involved regular burning and mowing have maintained the original species *Themeda triandra* and *Tristachya leucothrix* (Everson and Tainton 1984). Dormant season burning and double summer mowing resulted in the creation of dense veld dominated by *Themeda triandra*, *Trachypogon spicatus* and *Heteropogon contortus*. In other words, burning any time out of the growing season (winter or early spring) did not alter species composition (Tainton and Mentis 1984). In general, it was found that, as frequency of disturbance decreases, large productive species dominate the entire system whereas regular disturbances such as annual burning and mowing prevented the exclusion of smaller and less productive species. Another large transformation of the Tall Grassveld was observed in the veld fertilization trial (VFT). The Tall Grassveld was totally transformed by fertilizer application, for instance, in plots that received the highest level of nitrogen ($211 \text{ kg N ha}^{-1} \text{ a}^{-1}$), *Themeda triandra* and *Tristachya leucothrix* were completely replaced by *Eragrostis curvula* and other “invader” grasses (Tainton and Everson 1984). Nitrogen, therefore, appears to be the main element driving competitive interactions among species in Tall Grassveld (Barnes *et al.* 1987). The above-mentioned management induced dramatic transformation in the component species of the Tall Grassveld has raised many important questions. Its ecological and economic implications strongly demanded further investigation.

1.3 OBJECTIVES OF THE STUDY

The overall objectives of this study were therefore to:

1. Improve our understanding of the ecological mechanisms controlling the dynamics of species and cover change.

2. Provide a means of developing models for predicting the dynamics of key grass species and grassland structure in relation to the common disturbance factors in the region (KZN).

Within these broad objectives (illustrated in Fig. 1.1) several key questions were posed.

Study objectives and key questions

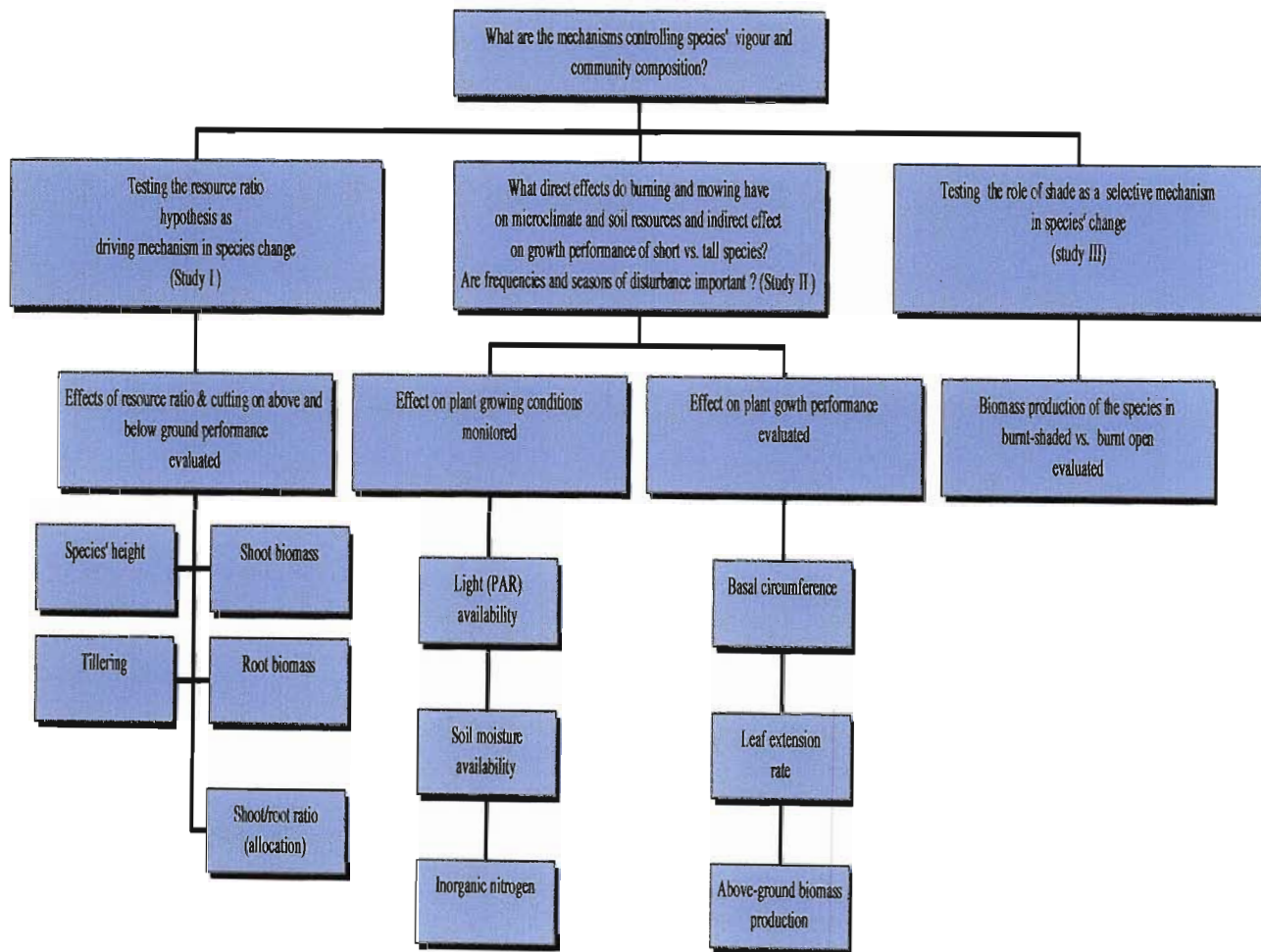


Figure 1.1 Structure of the study investigating on the effects of burning and mowing on microclimate and mechanisms of species change in the southern Tall Grassveld of KwaZulu-Natal.

CHAPTER TWO

The concepts of plant succession: disturbance, resources availability and their theoretical implications as determinants for species competitive success along the successional gradient: *a review of the literature*

2.1 INTRODUCTION

The principal goal of this study has been the promotion of a predictive understanding of management-induced compositional changes (succession) in the Tall Grassveld of KZN. In plant ecology succession is a broad subject and thus discussions surrounding it may radiate out into endless topics. Thus, to comply with the terms, it was desirable that the review on the present topic be summarized in two main sections.

1. It was imperative that successional theory, its developmental stages and the controversies surrounding the concept are sufficiently discussed. This was important in order to contextualise the recent developments in the subject.
2. Discussing the role of the major grassland disturbances in the area (KZN) i.e. fire and mowing, in relation to the above raised topics was also inescapable. However, a review of successional theory unavoidably leads to discussions of plant competition, resource availability and how this is mediated by various forms of disturbances (Sousa 1984, Peter *et al.* 1979, Tilman 1988). It may further require discussing on the contrasts in strategies of the life forms involved in succession (Bazzaz 1979, Grime 1979). The following review therefore has attempted to cover these and other related and apparently relevant topics.

2.2 PLANT SUCCESSION

Naturally, a review of successional theory must begin with a definition. Unfortunately, there is no generally accepted definition of succession. It is generally the case that for each theory of succession, there is a different definition to explain the process and its mechanisms (e.g. Clements 1916, Odum 1969, Grime 1979). Nevertheless, it is a matter of common observation that natural grasses occur in a number of easily recognizable communities. All such natural grass communities are established through gradual development, and for each community, a characteristic pattern in which a series of definite stage can be recognized. Such a gradual and “progressive” development of vegetation through a series of different plant groupings has been termed succession (Clements 1916).

There are two general types of succession: primary and secondary succession. Primary succession occurs when plants gradually become established in areas not previously vegetated because of the lack of soil development. Examples of primary succession include plants (e.g. lichens), which colonize a bare parent material such as a rock surface. This type of succession does not need disturbance to proceed. In contrast, secondary succession occurs in areas that were previously vegetated, but have had the pre-existing vegetation destroyed. In the case of secondary succession, much of the soil and plant propagules (such as seeds and rhizomes) remain intact (Grime 1979). Disturbances such as fire, logging, volcanic eruptions, landslides and cultivation are recognized to be the major causes that initiate secondary succession. In addition to primary and secondary succession however, depending on the nature of the causes initiating them, there are several types of successions. For instance, autogenic succession occurs after a rapid disturbance such as by fire and defoliation, whereas allogenic succession occurs due to gradual change in the environment (Grime 1979, McCook 1994). However, this traditional distinction between autogenic and allogenic succession has been suggested to be artificial, and they are not independent of each other (McIntosh 1981, McCook 1994). Though it is not generally acceptable, virtually all current discussions of succession consider only secondary succession, i.e. succession that follows disturbance. In light of the objectives of this project (stated earlier), this review will focus on secondary succession only. Classically, succession is considered as a recovery process of vegetation following disturbance (Grime

1979, Pickett *et al.* 1987, Bazzaz 1996). However, succession does not only refer to the recovery process of vegetation but it also involves a process of individual replacement and a change in the performance of individuals, which is commonly described as “the tradeoff” (Pickett *et al.* 1987). Such changes are partly brought about by the action of the plants themselves (Tainton and Hardy 1999). Alternatively man may exert influence on the vegetation and thus modification may vary according to the way man interferes with the system, so that changes may take place either slowly or rapidly, and in a number of possible ways.

In many ecology textbooks and University undergraduate courses in ecology for pedagogical purposes, succession is presented as a fairly simple and straightforward concept (McIntosh 1980). In reality however, succession is a complex and a very broad topic in plant ecology. It involves many processes such as seed source, seed dispersal mechanisms, germination, emergence and establishments of young seedlings, survival to maturity, reproductive behaviour and the interaction of all these with the environment (Raynal and Bazzaz 1973, Grime 1979). Therefore, it is extremely unlikely that any single factor or process will ever explain succession (Bazzaz 1979, Tilman 1982, Tilman 1988) and it is impossible to consider all possible causes and effects of succession into one review. In this context therefore, the term succession used here is in its simplest and narrow sense to denote vegetation recovery process after short-term sward manipulation by fire and defoliation (by mowing).

2.2.1 The importance of successional theory

Succession as a basic concept or theory of ecology has existed for over a hundred years and its significance persists. The concept has stood as a prime factor in the study of communities following disturbance. The understanding of succession and successional theory is as important as ever, on the account of research effort we see today (e.g. McCook 1994, Bazzaz 1996). The importance of successional theory was best described by Eugene Odum (1969) as critical for human society, in his own words: “*the principles of successional theory bear importantly on the relationship between man and nature therefore, the framework of successional theory needs to be examined as the basis for resolving man’s environmental*”

crises". Successional theory is the basis for much of the life history evolution, population dynamics, competitive interactions, nutrient dynamics, and community organization of plants. Practical issues such as the restoration of damaged ecosystems and predicting consequences of global change, also draw heavily on theories of succession. Its basic principles determine ecosystem development and apply the general rules to practical needs for promoting the reclamation of damaged lands. Moreover, the theory makes the central tenet of the understanding of community structure of all plant communities, and the dynamics of succession (Huston and Smith 1987, Bazzaz 1996). Resources management, rehabilitation and restoration, and ecosystem preservation, also greatly depend on successional theory (Bazzaz 1996). Thus, successional theory is the basis, which provides insight into how individuals, communities and populations change through time during the successional process.

When it comes to South Africa, the typical model of succession that had been applied to South African vegetation management up to the early 1980s had been Clementsian-Tansleyian in origin. These concepts of succession and the climax were introduced to South Africa by Bews (1916) and Phillips (1931) and were latterly based largely on the system proposed by Clements (Kruger 1984). It is a common feature of current literature around the subject that Clements' ideas are no longer influential in ecology (will be discussed latter). However, despite this fact his ideas have been widely used and misused by his followers world wide (McIntosh 1981, Crawley 1997b). In South Africa this approach was applied by many, and it is still continuing to influence approaches to resource management (Tainton 1981).

2.2.2 Development of successional theory

The historical development of successional theory is closely related to the development of the science of ecology. Although there is no general theory and model of succession yet, to fill the need for a theoretical context in succession, generations of authors have developed different theories. Indeed, the list of important works on succession can include hundreds of citations. Though it was impossible to include all the theories and views in one review, the following section attempts to outline some of the major and influential school of ideas surrounding succession and mechanisms of succession.

The old concept; historical perspective

That plant communities change is one of the oldest observations of the natural world (Clements 1916). Much evidence exists indicating that ancient humans have undoubtedly observed vegetation change. They saw the power of natural forces such as volcanic fires changing vegetation and used them, to “manage” ecosystems for their needs. Like any other primary concepts in ecology therefore, the idea of vegetation change (succession) and thus competition should have gradually emerged from the general experience of mankind (Clements 1916, 1928). In the formal sense however, the study of plant community dynamics in western science seems to have first appeared in the nineteenth century. Early ecologists have recognized regular, repeatable and apparently directional patterns of change in the species of a community. They soon understood that succession, its repeatability in an area and similarities in many areas should result from few underlying processes (e.g. Clements 1916; Gleason 1917, 1927, 1939). In an attempt to understand the underlying processes controlling succession, different processes have been considered important and several theories have been hypothesized (e.g. Clements 1916, Gleason 1917, 1927, Connell and Slatyer 1977, Grime 1979, Tilman 1985). The first theory was proposed by Frederic Clements (1916) and thus he is remembered as the father of successional theory.

Clements (1928) regarded succession as the growth, development and reproduction of a complex organism or superorganism, with the whole being the sum of the parts. He viewed plant communities as a complex quasi-organism to a predetermined climax. He assumed succession to be solely sequential. The assumption is that succession moves towards an inevitable, fixed and relatively stable climax. These concepts have been the source of much confusion (Drury and Nisbet 1973, Pickett and McDonnell 1989). In contrast, recent views of succession claim that succession is a multidirectional and probabilistic process, which can have more than one end point (Peter *et al.* 1979, Westoby *et al.* 1989). For instance, the state and transition model proposed by Westoby *et al.* (1989) and the “the multiple pathway model” by Peter *et al.* (1979) show that change in community composition is multi-directional rather than being restricted to uni-directional change. Several views of Clements therefore were disproved, and his ideas have remained a favourite target of critics of successional concepts in

the literature (McIntosh 1981). Although recent interpretations have tended to discount much of his early work, Clements' ideas still influence resource management (McIntosh 1981, Tainton 1981). Therefore, it has been cautioned by these authors that while using Clements's principles and terminologies careful interpretation is necessary.

Gleason (1917) is renowned for his "individualistic concept" of plant community structure. This author (1917, 1927, 1939) opposed rigid Clementsian views of orderly, progressive succession. He further argued that the holistic view point of Clements was inadequate in explaining the mechanism of succession. By contrast Gleason (1917) considered succession to be much less ordered. He considered that the nature of changes at a site depended entirely on the species making up the site. He argued strongly against the idea that any particular community functions as cohesive as an organism, but rather that successional communities are incohesive and random assemblages. He viewed succession simply as the result of differential longevity of plants. In his view, succession at any site would differ