

MONITORING SERIAL CHANGES IN
COASTAL GRASSLANDS INVADED BY
Chromolaena odorata (L.) R.M. KING & ROBINSON

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DECLARATION

I, Jeremy Marshall Goodall, hereby declare that this thesis comprises my own original work except where due reference is made to the contrary. This thesis has not been submitted for examination at any other university or academic institution.



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ABSTRACT

The objective of this study was to describe the impacts of the density of *Chromolaena odorata* (chromolaena) on species composition in coastal grasslands and to investigate serial changes in the vegetation following the implementation of a burning programme. The thesis deals with key ecological concepts and issues, so a comprehensive literature review is included.

Chromolaena invades coastal grasslands that are not burnt regularly (i.e. biennially). Grasslands that were not burnt for 30 years were seral to secondary forest. The successional pathway from open grassland to closed canopy forest varied according to soil type. Coastal grasslands on Glenrosa soils were characterised by savanna at an intermediate stage between the grassland and forest states. Shading ended the persistence of savanna species (e.g. *Combretum molle*, *Dichrostachys cinerea* and *Heteropyxis natalensis*) in forest, whereas forest precursors (e.g. *Canthium inerme*, *Maytenus undata* and *Protorhus longifolia*) only established where fire was absent. *Chromolaena* infestations were characterised by multi-stemmed adult plants of variable height (i.e. 1-3 m), depending on soil type. Regic sands did not support stratified woody vegetation and *chromolaena* infestations were self-supporting, reaching a maximum height of 1.5 m. Glenrosa soils supported tree communities and *chromolaena* reached more than 3 m in places. The density of *chromolaena* affected species composition in grasslands with moderate to dense stands (> 5 adult plants m^{-2} or $> 50\,000$ shrubs ha^{-1}). *Chromolaena* stands became monospecific when the number of adult plants exceeded $7\,m^{-2}$. Succession to forest also ceased once *chromolaena* became thicket-forming.

Fire-induced mortality of the *chromolaena* depended on grass fuel loads. Grass cover of 30% (c. $1\,000\,kg\,ha^{-1}$) was required to achieve 80% mortality of the parent infestation after the initial burn. Dense infestations could only be killed by running head-fires from adjacent grasslands into thickets. Under conditions where head-fires could not be used, infestations were slashed and burnt at the height of the dry season (July to August) to achieve an 80% kill rate. Seedlings were killed (99%) by annual burning in sparse ($\leq 10\,000$ shrubs ha^{-1}) to moderate ($< 50\,000$ shrubs ha^{-1}) infestations. The suppression of *chromolaena* and other alien species, establishing on bare ground after clearing dense infestations, required chemical control until grass cover was sufficient (i.e. $1\,000\,kg\,ha^{-1}$) to effect uniform burning. Certain secondary alien invaders (e.g. *Lantana camara*, *Psidium guajava* and *Solanum mauritianum*) persisted by coppicing profusely after fire and herbicides need to be integrated into burning programmes when these species occur. Grasslands on regic sands (e.g. *Ischaemum fasciculatum*, *Panicum dregeanum* and *Themeda triandra*) were more resilient to the modifying effects of woody vegetation, than grasslands on Glenrosa soils. Grasslands on Glenrosa soils did not revert to an open state but persisted as ruderal savanna grassland (e.g. *Eragrostis curvula*, *Hyparrhenia tamba* and *Cymbopogon validus*) once fire-resistant tree species (e.g. *Combretum molle* and *Heteropyxis natalensis*) had established.

Depending the objectives for land management and the vegetation's condition, coastal grasslands can be rehabilitated and managed in multiple states, i.e. grassland, savanna or forest communities. A state-and-transition model based on the empirical data recorded in the study is presented and shows *chromolaena* altering vegetation states from open grassland to *chromolaena* dominated thicket. The model illustrates *chromolaena* thickets as the dominant phase of a moist coastal forest/savanna succession, irrespective of soil type, in absence of appropriate land management practices (e.g. control burning and integrated control of alien vegetation). This model should aid in planning strategies for the control of *chromolaena* in subtropical grasslands in South Africa.

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1. LITERATURE REVIEW

This thesis reports on an eight-year study describing the impacts of *Chromolaena odorata* (L.) R.M. King and Robinson (chromolaena), before and after burning, on the integrity of coastal grasslands in KwaZulu-Natal (KZN). Key ecological concepts and issues in vegetation science that are discussed in the thesis needed clarification in a literature review preceding the research component. In Chapter Two topics of direct relevance to this study are discussed, namely the status and control of chromolaena, the ecology of coastal grasslands and the project aims.

The study of rangeland condition has been conducted from a predominately utilitarian perspective, with special cognisance to the role of livestock-grazing and fires (e.g. Clements 1916; Stoddart & Smith 1955; Ellison 1960; Noy-Meyer 1978; Westoby 1979; Tainton 1981; Trollope 1984). Unlike prairie grassland, the 'false grasslands' (*sensu* Mentis 1982) along the KZN and Transkei coast are believed to have been forged out of Coastal Forest following 'slash and burn' practices during the Iron Age (c. 2000 BP) (e.g. Feely 1980; Hall 1981). The impacts of the Iron Age and alien invasive plants (e.g. van Wilgen & Richardson 1985; le Roux & le Roux 1991) on coastal vegetation are largely descriptive though. To formulate hypotheses on the integrity of 'anthropogenic' grasslands it would be appropriate to first review fundamental ideas in rangeland science. The nature of the subject involves unavoidable references to grazing, however, which was not a component of this investigation. Pastoral practices were believed to have been introduced into the KZN coastal region after deforestation (Hall 1981) and were a factor in maintaining the coastal grasslands for over a thousand years. Chapter Two explores these anthropogenic influences in the development, and later degradation, of coastal grasslands based on empirical evidence.

1.1 Introduction to alien plant invasions

Alien invader plants, particularly woody species, are a major causes of ecosystem collapse worldwide. If left uncontrolled alien plants impact non-selectively on the environment, replacing species-rich plant communities with monospecific vegetation (Cronk & Fuller 1995). As weed density increases, internal resilience decreases, resulting in a breakdown in community structure, function and diversity. The breakdown of the vegetation component affects ecosystem dynamics and food webs. Resultant habitat loss is a direct threat to displaced fauna and rare plants (e.g. *Gerbera aurantiaca* - Hilton Daisy).

Chromolaena is posing a threat to the Black Rhino and Nile Crocodile habitats in Zululand. The unpalatable weed invades thicket vegetation that rhinos use for browse and protection, displacing an endangered species in the process. Nile Crocodiles make their nests on river banks where light and temperature are important in ensuring both embryonic-development and balanced sex-ratios. Chromolaena invades these areas and shades out nesting sites. This results in increased egg mortality and produces female-biased sex-ratios (Dr A Leslie pers. comm., Department of Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602).

Naturalised nitrogen-fixing species enrich nutrient-poor soils, facilitating the establishment of other alien species (Cronk & Fuller 1995). Some species accumulate large amounts of salt during their life cycle which they release once they die, boosting saline conditions and preventing natural succession from taking place (Kloot 1983). Invasive alien plants alter fire behaviour, or facilitate fires, increasing their severity and frequency, causing extensive damage to the natural vegetation and soil properties (Macdonald 1983; Macdonald & Jarman 1985; van Wilgen & Richardson 1985). Bush encroachment and injudicious grazing management have seen a reduction in regional carrying capacities and fuel loads. Fires, when they occur, are generally cool and do not result in great mortalities of woody species (Rutherford & Westfall 1994). Species such as *Lantana camara* are ecological indicators of poorly managed (includes sustained heavy grazing) range, where the quantity of fine fuels is below the requirements needed to induce shrub mortality. Woody alien species, especially *Acacia*, *Eucalyptus* and *Pinus* genera, have impacted greatly on hydrological processes in South Africa (Mueller-Dombois 1973). Versfeld *et al.* (1998) estimate 7% (3 300 million m³) of South Africa's mean annual water runoff is lost annually through the transpiration of alien plants in mountain catchments.

1.1.1 Traits of alien invasive species

General theories have been formulated about why some introduced species become naturalised. The absence of predators hypothesis supports the idea that problem species were introduced without their natural enemies and therefore have competitive advantages over indigenous species in every facet of their life cycles (Huffaker *et al.* 1976). Similarly Cronk and Fuller (1995) theorise that alien species have a greater reproductive potential,

characteristically producing greater quantities of seed than native species which are preyed upon by herbivores, pathogens and diseases. Consequently alien species have large residual seed banks.

The poorly adapted species hypothesis suggests native species are less well adapted to the specific conditions than alien species. The reason for species displacements would be easier to demonstrate as an outcome of the absence of predators hypothesis than by showing that alien species have superior niche dominance qualities. Elton's (1958) balance of nature hypothesis suggests species-rich communities with complex interactions are more resilient to invasion. The susceptibility of fynbos to plant invasions, however, was not significantly different to the other biomes in South Africa (Macdonald & Richardson 1986). Fynbos species are intolerant of shading caused by the taller growing alien species. The same may be said about other rangeland plants. Vacant-niche hypothesis assumes woody alien invasive species 'fit in' rather than competitively 'push out' native species in affected communities (Macdonald & Richardson 1986). This theory is not supported by empirical evidence (Cronk & Fuller 1995), but observation shows that alien species modify ecosystems and reduce species diversity, not add to it.

Although alien invader plants are known adversely to affect biological diversity (=biodiversity) (e.g. Drake *et al.* 1989), very little has been reported on how individual species affect plant community composition, structure, and function. The impacts of alien invasive species on ecosystem integrity and plant community succession are largely unknown.

1.2 Ecosystem integrity

Ecosystems are organised both structurally (populations, species and communities) and functionally (production and consumption components). Ecosystem integrity is the ability to maintain structural and functional organisation, and interactions, after disturbances (Limburg *et al.* 1986). Ecosystem integrity integrates many scientific disciplines, enabling management of natural systems for human benefit without harming ecological processes, structure or functioning of such systems. The sustainable use of natural vegetation therefore requires an understanding of plant succession, resilience vs stability, non-equilibrium vs

equilibrium, ecological redundancy, disturbance processes, niche theory, species functional groups and the management of biodiversity.

1.3 Succession

The study of plant community succession evolved from a period of holism, e.g. “super-organism” or monocl原因 succession (*sensu* Clements 1916) to reductionalism or individualistic succession (e.g. Botkin 1981, Huston & Smith 1987, Pickett *et al.* 1989). This section reviews the major contributions towards the development of succession theory. The issues revolving around monocl原因 and polyclimax states, namely stability vs resilience and equilibrium vs non-equilibrium are discussed separately in sections 1.4 and 1.5. The possibility that vegetation can function in alternative states is mentioned in subsection 1.5.1.

1.3.1 Obligate facilitative succession (monocl原因 theory)

The development and current understanding of plant community succession evolved principally from the pioneering work of Frederic Clements (1916). Clements understood succession as sets of climatically determined, universal sequences, culminating in a stable plant community that could progress no further. This so called end-state was called the ‘climax community’ determined by the climate. Clements described succession as a process comparable to the growth and development of a complex super-organism, where the organic whole (the climax state) had greater reality than the sum of its parts (species). The climax community remained in harmonious equilibrium with the greater environment, a product of reactions operating within the limits of the climatic factors of the region concerned. Climate, the stabilising controller of succession, determined what dominants (*sensu* Clements 1916) could grow in the region and what life forms would make up the final stage of development. Equilibrium states persisted in absence of catastrophes such as fire, flood, mismanagement, or until there was a fundamental change in the climate.

The development of vegetation or autogenic succession (Tansley 1920, 1923) was divided into primary and secondary succession (Clements 1916; Weaver & Clements 1938). Primary succession referred to the development of ecosystems on a sterile substrate (e.g. by the retreat of a glacier). Rock weathering processes made conditions favourable for the substrate to support life but any species that established arrived from outside the area, not from within it. Secondary succession was the development of vegetation on ground after a disturbance had

partly damaged or destroyed the existing vegetation. Colonisation and establishment took place from germinating seeds already in the soil. Both these definitions are still applicable but this thesis is only concerned with secondary succession.

According to Weaver and Clements (1938) obligate facilitative succession is made up of seres, i.e. vegetation sequences, after disturbance in both primary and secondary succession. Pioneer species induced changes in seres, making conditions more favourable for new species and less agreeable for earlier species. Seres therefore became progressively richer in species. In turn, species became more specialised in the progression towards the climax stage by reducing competition and successfully completing their life-cycles in the limited space available for growth and development.

Clement's theories from the outset were opposed by Tansley (1920), who questioned the exclusivity of climate and the extreme use of 'organism' in dealing with plant communities. In addition Tansley referred to another dimension of succession, allogenic succession, where changes, independent of the plant community, gradually altered the habitat, thus causing changes in the vegetation. Tansley's (1920, 1923) understanding of the 'climax state' was not restricted to the 'climatic climax' (*sensu* Clements 1916), but to any "stable and well characterised community" whose persistence was determined by many biotic and abiotic factors allowing for polyclimax states.

Gleason (1939) argued that succession was an individualistic process determined by species composition, by which successional changes could be explained by population dynamics, and not the 'embryological' development of the climax community. Whittaker (1951) was also critical of Clement's climatic concept and proposed that successional responses varied from site-to-site, leading to a multiplicity of endpoints. Clements (1916), nevertheless, still recognised the unique individuality of species in contributing towards vegetation states. The absolute finality of these states, however, was becoming increasingly untenable.

1.3.1.1 The role of obligate succession in North American rangelands

Weaver and Clements (1938) believed under certain conditions the climax community did not always develop. Managed disturbances could hold vegetation development at disclimax

(sub-climax) states. Stock farmers adopted the Clementsian paradigm under which grazing intensity was inversely related to the successional status of prairie vegetation (Stoddart & Smith 1955) and used grazing strategies to direct grassland condition towards preferred states (Ellison 1960). The theory was that grazing caused compositional changes leading away from the climax, but once the vegetation was rested, natural succession would bring the compositional structure back to the climatic climax.

1.3.1.2 Changing perceptions of plant succession in North American rangelands

Over the decades the unforeseen impacts of Clement's (1916) overemphasis of stability in plant communities were becoming serious. Prairie rangelands were being irreversibly changed at an alarming rate. Episodic climatic extremes in regions under the axe, cow and plough revealed the innate resilience of natural vegetation and the frailty of unsustainable agro-ecosystems (Worster 1985). Tornados and drought had reduced the wheat fields of the Great Plains to 'dust bowls'. Continuous heavy grazing weakened the herbaceous layer and caused soil erosion (Ellison 1960). Desirable species were replaced by less preferred species and invasions of new species from outside the area.

Ellison (1960) referred to range as "lands clothed mostly with native vegetation that cannot be grazed heavily with safety.". He proposed the replication of the exact composition before grazing would never be achieved under any form of grazing practice. Despite his intuition, Ellison failed to explore the role of grazing on the non-equilibrium dynamics of vegetation and so offered little opposition to Clementsian range succession.

Despite the premises that monoclimate theory (Clements 1916) suggested no damage could be permanent, denudation by cultivation, deforestation, overgrazing and the associated effects of soil erosion, non-equilibrium trends in rangelands were becoming increasingly acceptable (e.g. Turner 1971; Smith & Schmutz 1975; Noble 1986). Excessive disturbance and soil erosion imposed unique difficulties for orderly succession to occur. Succession ecologists began to accept that vegetation could function in alternative states, discontinuous and irreversible transitions and nonequilibrium communities (e.g. Tansley 1923, Gleason 1939, Whittaker 1951, Glendening 1952, Jenny 1961, May 1977, Westoby *et al.* 1989).

Clementsian range ecology underpinned the management of rangelands for many years. Blind acceptance of Clements's (1916) "super-organism" theory has done much damage to non-equilibrium systems through the implementation of veld management strategies that were based on inappropriate theories. Obligate facilitation, the development of the stable climax and organismic community behaviour are severely questionable concepts.

1.3.2 Individualistic succession (polyclimax theory)

The study of succession does not depend on the existence of a climax, but focuses on processes and uniquely spatial and temporal components, rather than a rare endpoint to the process (McCook 1994). Simulation modelling backed with manipulative experimentation presently form accepted mechanistically deduced principles of succession (e.g. Botkin 1981; Huston & Smith 1987; Pickett *et al.* 1989).

1.3.2.1 Resource allocation strategies

No organism can be simultaneously well-adapted to all environmental conditions, particularly the biological interactions of competition and predation (McCook 1994). Huston and Smith (1987) demonstrated the strategic resource allocation concept on sequential species replacements based on the following precepts:

- (a) "Competition between individuals for resources occurs in all communities;
- (b) Plants alter their environment, changing the availability of resources and adjusting the criteria for competitive success; and
- (c) Physiological and energetic constraints prevent species from maximising competitive ability for all circumstances, producing inverse correlations between certain groups of traits so that relative competitive abilities change over a range of environmental conditions."

The Huston and Smith (1987) simulations followed individual tree life cycles, modelling birth, growth and death as life history traits regulated by the competition for light, which in turn, was an absolute and individually based condition controlled by the neighbouring plants. Both primary and secondary succession were modelled as non-equilibrium processes, capable of interacting with disturbances to produce steady-state communities whose properties depended on abiotic conditions such as temperature, resource levels (e.g. availability of nitrogen and water) and frequency of disturbance. Sequential succession (McCook 1994), or successional replacement (Huston & Smith 1987), involved sequential peaks and declines in

abundance of different species. They predicted four types of sequential species replacements by modelling two species with inversely related traits.

- (a) Divergence: occurred when competitive abilities were initially equal but as the stand developed some species gained competitive advantages due to their regenerative ability and-or size.
- (b) Convergence: inverse of divergence, occurred when one species had a competitive advantage in early stand development but both reached equal competitive ability as the stand developed. Convergence resulted in similar final abundances of both species.
- (c) Total suppression: occurred when one species had immediate and lasting dominance over the other species. The suppressed species never achieved significant abundance, size and could disappear altogether, leaving a monospecific stand.
- (d) Pseudo-cyclic replacements: involved periodic reappearances of alternating species abundances, the patterns of which emanated from particular combinations of species traits. No species could dominate a site throughout the period of its growth because of the inverse correlation between stress tolerance, rate of growth, adult size, longevity and dispersal strategies.

In simulations involving five species, Huston and Smith (1987) showed early dominant species inhibiting growth of the next dominant but indirectly facilitating the final dominant. In addition they reported the arrival of a “super-species” which could reduce the relative abundance of both early-successional and mid-successional species. Alien invasive plants have characteristics enabling some species to suppress natural vegetation completely. The successional climax in such instances terminates in single-species stands.

Tilman’s (1985) resource-ratio hypothesis assumed tradeoffs between strategic allocations and competition resulted in species adaptations at different points along resource gradients. Under conditions of increasingly limited resources a species population at equilibrium with the lowest resource level would be competitively dominant. Emphasis was also placed on the strategic allocation of resources and tradeoffs between the roots and shoots. The resource-ratio hypothesis has limitations. It does not explain the causes of changes in resource levels, it accepts unrealistic equilibrium dynamics and is a population model ignoring variability in individual species responses to the biotic (competition and predation) and abiotic (fire and drought) processes.

1.3.2.2 Other succession models

Horn (1975) advocated the use of Markovian probability models to describe changes in

species composition of forest trees over time by estimating replacement probabilities under mature species. The estimate of these probabilities, compounded by the lack of theoretical or causal understanding discredited their use in formulating mechanistically deduced principles of succession. Markovian replacement models had predictive functionality that was more suited to management purposes. The model consistently revealed that initial composition was independent of a stable, single, end state. It is therefore an equilibrium model that derives projected outcomes statistically and ignores biological basis for species replacements. An additional weakness of Markovian replacement probability models in individualistic succession is that they are neither testable nor falsifiable (McCook 1994).

Grime (1977) developed the C-S-R three-way competition classification. In this system plants are either competitors (C), stress tolerant plants (S) or ruderal species (R). Competitive plants are fast-growing species forming dense canopies and accumulating copious amounts of litter. In relation to stress, e.g. shading or drought, these plants seek maximum production through morphological changes. Stress tolerant plants are slow growing with minimal litter production and lack morphological flexibility. These plants survive stress by reducing growth and reproductive activity. Ruderal plants are fast growing, short lived herbaceous species flowering at the end of the period favouring growth. In response to stress, ruderal species divert energy into seed production.

Grime's (1977) description of plant strategies was empirically based, with *post hoc* rationalisation that does not explain changes in species composition. It also lacks the power of other mechanistically-based approaches which consider tradeoffs between species. Species evolve unique traits of adaptation through processes of life history evolution, coevolutionary interaction and adaption to the competitive pressures. According to Huston and Smith (1987), plant strategies resulting in hierarchies of relative adaption to each different set of conditions are more complex than the C-S-R classification.

Connell and Slatyer (1977) presented an integrative model of succession that included facilitation, tolerance and inhibition. Earlier species ameliorate conditions which become suitable for the establishment and growth of new species but no longer suitable for their own survival. The tolerance model is similar to the facilitation model, the primary difference

being recruitment and replacement are not absolutes and coexistence of early and late succession species is possible. The intolerance model precludes any form of facilitation or sequential replacements, the earlier colonist suppresses or inhibits subsequent colonisations by other species. The model as it stands understates community succession. Facilitative succession, being mutually exclusive from inhibition, is unrealistic in a dynamic system controlled by many internal and external factors.

1.3.3 General principles of succession

Facilitative succession implicitly refers to the principle that the prior influence of earlier seres or species is an essential requirement for the establishment of later species (Clements 1916). Plant strategies, however, are likely to form a multidimensional continuum resulting in different hierarchies of relative adaption to each different set of conditions (Connell & Slatyer 1977, Tilman 1985; Connell *et al.* 1987; Huston & Smith 1987). Species with inversely correlated traits may, therefore, be adapted at different points long a successional gradient. Loehle (1988) considered that tradeoffs in species life-history strategies were a fundamental ecological principle. The frequency and intensity of disturbance are also likely to influence the course of succession. Disturbances produce directional changes in species composition, abundance and biomass, affecting hierarchies of adaption strategies and tradeoffs. The growing consensus that ecosystems are not stable communities (Holling 1973) imply that successions, or directional changes, are not needed for making assumptions about unique climax states (McCook 1994). The study of succession as a dynamic process is more important and these processes are still not adequately understood. Better understanding of community dynamics under applied conditions will lead to better management practices in the future.

1.4 Stability and resilience

Stability by definition means a state of balance in a body, which once disturbed, returns to an equilibrium state (Sykes 1982). Alternative terms for stability are properties of irreversibility and inflexibility (Kirkpatrick 1987). In ecological systems magnitudes of disturbance are counterbalanced to a degree by the internal dynamics of the system (Holling 1973). Disturbances larger than those which the system can absorb would result in changes in the stability of systems. Resilience suggests an ability to resume original form after disturbance

(Sykes 1982). Words synonymous with resilience are elasticity and flexibility (Kirkpatrick 1987). Stability and resilience are therefore two opposing ecological concepts, which under lax examination impart a sense of similarity. Stability is associated with monoclimate theory (equilibrium ecology) and resilience is referred to in systems with multiple stable states (disequilibrium or non-equilibrium ecology). Disequilibrium and non-equilibrium have both been used synonymously in ecology (Davis 1984; DeAngelis & Waterhouse 1987).

Resistance refers to the ability of ecosystems to absorb disturbance and retain biological structure and function (Begon *et al.* 1990). The region within which stability occurs is termed the domain of attraction (Holling 1973). The domain of attraction comprises boundaries which are variable, depending on the properties of the system. Populations forced towards these boundaries by external forces (e.g. change in burning regime), and/or a change in state variables (e.g. alien plant invasions), can undergo permanent change (Friedel 1991).

Resilience is inherent in natural communities and stability behaviour is the response to disturbance. Sustained disturbance will reduce resilience to a point where only marginal disturbance will trigger collapse. The specific causes of change are important. The properties of resilience and stability are most critical when it comes the manipulation and management of natural systems for human benefit. Plant abundances for example may vary discontinuously and irreversibly in response to changes in stocking rate (Glendening 1952; Noy-Meir 1978). The reduction or discontinuance of the driving variable may not result in recovery and may only be correctable through forced manipulation of the state variable, e.g. invasive plant control.

The persistence of ecosystems is determined by the resilience properties of the system. Stability is the ability of systems to return to an equilibrium state after a temporary disturbance, the more rapidly it returns and with least fluctuation, the more stable it is. These two terms refer to system properties but the results are the probability of persistence or extinction in resilience, and, fluctuation around specific states in stability. A system can therefore be resilient (persistent) and unstable. The relation between herbivorous insects and their host plants shows how instability in populations of both predator and prey ensures the survival and persistence of both. Populations of both species are regulated by equal yet

opposite crash and boom cycles (Huffaker *et al.* 1976).

Although knowing how stable ecosystems under management are, understanding the probability of systems persisting in an altered state is more crucial. In this respect managers need to understand non-equilibrium dynamics and the consequences of changes in the domains of attraction leading to permanently altered states, which may be less productive (concerning any specific set of objectives) than the original vegetation.

1.5 Equilibrium and non-equilibrium

Monoclimax theory (Clements 1916) does not hold for every system. In fact it is the exception, not the universal property of terrestrial plant communities. Non-equilibrium dynamics are most profound in grazing systems in arid climates (Westoby 1979) and are indicated by annual plant persistence, alternate stable states, woody plant invasions and irreversibility after soil erosion. It does not imply that mesic environments are equilibrium monoclimax systems, although rapid secondary forest successions in rangelands and fallow fields throughout the tropics (de Foresta & Schwartz 1991; Hochberg *et al.* 1994; Gignoux *et al.* 1997) can fool the observer into accepting equilibrium dynamics when in fact this is not the case. May (1977) advocated non-equilibrium ecology as the dominant theory of ecosystem change.

1.5.1 State and transition models

Non-equilibrium theory claims not all systems will return to the original state after disturbance and proposes catalogues of alternative stable states. Tansley (1935) believed random events on a landscape scale were an integral part of the multiple stable states phenomena (Jenny 1961). Vegetation is inherently unstable, the product of state factors such as climate, competition, stress, predation, nutrient enrichment, leaching and disturbance intervals. Non-equilibrium states thus equate to multidimensional landscape heterogeneity made up of alpha diversity states and beta diversity transitions between states and transitions.

The state and transition model in its original form organised vegetation changes into sets of discrete “states” and “transitions” (Westoby *et al.* 1989). Transitions between vegetation states were triggered by random or planned events, (e.g. cyclones, wildfires, invasive plant

control) which acted as catalysts for change in vegetation structure. The authors proposed the model as a practical way to organise information for management based on non-equilibrium dynamics and experimentation. Knowledge about a given range system derived from experimental trials, is organised into catalogues of possible alternative states and possible transitions from one state to another. The model schematically lists states, transitions, indicators, opportunities and threats which managers can use to detect symptoms of changes in vegetation and what to do to prevent further change from occurring.

Development of state and transition models in Australia (e.g. Ash *et al.* 1994; Brown 1994; Grice & Macleod 1994; Whalley 1994) during the 1990s has attracted both positive and negative responses. As an academic tool furthering the understanding of the spatial and temporal non-equilibrium dynamics of rangelands, it has proved extremely useful. The model, being simple and graphic, is also a very popular tool in the transfer of theoretical ideas into practical working knowledge for farmers and land managers. The application of the model in practice is bedevilled by the problems of insufficient catalogues of states and transitions. The model presently serves as a conceptual synthesis of the non-equilibrium dynamics in a few managed rangelands (Brown 1994; Ash *et al.* 1994; Grice & Macleod 1994). Mentis and Bailey (1990) uphold the state and transition approach under South African conditions, advocating not all African rangelands are stable.

1.5.2 Scale and disturbance

The term 'natural' in the sense of 'natural conditions' given to managing ecosystems may be irrelevant (Sprugel 1991). Given whole landscapes are made up of ecosystem-mosaics in a state of constant climatic adjustment, the notion of 'what is natural' becomes subjectively flawed. The controversy regarding 'natural conditions' (e.g. Bonnicksen & Stone 1985) relates also to the role of disturbance in natural systems (Sprugel 1991). Natural disturbances (e.g. wild fires, wind storms, hail etc.) are so common, assuming 'stable climaxes' is unrealistic for any ecosystem to maintain (Hanes 1971; Heinselman 1971; Habeck & Mutch 1973; Whitmore 1974; White 1979). The idea of orderliness and equilibrium are confounded by scale (Turner *et al.* 1993). An equilibrium landscape is one in which the parameter of interest (e.g. species composition) is roughly constant from year to year when averaged over the entire landscape (Bormann & Likens 1979), or when opposing processes (e.g. nutrient

input vs nutrient loss) are approximately balanced at a landscape level.

Shugart and West (1981) suggested a quasi-steady state landscape is at least 50 times the size of the average disturbance, but even at double this scale Baker (1989) failed to explain equilibrium in ecosystems. 'Wave forest' syndrome in North America is a non-equilibrium forest system whose persistence and diversity depend on uneven structure caused by episodic tree-toppling windstorms (Runkle 1982). The existence of natural forests throughout the world is therefore not a sufficient reason for proving the existence of stability, equilibrium or climax states in nature. Acocks's (1953) categorisation of climax Coastal Forest (Veld Type 1) assumes an ecological evenness that does not exist. This forest type is also sporadically subjected to severe climatic extremes, e.g. droughts (1992-1994) and cyclonic events (Cyclone Damoyna in 1984, the cutoff low pressure system in 1987 and Cyclone Eileen in 1999), encountering both monsoon-like rains and aridity (Tyson & Dyer 1975; Tyson *et al.* 1975; Tinley 1985; Lionnet 1993). In addition, the KZN coastal lowlands have been subjected to anthropogenic disturbances for 2000 years (Maggs 1977; Feely 1980; Hall 1981; Prins 1993).

Human beings have a culture of viewing themselves apart from nature (Grumbine 1997), which is often reflected in their approach to managing vegetation. Forest protection strategies in North America (e.g. McLain & Lee 1996, Sprugel 1991) for example have essentially resulted in a tradeoff between timber preservation and fundamental changes to vegetation. Insect infestations such as the spruce budworm, fire suppression, long-term drought, and flooding by beaver have changed the condition of the forest in ways not anticipated. Fire prevention efforts have simply pronged the incidence of fires but increased fire temperatures when forests do burn. There is also a correlation between budworm outbreaks and the age of forest stands. Random events therefore appear important for regulating the pulse of ecosystems and ensuring polyclimax states persist across landscapes and continents. Polyclimax states possibly exhibit equilibrium properties at scales that are patchy and short-lived in relation to the vegetation of interest. The vegetation component responsible for persistency in stable states is called the redundant component and is discussed further in the next section.

1.6 Ecological redundancy

Redundancy in an ecological sense means “surplus to the requirements” (Lawton & Brown 1994) of ecosystem structure and function, but not diversity. The kinds of biodiversity of greatest conservation value are those determining the ways ecosystems function. Taxonomic approaches to quantifying species diversity (e.g. species richness, alpha and beta diversity) assume all species have evolved equally (Gleason 1922, 1939; Whittaker 1972; Peet 1974; Whittaker 1977). Species-based approaches for targeting biodiversity conservation place emphasis on known urgencies. An ecosystem centred approach, however, is tactically sounder because it transfers the emphasis over to managing the habitat under which functional component species are conserved, including those rare and endangered (Walker 1992, 1994). Lawton and Brown (1994) posed two questions. “How much species redundancy is built into ecological processes and to what extent are patterns of biodiversity important in determining the behaviour of ecological systems?”.

Two approaches are possible, namely the “rivet hypothesis” of Ehrlich and Ehrlich (1981) and the “redundant species hypothesis” (Lawton & Brown 1994). The “rivet hypothesis” supports the idea that every species has some role in maintaining ecosystem integrity. In this analogy species are likened to the rivets holding a complex structure together, with limits about how many rivets can be removed from the superstructure before it collapses. This theory would conform to taxonomic approaches, although resulting indices of biodiversity would do little to advance the field of ecosystem integrity and management.

The “redundant species hypothesis” (Lawton & Brown 1994) assumes species diversity is secondary to sustained biomass (= abundance) of primary producers and their association with the other elements of the food web, e.g. consumers, predators and decomposers. This is the theory to which many ecologists subscribe. While the loss of biodiversity is of global concern (e.g. Glowka 1994), species loss may be tolerated up to some critical threshold because some species have greater functionality and importance than others (see keystone species, see Section 1.8.3.3).

At one end of the functional spectrum are “drivers” of the ecosystem of which they are a part, at the other end are “passengers” or “umbrella” species (Walker 1992). “Drivers” are usually

made up of several species which perform similarly yet vital functions maintaining homeostasis, e.g. nutrient cycling, microclimate regulation etc. The loss of “driver” species causes cascading effects in species losses, resulting in ecosystem transformation in systems without redundancy. Ecological redundancy refers to the guilds of species occupying functional groups maintaining ecosystem integrity. This ecological overlap provides a measure of safety to ecosystem function when exposed to disturbance. Such systems are considered resilient because the loss of a species within a guild can be functionally compensated for by the other, ecologically equivalent, member species.

In practice functional groups are the most dominant or abundant species, growth forms and life forms. The importance of high abundance (commonness) rather than rarity as selection criteria is more efficient at breaking down species diversity into functional groups which describe the major matter and energy in the system (Körner 1994). Keystone species (Section 1.8.3.3) will be underestimated by such a dominance-centred approach. No clear-cut guidelines on the identification of functionally dominating groups have been successfully applied and much is left to the individual’s objectivity.

Although the “redundant species hypothesis” is more manageable than its rival hypothesis, there remains great confusion in the development of methods which can be used for determining ecological redundancy (Lawton & Brown 1994). For example, how does one go about identifying which combinations of species are key components of ecosystem integrity as a corollary of species richness, abundance, function and structure? Spatial and temporal dimensions of the observer’s interpretation of landscape-level variability, ecosystem condition and successional status are also important. In ruderal ecosystems species composition will vary over time. Depending on the direction of change, biodiversity, species guilds and functional groups are likely to become more structured under conditions with minimal soil disturbance and normal climatic conditions. Apparent ‘passengers’ (noisy data) at one time scale may be ‘drivers’ (keystone species, Section 1.8.3.3) at another in systems that are changing.

A use of multivariate analysis is to summarise ecological redundancy by describing plant community composition, structure and function in low dimensional space (Gauch 1982).

This may have sensitised researchers into perceiving that ecological redundancy means we can afford to lose some redundant and noisy information without compromising biological integrity of ecosystems. This violates the importance for sustaining redundancy in nature. Ecological redundancy is a crucial element in the conservation of biodiversity. The “redundant species hypothesis” upholds this notion and therefore indirectly upholds the “rivet hypothesis” by maintaining biodiversity through correct habitat management. This aspect relates to the collective management of species and their respective roles and niches in the ecosystem. Does every species have a purpose? The perceived importance of species may be a condition imposed by scale or management objectives.

1.7 Niche theory

The niche concept is important to all of ecology, yet its theory remains confusing and its physical measurement is an intractable problem (Giller 1984; Arthur 1987). Central to theoretical ecology is the idea that absolute competitors cannot coexist together indefinitely (Hutchinson 1975 cited in Giller 1984). For two ‘competitive’ species to coexist would mean a discrete level of uniqueness accorded to both, i.e. separate niches. Two states of a niche are identified, the fundamental niche and the realised niche (Hutchinson 1958 cited in Giller 1984). The fundamental niche is the “total range of environmental variables to which a species must be adapted (physical, chemical and biotic), and under which a species’s population lives and replaces itself indefinitely” (Giller 1984). The realised niche is the actual set of conditions in which the species normally exists, evidenced by its population size and distribution in the community over space and time.

Niche width of a population is the absolute variety and amount of resources exploited. The niche of each species is then defined by a resource utilisation function (the distributions of a species’ activity) along a resource gradient. The niche is generated by both occupying species and the community being occupied. Intraspecific competition is inversely related to interspecific competition. Low interspecific competition increases a population’s niche width, making more resources available for specialisation. Interspecific competition restricts the resource utilization ranges of species. Increased niche separation is predicted as increased species diversity, and a related decrease in the size of the realised niches of component species. The process of self-thinning is a common trait arising from interspecific competition in tree and shrub communities.

If the resource utilization function between species is disjunct, empty niche spaces are created which are potentially available to immigrant species whose niches correspond to them.

‘Empty niche’ and ‘niche space’ mean the same thing (Arthur 1987). The concept of ‘space’ refers to the resource dimensions. Thus, ‘niche space’ is reserved for the environment and ‘niche’ for organisms. Predation and competition are the main causes of the realised niche. Niches are not discrete entities but a network of fundamental niche overlaps, resulting in simultaneous demands on some resources by two or more species populations. If the overlaps are very small, or the resources are not limiting, the outcome is coexistence. If the overlap zones cannot supply the demand for key resources, competitive exclusion of species that are less efficient will result. Although niche overlap might be small in plant communities, the commutative effect of competition can severely alter the size of the realised niche, even to the extent where it can no longer support some populations. This diffuse, interspecific, competition ‘squeezes out’ species under conditions of, for example, successional replacement. Self-thinning occurs when individuals’ roots overlap in competition for diminishing resources as the populations age, resulting in distributional changes over time.

1.8 Functional classifications of plants

The functional classifications of plants are arbitrary and inconclusive (Solbrig 1994).

Functional groups can be formed at any level of organisation and for any sort of function, so their number is limitless (Körner 1994). The scale of selecting functional groups is often chosen subjectively according to the aims of the research. Lower levels of complexity, e.g. positions of strategic organs on an organism as opposed to the entire organism, will allow for greater precision of describing deterministic processes at the ecosystem level, but with minimal relevance to the function of the superstructure itself. Inversely, grouping functional attributes based on shoot architecture will not sufficiently explain deterministic factors at a community level, but its functional relevance may be more conspicuous. The three functional groups most commonly referred and tested under South African conditions are life forms, growth forms and species and are relevant in this thesis.

1.8.1 Life forms

Rutherford and Westfall (1994) recommend the Raunkiaer (1934) life form classification for

its versatility in many vegetation types, simplicity and ease of application. Raunkiaer regarded the unfavourable season as the primary determinant of plant survival strategies, in which the defence and protection of shoots and buds are important during extreme cold or aridity. This system places emphasis on the position of the surviving buds in relation to the soil surface (Table 1.1).

Table 1.1 Raunkiaer (1934) life form classification (cited in Rutherford & Westfall 1994). Growth forms serve as examples only

Life form	Code	Bud position	Plant height	Growth form
Phanerophyte	P	>0.7 m above soil	>1 m	woody plants
nanophanerophyte	Pn	>0.7 m above soil	<2 m	shrubs
microphanerophyte	?	>0.7 m above soil	2-8 m	shrubs
mesophanerophyte	?	>0.7 m above soil	8-30 m	trees
megaphanerophyte	?	>0.7 m above soil	>30 m	large trees
Chamaephyte	Ch	≤0.7 m above soil	≤1 m	shrubs
Hemicryptophyte	H	at soil surface	-	graminoids
Phanerophytic herb	Ph	?	≤2 m	perennial forbs
Geophyte	G	on underground organs	-	bulbous plants
Therophyte	T	seed	n/a	ephemerals

The Raunkiaer classification has been modified to include fire life forms in South Africa (van der Merwe 1966 cited in Rutherford & Westfall 1994). Fire life forms are determined by the height of the renewable buds following the fire. Plants can be classified very differently by life form and fire life form, e.g. a fire intolerant woody species may be killed by fire (F) or sprout vegetatively from the root collar (e.g. P-FT or P-FCh).

1.8.2 Growth forms

No universal, all-embracing classification system exists for grouping plants and vegetation according to the structural attributes. Previous attempts indicate the impossibility of defining a single system appropriate under all conditions (e.g. Fosberg 1967; Campbell *et al.* 1981; Edwards 1983). The use of growth forms in this thesis prescribes to the classification system of Geldenhuys *et al.* (1988).

Growth forms are classified according to the shoot architecture, whereas life forms are more ecologically acceptable having been determined by general physiognomy (Rutherford & Westfall 1994). Geldenhuys *et al.* (1988) divided growth forms into three main categories,

viz. woody plants, herbaceous plants and epiphytes. This study relied only on woody and herbaceous categories. Each category was subdivided into growth forms according to the structural attributes (Table 1.2).

Table 1.2 Growth form classification system (Geldenhuys *et al.* 1988). DBH stands for ‘diameter at breast height’ (1.3 m)

Structure	Growth form	Size	Description
Woody plants	tree	>3 m	self-supporting
	shrub	<3 m, <100 mm DBH	self-supporting
	half-woody shrub	<3 m, <10 mm DBH	scandent, suffrutex
	liana	>10 mm DBH	not self-supporting
Herbaceous plants	vine	<10 mm DBH	not self-supporting
	graminoid	n/a	grasslike, sedges
	geophyte	n/a	bulbous plants
	fern	n/a	vascular non-flowering
	herb or forb	<2 m	angiosperms other than vines, graminoids and geophytes

1.8.3 Species

1.8.3.1 Evolutionary development on succession-related selection strategies

Possibly the most well regarded selection strategy is the theory of r- and K-selection (MacArthur 1962, Pianka 1970). This suggests that organisms lie on a continuum between two extremes of resource allocation representing two strategies for survival. Species with r-selected traits are considered to have evolved in unstable or newly formed habitats, e.g. disturbed conditions. The K-selected species, conversely, evolved at or near the carrying capacity of the environment. As a result, K-selected species use resources more efficiently, and their competitive ability is high.

Sequential succession occurs when life history traits of early and late (successional) species are inversely correlated (Huston & Smith 1987) and strategic allocation of resources results in a tradeoff between below and above ground tissue. Species that establish and reproduce the fastest at a specific level of a limiting resource will be competitively dominant. Thus in early succession when resources are ‘abundant’, r-selected species can establish as large populations of low diversity. In late succession resources are limited, realised niches are narrow, species diversity is at a premium, and empty niche space will competitively exclude species with r-selected traits.

Summarised, extreme K-selected species are characterised by being long-lived, reaching greater sizes, having prolonged vegetative stages, require low resource allocations for reproduction and are usually found occupying the later stages of succession. Extreme r-selected species, in contrast have shorter life-spans (e.g. annuals), smaller and largely herbaceous growth forms, place large resource allocations into reproduction and are early occupants in disturbed sites. Physical factors (e.g. perturbations) regulate populations of r-selected species, whereas K-strategists are maintained by biotic factors (e.g. pathogens, diseases, predators). These extreme scenarios are unlikely in practice, but the gradient between the two suffices for most species with inversely correlated traits (Radosevich & Holt 1984, Huston & Smith 1987).

Central to McCook's (1994) review on succession is the idea that correlations between traits, especially growth form, growth rate and shade tolerance, can explain autogenic succession. In other words r-selected species characterising secondary succession cannot occupy the same space in a continuum ending in a stable state. This may be true for native species but may not hold for alien invasive species that appear to establish and persist at any stage in succession.

1.8.3.2 Indicator species

The successional sequence from the early to the late stage incorporates increasing levels of stress and decreasing levels of disturbance. These factors have an important bearing on what kind of plants colonise a site. A common method of classifying species is by the life cycle of individuals, i.e. lifespan, the season of growth, method of reproduction and successional timing. Radosevich and Holt (1984) list three lifespan groups, viz. annuals, biennials and perennials.

Species have also been lumped groups according to stress-tolerance and successional status. For example, Dyksterhuis's (1949) range condition assessment for plant populations responding to overgrazing by livestock. This model groups species into three classes, namely decreaser, increaser and invader species. Decreaser species dominate in climax communities and decrease in abundance with increasing herbivory. Increaser plants are subdominant species of climax communities that increase under selective herbivory and range deterioration. Invader species are not part of the initial community but invade when

decreaser and increaser species become fewer and reduced in vigour. The main problem with the Dyksterhuis range condition method is the Clementsian idea of a single equilibrium state. Under South African conditions Dyksterhuis's model of range condition is too simple for application without modification. Hence increaser species have been subdivided into species that dominate in poor veld and increase with understocking or selective grazing (Increaser I), and Increaser II species increase with overgrazing (Trollope *et al.* 1990).

This classification becomes problematic when comparisons are made between systems controlled by disturbance as opposed to the rehabilitation processes (stress). Decreaser species, in the sense of grazing potential, are desirable plants (e.g. *Diheteropogon amplexans*) which follow undesirable pathways under injudicious grazing management. In contrast, increaser species are undesirable plants (e.g. *Chromolaena odorata*) which follow desired 'decreasing' pathways under weed control. Depending on the objectives of management, e.g. agricultural range vs restoration ecology, 'decreaser' and 'increaser' may be used inversely. The traditional nomenclature (*sensu* Dyksterhuis 1949) for indicator species is used in this thesis. Additional terms include ruderal species (pioneers, annuals, biennials) and seral species occurring during the intermediate stages of succession, but not initially nor at the end.

1.8.3.3 Keystone species

The activities and populations of keystone species determine integrity, resilience and persistence in biological communities (Paine 1966, 1969). The original application of the keystone concept was in marine ecology where the removal of a keystone predator altered the abundance of its prey, initiating many indirect effects, especially competition between species previously coexisting at lower densities. Keystone species have limited function under Paine's paradigm. They belong to the functional groups without redundant representation (Schulze & Mooney 1994), abolishing the idea of a relation between ecological complexity and stability.

Paine's (1966) concept has been broadened by ecologists to infer keystone species being important in ecosystem diagnosis by their sheer size or abundance (Power & Mills 1995 cited in Piraino & Fanelli 1999); also known as dominance (*sensu* Clements 1916). Khanina (1998),

for example, proposed only those species whose populations or biomass supported or altered the vegetation pattern of an ecosystem be considered as keystones, thus trees could be considered keystones in forest systems. In retort Vanclay (1999) suspected inconspicuous organisms such as mycorrhiza and other fungi may be more realistic candidates for the role of keystone species in forest communities.

Bond (1994) lists three types of keystone plants, viz. competitors, mutualists and system processors. Competitors were divided into either “climax” forest trees being keystones in suppressing understorey communities, or alien invasive plants which can invade heterogenous communities and reduce structure to monospecific stands. Keystone plant mutualists are species “providing critical support to large complexes of mobile links” (Gilbert 1980 cited in Bond 1994). “Mobile links” refer to animal pollinators and seed dispersal agents, where agents are totally reliant on the host plant, e.g. the fruits, over the season of critical shortage. The plant, however, is reliant on the agents for pollination and dispersal; a ‘chicken or egg’ scenario. Nitrogen-fixers have been suggested as keystone processor species facilitating nutrient cycling and litter decomposition. Frost and fire were also mentioned as abiotic determinants of vegetation change, implying environmental variables are equally important in the determination of ecosystem integrity. In summation Bond (1994) states “diverse and idiosyncratic nature of keystone species seem to defy generalisation,” and suggests that their identification and the role in ecosystem integrity difficult to appraise and apply.

It is suspected plants do conform to the general characteristics of keystone organisms (Paine 1966). Keystone species might be solitary or small guilds of predators, parasites, or pathogens near the top of the food pyramid, and not species at the bottom, i.e. producers. The biological control of weeds provides abundant evidence for why plants should not be considered keystone species. For example, *Sesbania punicea* (red sesbania) was introduced into South Africa about 150 years ago, and was until recently a major weed of wetlands and rivers. Twenty years of biocontrol has brought it under near-complete control due to the actions of three weevil species that feed off different parts of the plant (Hoffmann & Moran 1998). *Opuntia ficus-indica* (prickly pear), imported from Mexico about 250 years ago, infested some 900 000 ha of bushveld and Karoo vegetation in the Eastern Cape

(Zimmermann & Moran 1991). Nearly 90% of the originally infested area has been reclaimed for pastoral use by the actions of a cochineal insect and a phycitid moth. *Azolla filiculoides* (red water fern) was introduced into South Africa from South America in 1948 (Oosthuizen & Walters 1961 cited in Hill 1999) as an aquarium plant, but the weed soon invaded aquatic habitats throughout the country. The action of a single weevil species released in 1997 has brought red water fern under complete control. The *Azolla* example is an unusual case of where a single species assumes a keystone role in the dynamic states of ecosystems.

The consequence of keystone absenteeism is bottom up, not top down, e.g. monospecific unstratified alien vegetation. A more general term such as “ecologically dominant species” or “key species” (Odum 1971) should be used when drawing attention to plant impacts on vegetation structure and function. In weed-biocontrol, released agents (keystone species) and the target weed (key species) assume low level fluctuations in populations of both predator and prey. Eradication is seldom achieved. The temporal nature of individual species in the environment is brought sharply in focus when important alien invader species occur as infrequent determinants on a landscape scale because of predation. Ecologists should therefore consider the role of invertebrates and lesser organisms as determinants of vegetation structure, before targeting dominant plants as pivotal species.

1.8.3.4 Species diversity

Diversity takes into account the individual and its position in a community (alpha), the community in the landscape (beta), landscape level diversity (gamma) and overall gamma diversity of a region or biome (epsilon) (Whittaker 1972; Peet 1974; Whittaker 1977; Burton *et al.* 1992). All these approaches, however, use the number of species as a basic unit of measure, bringing the validity of biodiversity as a purposeful concept into question. Simply put, many functional groups (e.g. annual or perennial, evergreen or deciduous, position of renewable buds, nitrogen-fixers) coexist in plant communities, complicated further by the possibility that the community in question is at an unknown position of a theoretical continuum. The partitioning of species as functionally dependent units imply that they are not all created equally. The placing of equal emphasis on species, as is practised by the advocates of diversity indices is therefore ecologically unsound.

Walker (1992, 1994) conceptualised a way of reducing the decline in biodiversity by focussing on the aspects of biodiversity that are critical for maintaining the resilience of the ecosystem in question (see Section 1.6 Ecological Redundancy). The concept is not perfect. The loss of a key species can have a negative or positive consequence, depending on whether the species is invasive, a component of a stable or resilient community or simply a dominant species in a ruderal community. Arbitrary species at one *locus* may become keystone species in later succession, making it a very difficult concept to apply. This thesis deals with species richness, i.e. the number of species per unit area, and their relative abundance in an attempt to equate floristic diversity with ecosystem integrity.

1.9 Ecosystem Fragmentation

Large scale agricultural and forestry practices result in transformed landscapes consisting of remnant vegetation surrounded by developed land. Patchy habitats situated at different positions across the landscape with differences in soil type, topography, climate, habitat extent, ownership and management means vegetation is highly variable in composition, structure, condition and function. Such landscapes typify coastal vegetation on farms on the KZN coastal belt. The importance of fragmented ecosystems cannot be overstated. The conservation status of many endangered species depends specifically on the very small, isolated remnant vegetation.

The greatest threats to savanna, valley thicket, forest and grassland ecosystems in KZN are abusive grazing practices, cropping (especially sugar cane), afforestation and alien invasive plants (Scott-Shaw 1999). Fifty eight percent of the threatened plants in KZN are found in the grassland ecosystems. The grasslands of the KZN mistbelt, hinterland and coastal plain are very high conservation priorities because of their greater agricultural and urbanisation potential. The Karkloof Blue for example is a butterfly endemic to a one hectare patch of mistbelt grassland. Afforestation was presumably the cause of the initial decimation of the butterfly's home range.

Fragmentation of ecosystems results in changes to the biota of the remnant community. The most obvious effect is the increase in the proportion of the habitat falling in the edge zone. Isolation through agricultural land conversion can create ruderal ecotones and areas between

croplands and natural vegetation are highly disturbed. This condition can reduce the resilience of vegetation in small habitats, for example, by providing a niche for alien species through desisting with routine land-care practices (e.g. burning). Isolation and distance between similar patches may reduce the ability to maintain genetic heterogeneity through cross pollination or the ability for new species or ecotypes to colonise and establish.

Upon isolation, a remnant is likely to have more species than it can maintain and species will be lost as the changes caused by the fragmentation take effect (Saunders *et al.* 1991). The dynamics of remnants are driven largely by the factors arising in the surrounding landscape. These factors may range from farm-level conservation management to the ecological processes affected by a large-scale surrounding monoculture.

1.10 Conclusion

Alien invasive species are a serious threat to biodiversity on a global scale. Pre-adaption under similar growing conditions in the countries of origin plus the absence of natural enemies in the host country places unbalanced competitive attributes in favour of exotics over indigenous species. Besides direct invasion, hybridization and the evolution of new taxa following introductions is of concern to conserving genotypic biodiversity. Hybrid swarms of *Lantana camara* have not only made effective biocontrol almost impossible, but also pose a threat to the only South African lantana species, *L. rugosa*.

Functional and structural approaches grouping species into guilds for better understanding of the relations between biodiversity and resilience are an improvement to the traditional species-centred methods. This approach is not perfect. It does not take into account absolute species composition (i.e. redundancy, commonness and rarity). Biodiversity has become an emotive issue and an inadequate understanding of the mechanics determining diversity, and sensational reporting, have made the serious ecologists reluctant to tackle the “flavour of the month” with great enthusiasm (Walker 1992). Meanwhile, biodiversity rests on current understanding of ecosystem integrity for managing habitats as functional systems. Principles of adaptive management (e.g. Haney & Power 1996; McLain & Lee 1996) are needed to maintain monitored objectives and to prevent ecological states from shifting into transitions that lead to ecosystem degradation.

2. STATUS AND CONTROL OF CHROMOLAENA IN KWAZULU-NATAL

2.1 *Chromolaena odorata*

2.1.1 Current distribution in South Africa

2.1.1.1 Rate of spread

Chromolaena odorata (L.) R.M. King and Robinson is an asteraceous shrub of South American origin (King & Robinson 1970) that was accidentally introduced into South Africa via Durban sometime in the 1940's. The weed is known locally as *paraffienbos* (Afrikaans), Triffid weed or chromolaena (English) and *usandanezwe* (Zulu). In this manuscript I call it chromolaena. Chromolaena has become a major weed problem in South Africa and in many other areas of the Old World tropics and subtropics, from West and Central Africa through India to the Philippines and Indonesia (Gautier 1994).

Over a 50-year period from 1945 chromolaena had invaded extensive tracts of land south of Port St. Johns to north of Louis Trichardt (about 1 125 km = 22 km y⁻¹). In KZN chromolaena has been unable to establish west of Pietermaritzburg (where it established in 1982) and Melmoth and is restricted to areas below an altitude of 800 m (Egberink & Pickworth 1969; Liggitt 1983; Henderson 1989). Chromolaena is also extensive in the low altitude parts of Swaziland, Mpumalanga and Northern Province (Goodall & Erasmus 1996). In these subtropical semiarid to humid regions chromolaena has recorded its highest rate of spread, spreading from Ndumu Game Reserve (1985) to Venda in 10 years (45 km y⁻¹). The highest altitude infestation was recorded at Tzaneen in 1994 at 1 250 m.

2.1.1.2 Vegetation-veld types invaded by chromolaena

Vegetation was graded according to the combined impacts of current chromolaena density and distribution (severity). Vegetation types follow the classification of Low and Rebelo (1996), 'LR', and Acocks (1953) veld types with the prefix 'A'. Low and Rebelo's veld types were classified according to structure and floristics whereas Acocks based his veld types on agricultural potential. Low and Rebelo's system is thus more ecologically relevant. The coarse resolution of Acocks's vegetation classification is further emphasised by incidences of veld types covering more than one vegetation type.

(a) Severe (mesic to semiarid), infestations not restricted to watercourses:

- Coastal Forest-LR1 (Coast-belt Forest of Natal & Transkei-A1a, Dune Forest-A1d). Invasions into disturbed forest gaps prevents forest regeneration. As more gaps appear and are colonised by chromolaena, the forest canopy becomes gradually fragmented and vegetation is transformed into weedy scrub (Goodall & Erasmus 1996). A model predicting rates of canopy breakdowns in Coastal Forests using remote sensing showed full canopy forest could be fragmented by 90% in 45 years (Goodall *et al.* 1996b).
- Afromontane Forest-LR2 (Pondoland Coastal Plateau Sourveld-A3, North-eastern mountain Sourveld-A8). Coast Scarp forests (Cooper 1985) growing on the coastal ridges often comprise endemic species and are threatened by chromolaena and the increased risks of fire damage.
- Valley Thicket-LR5 (Northern Valley Bushveld-A23a). Major river valleys, e.g. Mkomazi, Mgeni and Tugela valleys from the coast up to 80 km inland. Infestations cover whole hillsides near the coast.
- Lebombo Arid Mountain Bushveld-LR13 (Zululand Thornveld-A6, Lowveld-A10). Infestations of chromolaena occur in Ubombo (KZN) and all along the eastern boundary of Swaziland with Mozambique. Extensive thickets occur in deciduous woodland.
- Sour Lowveld Bushveld-LR21 (Lowveld Sour Bushveld-A9). A region incorporating the middleveld of Swaziland, Mpumalanga (Sabie, Tzaneen) and Northern Province (Louis Trichardt to Punda Maria). Extensive infestations exist in evergreen and deciduous woodlands. This vegetation type is still in the early stages of invasions. Strategies to contain the spread of the chromolaena in this region (Goodall *et al.* 1996a) were never set up. Further spread is therefore expected.
- Coastal Bushveld-Grassland-LR23 (Coast-belt Forest of Natal & Transkei-A1a, Zululand Palm Veld-A1b). Mosaic vegetation of coastal forest, open grassland and palm veld has been severely affected by chromolaena, being one of the first vegetation types exposed to the weed in the 1950s.
- Coast-hinterland Bushveld-LR24 ('Ngongoni Veld-A5). Restricted to the coastal plateau around Melmoth and Eshowe areas comprising of grassland, evergreen savanna and forest mosaics.
- Natal Lowveld Bushveld-LR26 (Zululand Thornveld-A6). Thornveld areas of Hluhluwe, Umfolozi, Ndumu and Mkuzi game reserves. Chromolaena poses a threat to nature conservation and ecotourism.

(b) Moderate (arid to semi-arid), infestations severe but restricted to watercourses:

- Mopane Bushveld-LR10 (parts of Lowveld-A10, Mopani Veld-A15). Chromolaena is invading riverine vegetation and transforming *Ficus sycomorus* forest.
- Mixed Lowveld Bushveld-LR19 (Lowveld-A10). Nucleus infestations occur in Northern Swaziland and in the former Venda homeland north east of Louis Trichardt. Potential exists to degrade many kilometres of *Ficus sycomorus* riverine forest.
- Sweet Lowveld Bushveld-LR20 (Lowveld-A10). The same as LR19.

(c) Unknown, sandy soils or frost may resist establishment, rainfall not limiting:

Sand Forest-LR3 (Coast-belt Forest of Natal & Transkei-A1a, Zululand Palm Veld-A1b).

Soutpansberg Arid Mountain Bushveld-LR11 (North-eastern Mount Sourveld-A8, Sourish Mixed Bushveld-A19, Sour Bushveld-A20).

Chromolaena is a threatening North-eastern Mountain Sourveld (see LR2) and occurs in adjacent Lowveld Sour Bushveld (see LR21). Invasion is expected at some stage.

Subhumid Lowveld Bushveld-LR22 (Lowveld-10). Restricted to Ndumu and Tembe reserves. *Chromolaena* is already a problem in parts of Ndumu.

2.1.1.3 Potential for further spread

The neotropical origin of *chromolaena* (King & Robinson 1970) suggests that the plant is sensitive to frost, confirmed by its establishment only in the frost-free areas (Figure 2.1).

Chromolaena continues to expand its range into more marginal environments. In the lowveld and arid lowveld of Mpumalanga and Northern Province, in areas where rainfall is below 500 mm per annum (Figure 2.2), aridity restricts infestations to riparian zones. The ability to invade, establish and propagate in arid ecosystems suggests an enormous potential for spread in the savanna biome of South Africa and Swaziland (Goodall & Erasmus 1996).

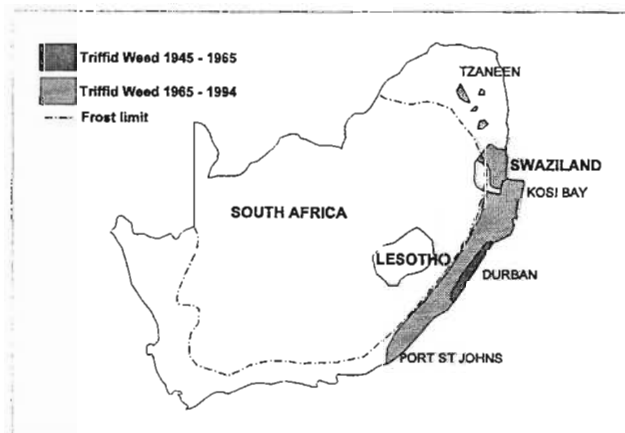


Figure 2.1: Spread of *Chromolaena odorata* from 1945 to 1994 (after Goodall & Erasmus 1996).

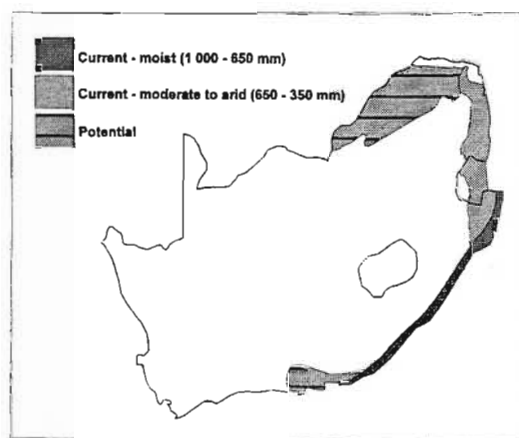


Figure 2.2: Current and potential distribution of *Chromolaena odorata* in South Africa based on vegetation and rainfall (after Goodall & Erasmus 1996).

2.1.2 Ecological impacts

Chromolaena is a serious weed problem in indigenous forest, grassland and savanna. The plant is allelopathic and the leaves contain essential oils (Hamilton *et al.* 1993; Biller *et al.* 1994), rendering it flammable. Once habitats become invaded, they are rapidly degraded by smothering, competition and allelopathy. In forests, *chromolaena* assumes a suffrutescent habit where it scrambles into the canopy and smothers trees. In grassland and savanna it forms compact half-woody shrubs up to two metres tall, becoming thicket forming, reducing species richness and carrying capacity.

The presence of dense infestations of any alien invader suggests excessive disturbance and mismanagement. *Chromolaena* in savanna or low altitude grassland is an indicator of grazing mismanagement, either by selective- or over-grazing. Severe soil erosion also accompanies overgrazed rangelands on the coastal lowlands (Goodall & Morley 1995). *Chromolaena* is also an indicator of veld neglect, i.e. lack of veld-burning, leading to vegetation transformation. Its presence and abundance in open grassland have been associated with the absence of fire and on forest margins it carries fires from neighbouring grasslands into the forest interior, killing trees and shrubs (Macdonald 1983).

The expansion of sugarcane cultivation in KZN during the 20th century has been responsible for large scale fragmentation of a ubiquitous forest, savanna and grassland mosaic vegetation. Land transformation between 1937 and 1991 (Plate 1) on a farm near Scottburgh show expanding cultivation initially resulted in grassland and forest fragmentation. Between 1937 and 1966 grasslands became increasingly dominated by an assortment of woody indigenous plant species. The assumed lack of burning of these fragmented ecosystems resulted in savanna-forest successions. Wooded communities after 1966, however, did not exhibit normal development. Instead *chromolaena* rapidly replaced grass and suppressed further woody plant recruitment. *Chromolaena* appears to destroy resilience in grasslands more rapidly than in forest and woodland successions.

Some game farms in Zululand, once used for cattle ranching and growing of crops, have now inherited problems associated with overgrazing and 'old-lands', typically bush encroachment but also *chromolaena* infestations. Infestations not only affect grazing and browse

availability but also the ability of invaded landscapes to support diverse populations of life forms. This implies that infestations of chromolaena effect breakdowns in the food web, resulting in a decline in species diversity across the trophic spectrum. Chromolaena therefore has a direct bearing on the production potential of lucrative renewable natural resources, i.e. trophy animals and game viewing, which in turn, determines how much money is put back into land management. Dense thickets of chromolaena also obstruct game viewing and provide ideal habitats for the concealment of snares. The cost of clearing dense, extensive infestations is prohibitive, often exceeding the value of the land itself.

2.1.3 Chromolaena control research

2.1.3.1 Mechanical control

Slashing and uprooting of chromolaena is labour intensive (85 man days ha⁻¹) and control is short (Goodall & Erasmus 1996). The method causes high levels of disturbance, creating an ideal environment for further weed germination. Labour intensive techniques are best suited to fallow cropping systems where clearing efforts can be combined with soil preparation under shifting cultivation in resource-poor regions (Muniappan & Marutani 1991; Slaats 1995). Follow-up operations involving slashing and ring-weeding up to four times per annum are required to prevent chromolaena from interfering with crop production. In South Africa mechanical control is usually practised with the application of herbicides. Examples include slashing tall growth (a) to promote coppice that can be sprayed later, or (b) applying herbicide to the stumps (Erasmus 1988).

2.1.3.2 Cultural control

Chromolaena has become an important component in shifting agriculture in West Africa (de Foresta & Schwartz 1991; de Rouw 1991). Rainforests are cleared for crops, as were coastal forests in KZN during the Iron Age (Section 2.2.3). When crop production in rainforest clearings becomes uneconomical the farmers move into new areas and repeat the process. Abandoned fields are soon invaded by chromolaena, preventing forest succession. A method of nutrient recycling by mulching with chromolaena has been developed in fallow cropping in West Africa (Slaats 1995). Fallow-cropping with chromolaena is preferred to clearing forest, the latter yielding a lower return on the energy invested during labour intensive site preparation (Roder *et al.* 1995; Slaats 1995). Chromolaena also displaces *Imperata*

cylindrica which is a serious weed of crops and fallow land in the tropics (Ivens 1975).

Fallow-cropping with chromolaena has not been tested in South Africa. The agricultural benefits are overshadowed by the ecological impacts. New research intends to determine its potential in economically depressed regions where crops could be cultivated in place of dense chromolaena infestations. Great care is needed to ensure the chromolaena is not promoted as a new 'agroforestry wonder-plant'. Mulches, leguminous ground covers and signal grass (*Brachiaria decumbens*) were also found successfully to compete with and reduce the incidence of chromolaena (Wu & Xu 1991) and are indirect methods of control. In rural areas it is hoped that clearing of dense infestations will be integrated with crop production on otherwise useless ground.

2.1.3.3 Biological control

In its country of origin chromolaena is not invasive, although it is sometimes a minor problem during plantation establishment. No control methods other than slashing are required in the Neotropics, the reverse of the situation in Africa and Asia. The only logical explanation is the cumulative effect of biotic factors, principally host-specific insects, other arthropods and diseases, which attack the plant throughout its range in the New World, but are largely absent from Asia and Africa (Cruttwell McFadyen 1991).

Biocontrol involves the use of natural enemies, especially insects and fungi, from the weeds' countries of origin, to decrease reproduction and growth to a level where other control methods can be more effectively employed. Chromolaena biocontrol research began in 1988 with the aim of introducing a suite of insects to attack different parts of the plant (leaves, stems, roots, flowers). In 1989 a defoliating moth *Pareuchaetes pseudoinsulata* was released with unsuccessful establishment in the wild (Zachariades *et al.* 1999). Another defoliating moth *P. aurata aurata* was released more numerously between 1990 and 1993 but it was also unable to establish in the field. Several other insect species have been imported, cultured and tested but only *P. insulata* has been authorised for immediate release, but no field data are available yet. Several species still under quarantine appear promising, namely *Melanagromyza eupatoriella* (stem-tip borer), *Lixus aemulus* (stem borer), *Calycomyza* sp. (leaf miner) and *Longitarsus* sp. (root borer). Research on these insects is at differing stages

but one species is due for release at the end of 2000, followed by another species in 2001. If the remaining insects prove host-specific, they should be introduced into the wild by 2004 (Zachariades pers. comm., Plant Protection Research Institute, Private Bag X6006, Hilton 3235). Once an agent is released, it takes several years for it to have an impact on the weed populations, if it does establish a population.

2.1.3.4 Chemical control

Chromolaena has conclusively proved easy to kill by herbicides. A number of herbicides were screened between 1983 and 1993 (Erasmus 1985; Erasmus & van Staden 1986a; Erasmus & van Staden 1987; Erasmus 1988; Goodall 1997) and by 1995, seven formulations comprising 16 products were registered for *chromolaena* control (Table 2.1). These include 11 foliar, two cut-stump and three soil applications (Vermeulen *et al.* 1995). Commercial enterprises employ chemical control effectively, e.g. forestry companies, but this method is inappropriate for unskilled subsistence farmers in South Africa.

Table 2.1 Herbicides registered for the control of *Chromolaena odorata* in South Africa (Vermeulen *et al.* 1995)

Active ingredient	Site of application	Herbicide mixture (% concentration)	No. products
glyphosate 359 g ℓ^{-1}	foliage	1 ℓ /100 ℓ water	7
triclopyr 480 g ℓ^{-1}	foliage	375 ml/100 ℓ water	1
triclopyr 480 g ℓ^{-1}	stumps	1 ℓ /100 ℓ diesel	1
metsulfuron methyl 600 g kg^{-1}	foliage	25 g/100 ℓ water	2
sulfosate 720 g ℓ^{-1}	foliage	0,67 ℓ /100 ℓ water	1
imazapyr 100 g ℓ^{-1}	stumps	2 ℓ /100 ℓ water	1
tebuthiuron 200 g kg^{-1}	soil	1 g/m ²	2
tebuthiuron 752 g kg^{-1}	soil	1 kg/10 ℓ water	1

2.1.3.5 Integrated Control

At present effective integrated control of *chromolaena* is only feasible by combining mechanical, cultural and chemical control, depending on the type of ecosystem invaded and the density of infestations (Table 2.2).

Table 2.2 Integrated strategies for the control of *Chromolaena odorata* in different situations (Goodall *et al.* 1996a)

Habitat	Density	Strategy
Savanna	sparse	Spot-spray leaves with triclopyr, or slash and apply imazapyr to stumps, or uproot plants by mattock. Remove seedlings by hand in future follow-up operations, or spray with triclopyr.
	dense	Spray leaves with triclopyr if plants are < 1.2 m. Sash taller plants and apply imazapyr to stumps, or spray the regrowth with triclopyr. Follow up with regular spraying until it becomes feasible to remove seedlings by hand.
Indigenous forest	sparse	Spray leaves with triclopyr if plants are < 2m. Slash taller plants and apply imazapyr to stumps, or spray the regrowth with triclopyr. Plants may also be uprooted if populations are low enough to warrant the expense. Remove seedlings by hand in future follow-up operations, or spray with triclopyr.
	dense	Spray leaves with triclopyr if infestations are < 1.2 m. Sash taller plants and apply imazapyr to stumps, or spray the regrowth with triclopyr. Follow up with regular spraying until it becomes feasible to remove seedlings by hand.
Timber plantations	sparse	Spray leaves with triclopyr if plants are < 2m. Slash taller plants and apply triclopyr to stumps, or spray the regrowth with triclopyr. Plants may also be uprooted if populations are low enough to warrant the expense. Follow up control depends on the silvicultural policy.
	dense	Spray leaves with triclopyr if infestations are < 1.2 m. Sash taller infestations and apply triclopyr to stumps, or spray the regrowth with triclopyr. Follow up control depends on the silvicultural policy.
Fallow land	all densities	Slash, uproot and burn infestations or incorporate debris as a form of green manure. Follow-up with manual weeding (hoeing) or using registered herbicides appropriate for the specific crops.
Border infestations	dense	If accessible by vehicle chromolaena thickets growing along forest margins, watercourses and roadsides can be sprayed with triclopyr from LDV and tractor-mounted sprayers (Goodall 1997).
Gardens	all densities	Remove seedlings by hand. Slash and uproot taller plants.
Municipal	sparse	Spot-spray leaves with triclopyr, or slash and apply imazapyr to stumps, or uproot plants by mattock. Remove seedlings by hand in future follow-up operations, or spray with triclopyr.
	dense	Spray leaves with triclopyr if plants are < 1.2 m. Sash taller plants and apply imazapyr to stumps, or spray the regrowth with triclopyr. Follow up with regular spraying until it becomes feasible to remove seedlings by hand.

2.1.3.6 Rehabilitation in coastal forest

Trials in infested coastal forest at St. Lucia compared control efficacy of mechanical control (uprooting and uprooting combined with burning) and chemical control integrated with grass planting and fertilization (Erasmus 1991). Fire reduced the intensity of reinfestation and

improved establishment of sown grasses. Grass establishment two years later was poor in unburnt plots due to the thick mulch layer left after clearing. *Setaria megaphylla* grew the best where chemical control was applied (2.5 t ha^{-1}) compared with the next best *Panicum maximum* (1.4 t ha^{-1}). *P. maximum* grew best in both manual control treatments but *Chloris gayana* yields were also significant. Natural grasses establishing in plots that were not planted was highest in the plots treated with herbicides (0.9 t ha^{-1}) and lowest in the plots which were burnt (0.4 t ha^{-1}). Nitrate and phosphate application increased grass yields but over-sowing, or planting of grass, was expensive and was considered only feasible in situations where large areas of exposed soil were left after clearing chromolaena.

2.1.3.7 Developing landscape level control strategies

In an attempt to find tactical solutions to deal with the chromolaena problem on a large scale a control strategy was developed embracing both 'big picture' (Goodall *et al.* 1996a) and sustainable chromolaena control on a local scale (Goodall & Naudé 1998). The strategy comprises two functioning levels that are interdependent. The "macro strategy" analyses the problem on a national or regional scale without being prescriptive while "micro strategies" focus on the planning and management of chromolaena in prioritised areas on farms, nature reserves and plantations. Macro strategies incorporate (a) inventories integrating weed surveys, mapping and modelling of chromolaena spread; (b) setting up planning, management and regulatory structures; (c) identifying regional priorities; and (d) allocating strategic resources. Micro strategies consist of management plans containing control strategies for treating key areas. The success of managing chromolaena on a regional scale depends on the collective commitment of all the affected parties and an organised management structure at the macro level that can promote job empowerment opportunities and deliver on coordinated objectives.

2.2 Ecology of coastal grasslands

The debate concerning the development of the "false grassland biome" (Mentis & Huntley 1982; le Roux 1995) or savanna biome (Rutherford & Westfall 1994) is ongoing. Arguments revolve around the role evolutionary development (Werger 1978; Cowling *et al.* 1997) and the more recent modifying effects humans have had on the vegetation for the last 2000 years (e.g. Feely 1980; Hall 1981; Prins 1993). Acocks (1953) used Clementsian ecology (e.g.

Clements 1916) to classify vegetation. Under this system savanna and grassland along the KZN and Eastern Cape coast became known as Coastal Forest and Thornveld (Veld type 1). Acocks dismissed fire as a controlling factor in maintaining grassland over millennia. He also based his assumptions on outdated archeological theories where the 'climatic climax' vegetation could be traced back to 600 BP, the point where he believed Iron Age man began influencing the vegetation dynamics in southern Africa.

2.2.1 Geology and development of vegetation in KwaZulu-Natal

The Natal monocline was believed to have been formed during the late Pliocene epoch from the same tectonic upheavals that substantially elevated the interior plateau (King 1978). At the end of the Tertiary period King hypothesised a marine environment once inundated the coastal plain, situated about 100 m below its present position. King's (1978) theory of the Natal monocline developing out of a flat Gondwanaland land surface has been superseded by the theory that the Drakensberg was already present at the time of intercontinental drift (Partridge & Maud 1987). This hypothesis, however, did not change the fact that the parts of coastal lowlands of KZN were once a marine environment that impacted on the soil and vegetation patterns of present. On the east coast the Paleozoic-Mesozoic base material of the Karoo system falls away to below sea level and deposits of glacial, marine and aeolian origin form the basis of present-day coastal lowlands of KZN (Tinley 1985). Soil types are largely regic sands merging with tillite deposits (Glenrosa form) with increasing altitude and rolling topography (MacVicar *et al.* 1991; Camp 1997).

The Cainozoic era preceded a change in Africa's mesic tropical climate to one of increasing aridity. Rainforests covering most of the land surfaces before upheaval were largely replaced by savannas, subtropical forests and deserts. Wooded savannas and open grasslands covered the interior plateau and Drakensberg region as recently as 10 000 BP. Subtropical forests on the KZN coast and hinterland were believed to have remained unchanged for millions of years owing to the atmospheric and oceanic circulations controlling the climate of southern Africa (Axelrod & Raven 1978; King 1978; van Zinderen Bakker 1978; Hall 1981; Tinley 1985). The interface between savanna and the subtropical forest belt in the early part of the Holocene remains uncertain. How far into the hinterland and lowland bioclimatic zones had savannas and grassland spread before the arrival of Iron Age man, is debatable. The presence

of *Themeda triandra* in the sward has been used to defend the antiquity of 'false grasslands' (Mentis & Huntley 1982). This 'preferred state', however, is not enough to explain why higher order communities such as forest, remains the domain of attraction in *Themeda/Aristida* coastal grasslands (Henkel *et al.* 1936; Bayer 1938; von Maltitz *et al.* 1996).

2.2.2 Prehistoric vegetation (BP 10 000) on the coastal lowlands

Archaeological research supports the notion that the coastal plain was predominantly under forest before the arrival of Iron Age man (Werger 1978; Feely 1980; Hall 1981). Hall (1981) believed Stone Age Man, who were hunter-gathers, had little influence on Holocene landscapes (10 000 BP). Hall described dune forest covering the entire dune cordon of KZN, merging into an array of other lowland subtropical forest types to the west. Endemic hygrophilous grasslands occurred in the lake district of north eastern Zululand which resisted forest succession due to high water salinity and anaerobic conditions resulting from inundation (Hilliard 1978; Moll & White 1978). Coinciding with extreme growing conditions, a process of specialisation occurred in the hygrophilous grasslands and forest communities, resulting in many endemic floras (Hilliard 1978; Moll & White 1978). Hall (1981) did not suggest the existence of open terrestrial grassland on the coastal lowlands during this period.

2.2.3 First farmers of the Iron Age

Man as a settler, it was suggested, first arrived on the Zululand coastal plain as a communal influx of peoples in 1 700 BP (Hall 1981, 1987; Prins 1993). This theory differs from Acocks's (1953) notion that the Iron Age began in 600 BP by more than 1 100 years. Hall (1987) described an eastern stream of Black races from Moçambique, called the 'Matola Tradition', colonising the coast to slightly north of Durban between 1 800 BP and 1 600 BP. Between 1 600 BP and 1 100 BP a second stream from Zimbabwe colonised the eastern interior and south coast of Natal and Transkei, known as the 'Lydenberg Tradition'. Towards the end of the first millennium a great northern migration lasting for several centuries took place along the entire length of the KZN coastal belt.

Hall (1981) describes coastal grasslands as secondary communities resulting from 'slash and burn' agricultural practices. Early Iron Age farmers occupied areas for two to three seasons

until soil fertility failed to sustain crop production levels. Shifting agriculture was the only farming system that could sustain crop production demands under increasing human influx. Small plots for growing subsistence crops were cut into the forest at frequent intervals, causing rapid deforestation. Infertile fields were abandoned and these reverted to secondary grasslands. Early iron age practices, in Hall's (1981) opinion, affected the very structure of the biota rather than merely extracting a living from it.

2.2.4 Late Iron Age (1000-early 19th century) agriculture

According to Hall (1981) human settlements became well established during the Late Iron Age and dune forest clearing had progressed to such an extent that secondary grasslands were extensive. Besides shifting agronomic practises, domestic cattle grazed on these 'man-made' rangelands. At the time of Hall's (1981) study the 'no-burning policy' of many commercial farmers and the Natal Parks Board (now KZN Wildlife), documented open grassland reverting to wooded savanna in a succession that would culminate in closed savanna and forest. Farmers and conservation officials perceived this tree-dominance as bush encroachment. Hall hypothesised, Late Iron Age farmers were likely to have opened the savannas and forests and kept them open.

2.2.5 The Late Iron Age system in stress

The coastal plain, hinterland and upland regions supported self-contained communities during most of the Iron Age (Hall 1981). The demand for basic resources increased as the Iron Age progressed. Depletion of soil nutrients was believed a major problem on the coast while drought in the hinterland was more prevalent. Grazing large herds on upland sourveld was only possible during summer and these were moved onto the sweetveld of the river valleys during the dry months. The harsher conditions forced communities to integrate and share their basic resources, according to Hall (1981). For example, Hall mentions iron smelting was practised on the coast and hinterland because of the timber abundance for smelting purposes. Towards the end of the Iron Age farmers had greatly modified the vegetation of the KZN lowlands and hinterland and the forest-savanna-grassland mosaic was well established by the time Europeans began settling in the province (Henkel *et al.* 1936; Bayer 1938; Reitz 1938; McCracken 1995, 1996).

It seems ironical that sugar cane farmers have received the full brunt of the blame for deforestation on the coast. It is believed sugar planting converted more virgin grassland and savanna (Hoffman 1996) than the deliberate targeting of forests, which were expensive to clear for arable land (Watson 1932; Dodds 1933). These chivalrous accounts of an expanding colonial sugar empire cannot disguise the impression of complete disregard for natural vegetation. Iron Age agriculture practices, presumed by Hall (1981) as the main culprit of deforestation, have not desisted in KZN (Weisser & Marques 1979; Weisser & Muller 1983). Ongoing deforestation at Dukuduku supports this notion.

2.3 Geographical region and subject of research

The region of interest is the coastal lowland of KZN, a long but narrow belt of land with an elevation ranging from sea level to 450 m, situated between Moçambique and the Eastern Cape province. The natural vegetation falls into the taxonomic region called the Tongaland-Pondoland Regional Mosaic (Moll & White 1978). Lowland Subtropical Forest of the Indian Ocean coastal belt, savanna and grassland occur in a ubiquitous ensemble in areas where agricultural land use is not agronomic. Forest is distinguished from savanna and grassland based on the absences of (a) C4 grasses in the herb layer and (b) fire as a determinant in the development of hemicryptophyte vegetation (O'Connor 1985; Rutherford & Westfall 1994). Coastal grassland is the subject of research in this investigation.

The coastal hinterland (450 to 900 m above sea level) is a region of transition between the tropical climate of the coast and the temperate mistbelt region. In many respects the subtropical vegetation of the hinterland is similar to that found on the coastal plain, but more importantly, it is also severely affected by chromolaena. Any implied effects of chromolaena in grassland ecosystems on the coast may also be inferred or interpreted as including the grasslands of the hinterland region.

2.4 Aims

Research on chromolaena control, other than biocontrol, is relatively saturated (see 2.1.3.4). Research on the biology (phenology, reproduction and seed germination) (Erasmus 1985; Mbalo & Witkowski 1997), rate of spread (Liggitt 1983; Henderson 1989; Goodall *et al.* 1994) and autecology (Wilson 1995) in South Africa is also voluminous. No work on

measuring the impacts of *chromolaena* on ecosystem structure and function has been carried out in South Africa in the past.

Coastal grassland ecosystems are threatened by agricultural, silvicultural, urban and recreational expansions. Coastal farmers perceive fragmented habitats as not being viable and consequently patchy grasslands are not managed properly. This study aims to describe the impacts of *Chromolaena odorata* density on species composition in coastal grasslands and serial changes in the vegetation following the implementation of a burning programme. Due to budget and time constraints the project attempts to quantify 'before and after' changes in sites over time using simple, cost-effective, repeated measures sampling techniques, in unreplicated plots. It is therefore a descriptive account of vegetation changes over time within sites.

2.4.1 Key questions

- (a) Is species composition, richness and therefore function of coastal grasslands affected by *chromolaena* density and the absence of fire?
- (b) Is fire an effective control method for reducing and suppressing *chromolaena* in grassland?
- (c) What implications do woody alien plant invasions and indigenous trees and shrub successions have on the resilience and (non) equilibrium properties of coastal grasslands?

2.4.2 Main patterns of interest

The study covers a period from July 1991 to June 1998. Extensive data was collected (see Chapter 3) for the purposes accounting how fire and alien vegetation influenced the dynamics of coastal grassland communities over time. These dynamics include:

- (a) Patterns of change in species richness and frequency constrained by (i) sample size, (ii) minimal area and (iii) scale;
- (b) fire tolerance of *Chromolaena odorata*;
- (c) successional changes of woody alien and native species;
- (d) successional changes of herbaceous species

The research findings will be consolidated into a management model for relic coastal grasslands.

3. METHODS

3.1 Monitoring technique

3.1.1 Choice of sampling method

Several authors propose the use of quadrats to record the species composition in grasslands because the technique is more consistent and repeatable than other techniques (Walker 1976, Everson & Clarke 1987, Panagos & Zacharias 1995). The quadrat method was more superior in accounting for species than the point-canopy intercept method because the operator is required to record all the species found inside the sample unit (Panagos & Zacharias 1995). Monitoring data derived from quadrats are preferable to point based data because they provide a measure of community composition, plant density and species diversity (le Roux 1995). In studies where data are required to quantify change over time, permanent transects comprising contiguous quadrats have an added advantage (Austin 1981). The smallest sampling unit can be compared directly or cumulatively, accounting for changes at multiple scales.

Small scale periodicities in vegetation are prone to spatial autocorrelation if systematic sampling using contiguous quadrats are used. Quadrats must be spatially independent to categorise and draw conclusions about species associations in plant communities (Jonsson & Moen 1998). Contiguous quadrats are, however, needed in repeated-measures experiments partly to categorise vegetation, but principally to quantify and explain changes between temporal observations. Serial comparisons in nested sampling units can qualify multi-species associations occurring at many scales of interest (Austin 1981, Critchley & Poulton 1998), despite degrees of relative similarity of nearby quadrats. In addition, the analysis of species-area curves and corresponding minimal area are independent of sampling design, as only the accumulation of new species in relation to the sequence in sampling is analysed.

One problem associated with transects is the inherent heterogeneity of the sample area, being narrow and long, in confounding the vegetation/environment relation, but criteria for optimising plot-size by minimising edge-effects have not yet been defined. The study of serial patterns in species composition using permanent transects is validated by the need for exact repetition of field procedures, ensuring comparability between successive sets of data (Greig-Smith 1983, Mentis 1984). The aim is not to measure alpha diversity but from

successive sets of data, extract exact differences that account for the changes.

3.1.2 Monitoring strategy

Based on the considerations described above, fixed-belt-transects comprising 1 m² and 25 m² contiguous quadrats were used to monitor herbaceous and woody plant compositions in coastal grasslands with variable densities of *Chromolaena odorata*. The size of quadrats used for sampling herbaceous and woody species follows the guidelines recommended by Gauch (1982). Large quadrat size helps reduce excessive variances between quadrats, patchiness of the vegetation gradient being sampled and the boundary-to-area-ratio of quadrats (Greig-Smith 1983).

Permanent transects were located in even stands at the start (t_0) and positioned perpendicular to the contour interval to include aspect. Transects varied according to the size of each site. Standard transect length was set at 25 m (Table 3.1), excepting Site 1 and Site 3. Site 1 was used as a benchmark site (Section 3.2.1) and only monitored intensively for one season. More importantly, no alien species were found. Site 3 was the locale of a separate study on sampling intensity (Section 3.1.1) in which transects of diminishing size were laid out parallel to one another at five metre intervals and monitored intensively for the duration of the study.

Sampling error in transects was a factor common to all sites, resulting from failure to detect certain species in quadrats. Monitoring was carried out during the growing season (October to May). To reduce sampling error, two observers and a recorder conducted monitoring of the herbaceous community in quadrats (1 m²), during routine biannual surveys (spring, late summer) from 1991 to 1998. An exception to this occurred in the 1996/97 season. Site 3 and Site 4 were monitored in late September 1996 and early February 1997, a census covering only four months. Herbarium specimens of live herbaceous species rooted inside quadrats were collected from outside the transects and identified at the Bews Herbarium (University of Natal, Private Bag X01, Scottsville 3209). Both herbaceous and woody species were recorded as either present or absent in quadrats, with $n_i = 0$ or 1. This was used to calculate frequency of occurrence of each species (F_i) by dividing the sum of quadrats containing the i th species into the sum of quadrats in the transect (Equation 3.1).

Equation 3.1:

$$F_i = \frac{\sum n_i}{\sum n} \times \frac{100}{1}$$

An exception to this rule were the enumerations of alien woody species where it was required to have both (a) population counts according to size class, and (b) relative frequency of occurrence. For example, *Chromolaena odorata* (n_{Co}) was recorded as population counts per quadrat (n) and percentage frequency per transect (e.g. where n_{Co} per quadrat $\geq 1=1$).

Percentage estimated grass cover was measured in each quadrat during the late summer surveys. Grass cover was recorded as an average calculated from two independent observer estimates. In addition, 0.25 m² quadrats were used for harvesting grass in five representative quadrats in each transect. Grass clippings were weighed, separated into grasses and herbs, oven-dried at 90°C for 48 hours and reweighed. Grass dry matter values (DM g m⁻²) were then plotted as calibration curves of cover to yield and used for estimating the seasonal grass fuel production at each site over time. Aerial cover, however, was assessed far more intensively than phytomass and was used with species data for interpreting restoration responses to some determinants (e.g. aspect, soil, woody species and fire).

Population counts of woody species were carried out during annual assessments before winter burning treatments (July/August) in contiguous 5 m x 5 m quadrats on either side of transects, a method similar to that used by Walker (1976). Woody species were counted as individuals and grouped into the following height classes: ≤ 1 m, $>1 \leq 2$ m, $>2 \leq 3$ m, $>3 \leq 4$ m, $>4 \leq 5$ m and > 5 m. To prevent counting the same woody species more than once each 25 m² quadrat was divided into quarters. Censuses were systematically conducted in each quadrant. The woody plant plots were laid out in transects of 25 m, i.e. sites 1a, 1b, 3a, 3c and 3d were left out (see Table 3.1).

Species were classified into three hierarchical levels for analysis, i.e. species, life forms and growth forms, the most important being the individual species themselves (O'Connor 1985). Species were then ascribed to life forms under the following groups: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes (Raunkiaer 1934). Rutherford and Westfall's (1994) fire-life forms were used as indicators of change. Growth

forms were mentioned for greater clarity concerning the applications of the three hierarchical classification systems. Growth forms of Geldenhuys *et al.* (1988) were adopted and divided into trees, shrubs, shrublets, lianas, vines, graminoids, geophytes, herbs (forbs), succulents and ferns.

Nomenclature: the scientific names of species conform to Arnold and de Wet (1993).

Referencing format is in accordance with African Journal of Range and Forage Science (1999).

3.1.3 Statistical tests

Permanent transects with contiguous quadrats were not replicated and run the risk of pseudo-replication. To avoid this, linear regressions were used to detect differences in species richness over time in samples of variable size. Curvilinear regressions were used to measure serial differences in species-area curves in of 25 m.

One-way Analysis of Variance with *post hoc* comparison of means using Friedman ANOVA was used to detect significant differences in species richness between surveys in relation to chromolaena density and fire. The significance of differences in richness between sites was ascertained by Scheffé test. Succession and species composition of sites were examined using multivariate techniques, namely unconstrained and constrained ordinations and cluster analysis (TWINSpan). The specific analyses will be covered in greater detail in chapters five and six.

3.2 Description of sites

For purposes of this investigation sites were selected with the following criteria:

- (a) grasslands which were open communities in 1937 despite recent habitat degradations;
- (b) occurring within three kilometres of the littoral dunes;
- (c) at an altitude not more than 100 m;
- (d) confined to Veld Type One (Acocks 1953); and
- (e) infrequently or not grazed.

Chromolaena was first reported as a weed-problem on the south coast in 1955 (Egberink & Pickworth 1969). Old aerial photographs (1937 and 1966) were used to validate sites

described in point 3.2a above (Plate 1). Degradation taking place after 1966 is associated with sugarcane expansion, i.e. conversion of virgin soil to arable lands, causing grasslands unsuitable for cultivation becoming fragmented. Excluded are communal rangelands, typified by a cropped sward, or more poignantly, free of chromolaena and other woody species, in accordance with point 3.2e.

The criteria for site selection, and the rarity of coastal grassland communities (le Roux 1995), meant sites chosen were highly variable. The major variations include differences in aspect, soil form and consequently species composition. Differences in condition in relation to chromolaena density are in keeping the objectives of the study. I did not see the large degree of variation as a discredit to the study because the primary focus was the descriptive analysis of temporal changes within communities. None of the sites chosen had been grazed in recent years. For logistical reasons, I restricted sites to an area between the Mkomazi and Mtwalume rivers (*ca.* 40 km apart) on the KZN south coast. Sites are briefly described below.

Coastal grasslands are low elevation fire-climax communities with a potential forest domain in the absence of fire (Tainton 1981). In the Transkei region of the Eastern Cape coastal grasslands characterised by short grassland are composed almost exclusively of *Aristida junciformis* with associations of *Themeda triandra* and *Tristachya leucothrix* (Acocks 1953). In tall grassveld *Cymbopogon* species predominate, but this type of veld has a limited patchy distribution. Both community types were represented in this study.

3.2.1 Site 1

Site 1 is a three hectare open grassland at Elysium (30°28'52"S, 30°38'07"E) on a lowland hillock (alt. 30 m) 500 m to the west of the littoral dunes. The hillock slopes in the south to form the mouth of the Mtwalume River. Three locales typify the terrain, namely east (Site 1a), crest and west (Site 1b) facing slopes (Plate 1, a and b). Soils at Site 1 are regic sands (MacVicar *et al.* 1991). Soil texture varies from sand (86:8% sand:clay) on the eastern aspect to sandy loam (74:15% sand:clay).

The site experiences irregular wildfires with magnitudes of *Brachiaria serrata*, *Digitaria eriantha*, *Diheteropogon amplexans* and *Themeda triandra*. The scarcity of indigenous woody species kept as scrubby shrublets (0.5 m) by fire and salt-laden sea breezes, and the absence of exotic species, fulfilled the requirements of using this site for benchmark purposes. Monitoring was carried out during the 1992/93 biological year. Fuel loads at the start of the investigation were estimated at 2.5 and 5.0 t DM ha⁻¹ at Site 1a and Site 1b respectively.

3.2.2 Site 2

Site 2 is a one hectare pocket of gently undulating grassland (Site 2a) bisected by a natural drainage depression (Site 2b), in a coastal forest clearing (30°14'26"S, 30°46'26"E) at Clansthall. Soils are regic sands with sand:clay percentages of 85:9 at 2a and 75:19 at 2b. It is situated one kilometre from the littoral dunes and has a maximum altitude of 60 m. The grassland has been reduced in areal extent since 1937 by secondary forest expansion (Plate 1, c to e) in areas not converted to sugar cane. Site 2 was moribund in 1991, the last fire, according to the farmer, occurred in 1960, but the area was mowed by tractor in 1988.

Site 2 is characterised by open mesic grassland on well drained loamy sand (Site 2a). One metre tall chromolaena was the dominant woody species in 1991 (1.2 plants m⁻², 60% frequency), with occasional *Albizia adianthifolia*, *Brachylaena discolor* and *Syzygium cordatum* occurring as dwarf shrubs. Site 2b is on sandy loam soils and occurs in the drainage line. It was historically sedgy-grassland, but is never inundated by water. Subsequent to 1966 the site was modified and visibly desiccated by a 1.5 m thicket-forming infestation of chromolaena (17.7 plants m⁻², 100% frequency). The grass fuel loads at the start of the investigation were estimated at 13.2 and 0.3 t DM ha⁻¹ at Site 2a and Site 2b respectively.

3.2.3 Site 3

Site 3 (alt. 80 m) near Clansthall, is situated on north facing slope (30°14'43"S, 30°45'07"E) that drops down steeply to Mahlongwana River, 2.5 km inland from the sea. Soil form is Glenrosa (MacVicar *et al.* 1991) and soil texture was classed as sandy clay loam (56:23% sand:clay). In 1937 the grasslands in this locality were quite extensive. Cultivation of

surrounding grasslands during the late 1960's resulted in the establishment of scrub forest (Plate 1, f to h). Grass cover had been reduced to *ca.* 30% (2.7 t DM ha⁻¹) by 2 m Chromolaena bushes (5.2 plants m⁻², 76% frequency). *Combretum molle*, *Dichrostachys cinerea* and *Heteropyxis natalensis* were the dominant tree species with heights ranging from 1 to 5 m.

3.2.4 Site 4

Site 4 (30°14'43"S, 30°45'05"E) is located on the same slope as Site 3 at an altitude of 100 m and has the same soil form and textural properties. Open grassland has been transformed to scrub forest, without a herbaceous layer, dominated by 3 m chromolaena thicket (11.7 plants m⁻², 100% frequency). *Canthium inerme*, *C. molle*, *D. cinerea*, *H. natalensis* and *Protorhus longifolia* trees up to a height of seven metres were interspersed above the chromolaena under storey.

Table 3.1 Location and specifications of belt transects used in monitoring coastal grasslands

Site	Transect m	No. Quadrats		Aspect N=360/0°	Slope n°
		1 m ²	25 m ² (total area m ²)		
Site 1a	60	60	0	90	15
Site 1b	80	80	0	270	16
Site 2a	25	25	10 (250)	220	14
Site 2b	25	25	10 (250)	150	2
Site 3a	30	30	0	360	18
Site 3b	25	25	10 (250)	360	17
Site 3c	20	20	0	340	18
Site 3d	15	15	0	320	15
Site 4a	25	25	10 (250)	360	21
Site 4b	25	25	10 (250)	360	21

3.3 Soils

The coastal lowland of the southern KZN monocline, with the offshore continental shelf at 110 m below sea-level, consists of buried soils of sedimentary origin underlying an overburden of aeolian sand about 3 km inland (Tinley 1985). Topsoils in the study areas have been formed by either sand accretion at sites less than 60 m above sea level (Sites 1 and 2 = regic sand) or by glacial sedimentation, Glenrosa form, (Sites 3 and 4) at altitudes above 60 m.

3.4 Climate

The entire province falls into the summer rainfall region with 16 to 20 year oscillations typified by quasi-10 year periods of high rainfall followed by periods of low rainfall (Tyson *et al.* 1975, Tyson & Dyer 1975). Similar patterns were confirmed in rainfall data from a Clansthall farm with records dating from 1927 (Figure 3.1). The Great Escarpment causes marked discontinuity of climate between the interior and coastal maritime types. Mean annual rainfall ranges from 1 000 to 1 600 mm per annum on the coastal lowlands (up to 450 m a.s.l.) but becomes more variable in the adjacent hinterland (450 to 900 m). Low stratiform cloud such as sea fog or coastal drizzle has been important in the development of the beach and dune system in KZN. The study commenced in July 1991 and ended in July 1998 and seasonal rainfall patterns at Clansthall (sites 2, 3 and 4) over this period are presented (Figure 3.2).

Droughts are common on the coast (Figures 3.1 and 3.3), with 12 occurring between 1926 and 1999 (one in six years). Drought occurred at the beginning of the study and ended in the 1993/94 biological years. This drought differed from previous ones in that the duration of aridity was much longer. Its effects on the sugar industry were severe (Lionnet 1993), however, minimal impacts were observed on the natural vegetation. Effects of drought on the grassland communities are discussed in Chapter 6.

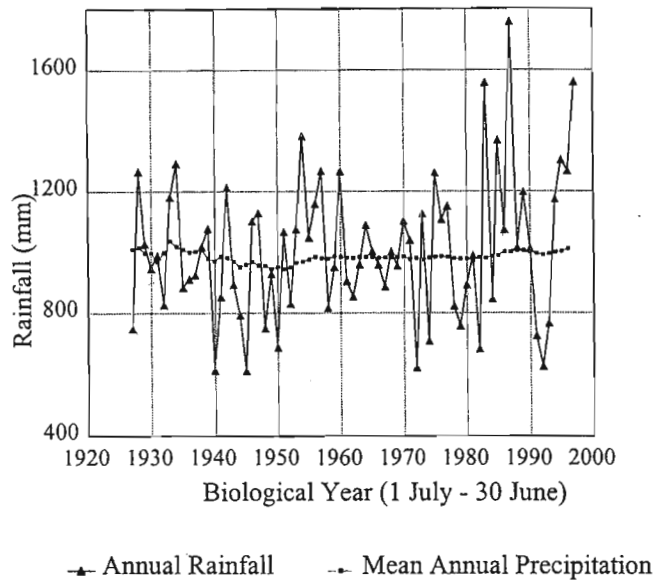


Figure 3.1: Annual rainfall according to biological years (July 1st to June 30th) at the Clanshall sugar estate. Records date back to 1927.

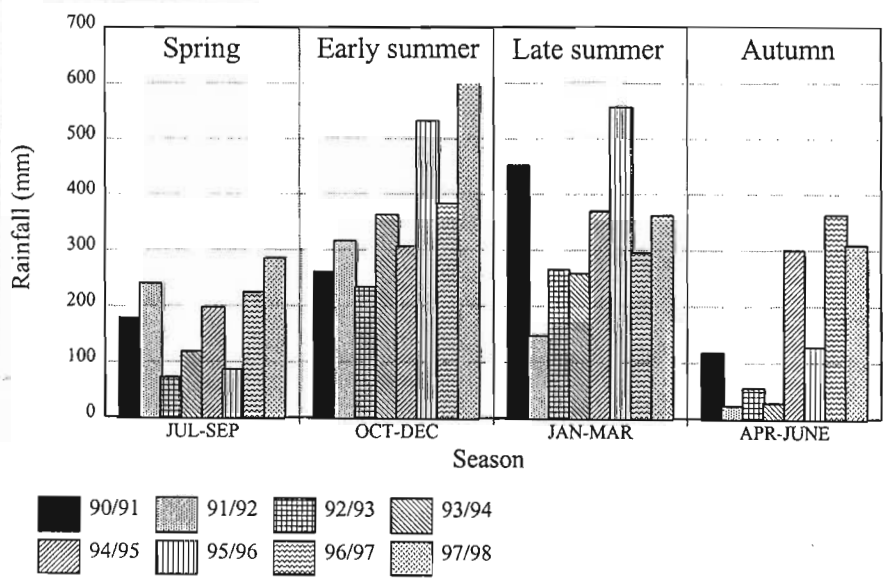


Figure 3.2: Annual rainfall according to season at Clanshall during the study period (1990/91 to 1997/98).

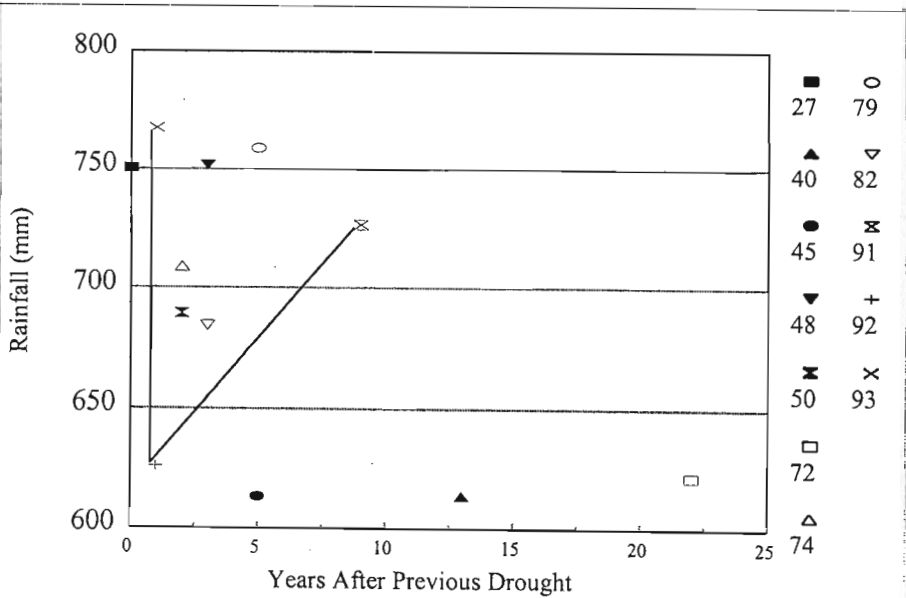


Figure 3.3: Incidence of drought at Clanshall, the values in the legend are the years in which the droughts occurred (e.g. ■27 = 1927/28 biological year).

4. SERIAL PATTERNS OF CHANGE IN PERMANENT TRANSECTS

4.1 Statement of the problem

“All boundaries are arbitrary, distinctions drawn in space by the observer...containing the record of interactions across it” (Canny 1981).

The interpretation of plant community changes over time and locality are conditional on the scales of interest. This chapter aims to describe patterns of change over time in coastal grasslands invaded by *Chromolaena odorata*. Aspects of interest are the effects that (a) transect length; (b) species richness-by-area and (c) species frequency-by-sample size have on the types and amounts of change in ecological condition states.

Grassland sites occurred as patchy habitats confined by coastal forest remnants in a landscape planted largely to sugarcane. A prerequisite for monitoring communities in permanent transects was to exclude from samples species associations characterising edge effects. The smallest patch of grassland occurred at Site 2 and had a width of 25 m at its narrowest end. Sites 1, 3 and 4 could hold longer transects but for consistency, transects were standardised at 25 m.

4.1.1 Sampling intensity

How is efficient sample size determined to achieve a reliable representation of community differentiation along spatial and temporal gradients (Hume & Day 1974)? To assess the effectiveness of the standard sample size one would need to know how many species are accounted for at sizes smaller and larger than transects of 25 m. This section reports on the differences in species richness in transects of variable length and the most area-effective sample size over the study period.

4.1.1.1 Test one

Test the null hypothesis of no significant difference in species richness over time in transects longer than 25 m.

4.1.2 Species-area curves

The species-area curve expresses the relation between the number of species and the area in which they occurred. Species-area curves increase exponentially initially but become increasingly horizontal as unity in area and number of individuals gets progressively negligible (Juliano 1993). The true characteristics of communities only appear once a threshold minimum area has been examined. The point where the curve levels off is an indication of the minimal area required for effective sampling. Species-area curves are also used to estimate how much potential variation occurs beyond the scale of interest. This section reports on (a) verification of the most effective sample size; (b) curve dynamics over time and (c) some observed biological responses.

The purpose of the point (c) above, despite differences in initial chromolaena density, topography and soil form, was relating 'within' site condition over time to species-by-area relations. This is a descriptive approach because independent transects were not replicated.

4.1.2.1 Test two

Test the null hypothesis of no change in species-area curves over time concurrent with annual fires. Included is a spatial component of sites degraded to varying extents by chromolaena. The temporal dimension is the within community record of 'states of change' in species richness after fire.

4.1.3 Scale

Random quadrats that are the same size measure treatment effects at a single scale. Contiguous quadrats (sub-sample) along belt-transects (sample) can monitor treatment effects at scales ranging from sub-sample to sample sizes. This can be achieved by treating samples as nests containing a record of the cumulative abundance of all the species found in transects. By accumulating local abundances along transects, i.e. combining sub-samples in sequence (e.g. 1, 1+2, 1+2+3, 1+2+3...+N), one might observe differing species responses at a range of scales. Transects made up of 25 contiguous 1m² quadrats were used for monitoring in coastal grasslands communities. The effects of fire could therefore be viewed at scales ranging from 1 to 25 m². This section reports (a) types of species response to chromolaena density and fire at the sample scale of 25 m²; (b) absolute change at scales from 1 to 25 m² and (c) the

inability to detect changes from sub-sample to sample size.

4.1.3.1 Test three

Test the null hypothesis that scale does not influence species local frequency.

4.2 Methods

Permanent transects were sampled in the same systematic manner throughout the duration of the investigation, starting with the first quadrat in each transect. Species richness in the first quadrat may not typify richness in subunits making up each transect. Richness data were transformed into normally independent distributions (NID) using true means from random forward and reverse extractions in randomly selected quadrats as an attempt to reduce observer bias. Quadrats remain spatially dependent nonetheless.

Seasonal compositions of samples were arranged into two-way community tables of quadrats-by-species. Populations of species were calculated by totalling their presence values in columns. Species richness was calculated by adding new species, as quadrat numbers accumulated, to the population in the first quadrat.

4.2.1 Sampling intensity

The trial was carried out at Site 3 (see Section 3.2.3 for site details). Four parallel transects were laid 5 m apart (Figure 4.1). Each successive transect diminished by 5 m with a maximum length of 30 m (A in Figure 4.1) and a minimum length of 15 m (D). Monitoring in transects began in the 1992/93 biological year (1 July to 31 June) and the trial was stopped on the 30 June 1998. Monitoring was not done in 1995/96 due to budget constraints. Annual veld burning was carried out according to burning regulations (Forest Act 122 of 1984, Forest Amendment Act 25 of 1989). Fire intervention history is as follows: 1st fire 20/1/93 (wild fire during mid-season drought), 2nd burn 22/9/94, 3rd burn 3/10/95, 4th burn 18/9/96 and 5th burn 3/9/97.

Transects were not randomly positioned and quadrats were not spatially independent. The problem of pseudo-replication meant Analysis of Variance could not be used to detect statistical differences in species richness over time within and between transects. Instead,

time series data were subjected to regression analysis on Genstat 5 (Anon. 1998).

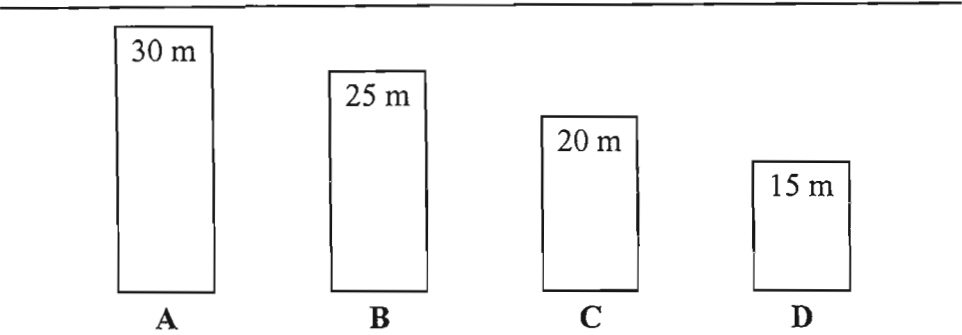


Figure 4.1 Sampling intensity study showing the positions of transects (A to D) and transect lengths (m).

4.2.2 Species-area curves and minimal area

Standard transects of 25 m (Table 4.1), accounting for 21 samples in five sites over seven seasons, were used for comparing species-by-area relations (see Section 3.2 for site descriptions). Raw species-by-area data were first plotted to determine the general shapes of the curves. All were essentially asymptotic due to accumulation of new species with increasing area. The exceptions were samples with initial monospecific stands of chromolaena (sites 2b, 4a and 4b).

Table 4.1 Samples-by-season matrix of spatio-temporal data used in the analysis of species-area curves, minimal area and scale

Years	Site 2a	Site 2b	Site 3b	Site 4a	Site 4b
Time 0	'90/91	'90/91	'92/93	'90/91	'90/91
Time 1	'90/91	'90/91	'93/94	'90/91	'90/91
Time 2	-	-	'94/95	-	-
Time 3	-	-	-	-	-
Time 4	-	-	'96/97	-	-
Time 5	-	-	'97/98	-	-
Time 6	'96/97	'96/97	-	'96/97	'96/97
Time 7	'97/98	'97/98	-	'97/98	'97/98

Genstat 5 (Anon. 1998) was for fitting exponential curves (Equation 4.1) to raw data and for conducting analysis of parallelism between curves (curvature).

Equation 4.1:

$$y_i = a + \beta \exp(-kx_i) + \varepsilon_i$$

or: $y_i = A + B \times R^x$
where: $R = \exp(-k) = \text{curvature}$
 $x_i = \text{accumulated area of the } i\text{th quadrat}$
 $A = \text{asymptote}$
 $A + B = y \text{ intercept}$

Equation 4.2 was used for determining x_i on an exponential curve for the calculation of percentage minimal area.

Equation 4.2:

$$x_i = \frac{\log_e \left(\frac{\left(A \times \frac{n}{100} \right)}{B} \right)}{\log_e(R)}$$

Where: n = required minimal area level (e.g. 95) as a percentage of the asymptote.

4.2.3 Scale

Serial data from sites 2a, 2b, 3b, 4a and 4b were transformed into matrices of species-by-cumulative area. The smallest scale was equal to the area of the first quadrat (1 m²) and the largest scale was equal to the sum of all quadrats in the transect (25 m²). Turnover was determined by subtracting species presence values from earlier and later surveys, producing change profiles at the scales from 1 to 25 m².

Change in species local frequency between two observations can be positive or negative values. Negative values show a decline in frequency, positive values show increases and zeros denote no change in species frequency over time. The measurement of absolute change is called **sensitivity** (after Critchley & Poulton 1998) and is calculated by summing the modulus of change values (e.g. -1+1=2) down each column (Appendix D). The inability to detect change is called 'blindness' and is calculated by counting the number of zeros in each column. Optimum scale was originally based on a parabolic principle for nested quadrats whereby changes in species local frequency are detectable in both directions (Critchley & Poulton 1998). Changes in local frequency that are closest to the midpoint of the transect area, i.e. 12.5 m², was considered the optimum scale. Optimum scale can only be determined from change profiles that show changes in opposite directions. Effective optimum scale should reflect changes values that are higher than the change values at the 25 m² scale.

Absolute change and blindness data were analysed with Genstat 5 (Anon. 1998) using linear and exponential models.

4.3 Results

4.3.1 Effective sampling intensity

Trends in the raw data suggest that the 25 m transect (B) had greater similarity to the 30 m transect (A) than it did to both 20 (C) and 15 m (D) transects (Figure 4.2). Chromolaena populations were comparatively similar in the 1992/93 biological year, namely 4.1, 5.2, 3 and 2 m² in A, B, C and D respectively. All transects showed increases in species richness over time coinciding with annual burns and declining chromolaena populations. The dip in richness during the 1996/97 is attributed to a monitoring season covering only four months (Section 3.1.2).

Statistical differences between the 25 and 30 m sample sizes were negligible throughout the study period (Figure 4.3). The 30 m transect yielded only six additional species from six years of data. Transects of 20 and 15 m were repeatedly inferior to the transects of 25 m. The relation between richness and sample size also appears consistent. Species richness increased at the same rate across all transects shown by the parallel lines. Twenty-five metre transects remained the most area-effective sample size throughout the study period. The null hypothesis of no significant difference in species richness over time in transects longer than 25 m is upheld.

4.3.2 Species-area curves and minimal area

4.3.2.1 Species-by-area relations

Species richness increased with increasing sample area at all sites over time (Figure 4.4). Curvature (R) in species-by-area relations were nonparallel over time ($P < 0.05$). Exponential curve-fitting analysis (Equation 4.1) established that curvature was not different ($P > 0.05$) at Site 3b only. The null hypothesis of no change in species-area curves over time was therefore falsified.

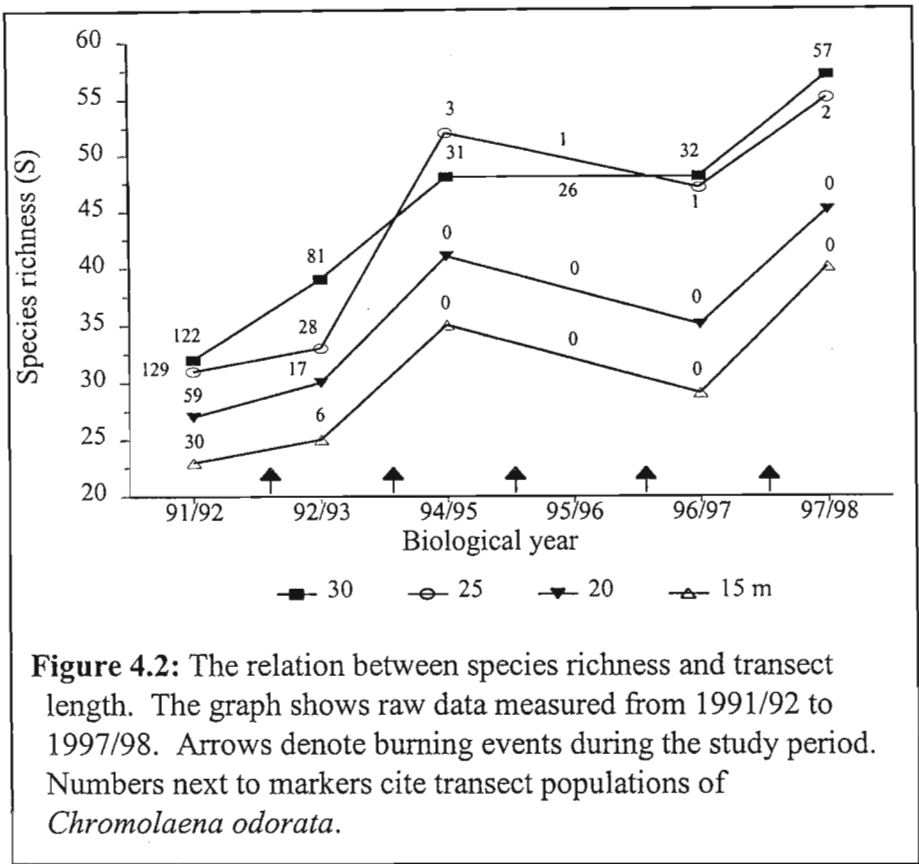


Figure 4.2: The relation between species richness and transect length. The graph shows raw data measured from 1991/92 to 1997/98. Arrows denote burning events during the study period. Numbers next to markers cite transect populations of *Chromolaena odorata*.

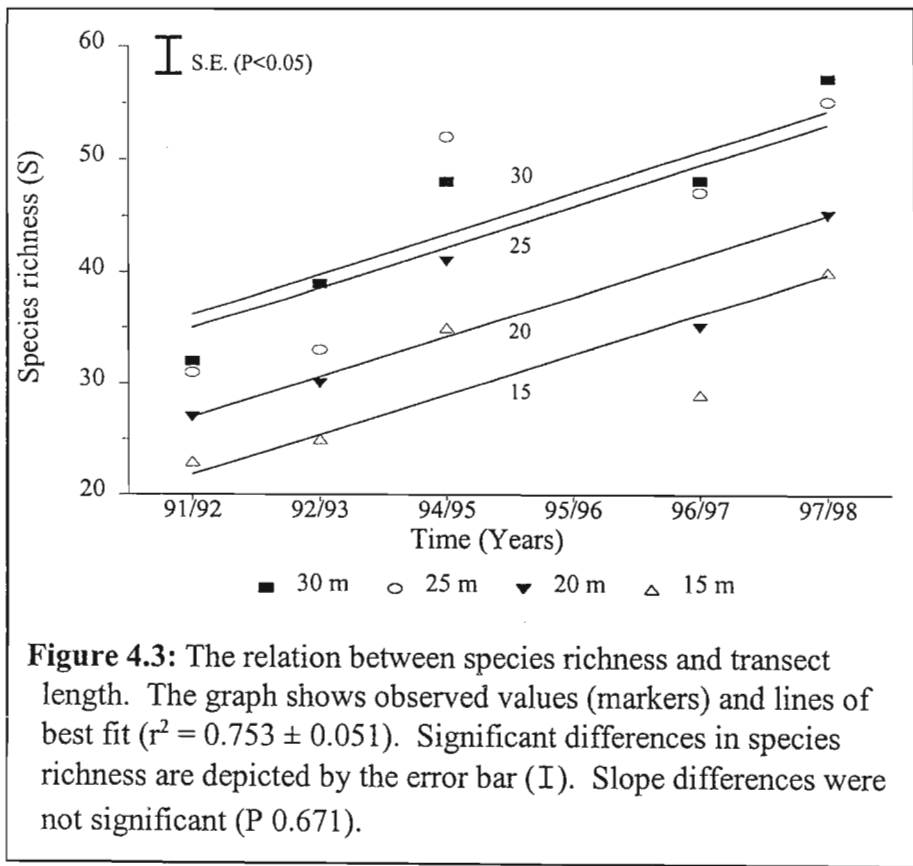


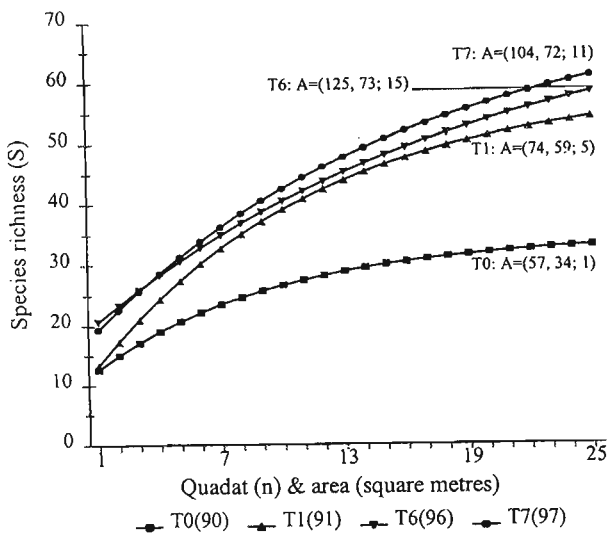
Figure 4.3: The relation between species richness and transect length. The graph shows observed values (markers) and lines of best fit ($r^2 = 0.753 \pm 0.051$). Significant differences in species richness are depicted by the error bar (I). Slope differences were not significant (P 0.671).

The temporal dynamics reflected in the species-area curves varied from site to site. Site 2a had 33 species in 1991/90 and maintained steady increases over the study period, reaching 61 species in 1997/98. Site 2b and 3b followed the same pattern of sustained increases in species richness over time. A shorter monitoring period in 1996/97 resulted a decline in species richness being recorded at Site 3 (Figure 4.4c). Initial chromolaena density appears to have had a residual impact on the temporal dynamics of species-area curves. Sites 4a and 4b, initially dense in chromolaena, produced curves with inconsistent directions of change. Gains in species richness during the first half of the study were unable to maintain the impetus of directed change and both sites showed signs of non-equilibrium towards the end of the study.

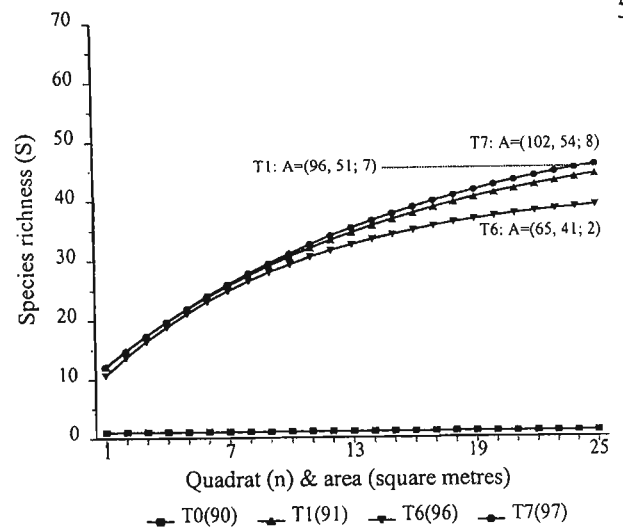
Exponential curves of species/area-by-location data yielded similar results to the species/area-by-time analyses. Species richness in 25 m² transects were summarised using fitted values of species-area curves from the first two and last two field surveys (Figure 4.5). Species richness varied across sites over time ($P < 0.001$). Increases in richness occurred where chromolaena populations declined under routine veld burning. Chromolaena populations were not effectively suppressed by fire at Site 4b.

4.3.2.2 *Minimal area*

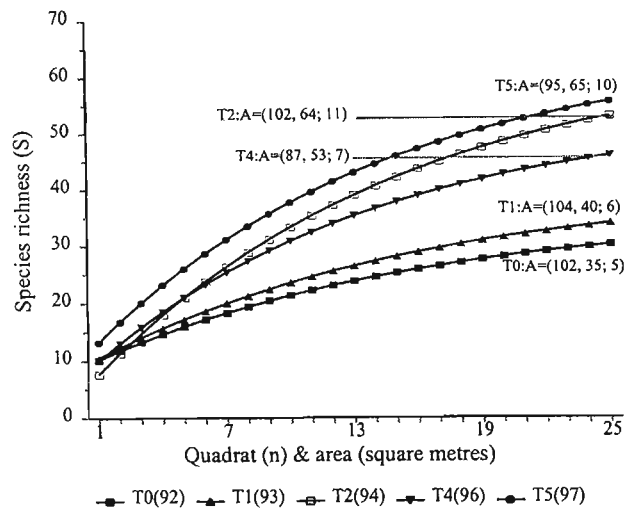
Asymptotes occurred consistently beyond the length of transects and the physical boundaries of each site (Figure 4.4). The difference between the asymptote and transect richness (see Figure 4.4 caption, last sentence) increased over time at sites 2a, 2b and 3b. Asymptotes fluctuated strongly at sites 4a and 4b but differences in richness still increased at 4a before the site showed signs of failure to restore itself in 1997/98. Transects were only partially able to reveal an appropriate minimal areas of 90 to 95% (Table 4.2). Directions of change in proportions of asymptotes contained within transects could not be determined under conditions of increasing or fluctuating heterogeneity. The proportion of asymptotes revealed by 25 m² transects did not seem significantly different overall.



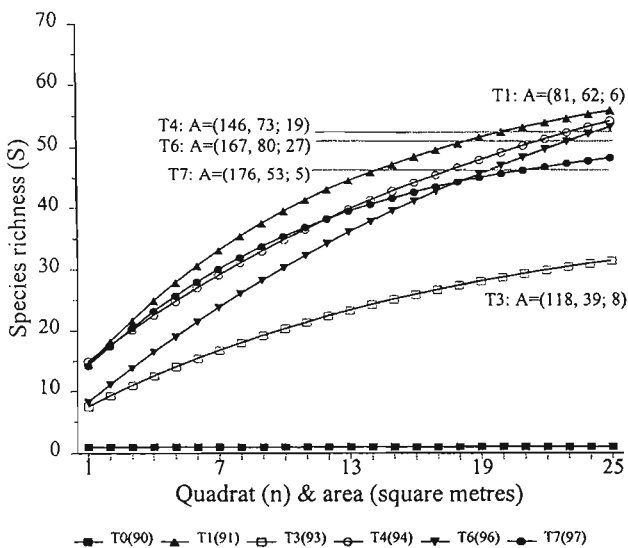
(a) Site 2a: curvature (R) $P < 0.001$, $r^2 = 0.99 \pm 0.01$



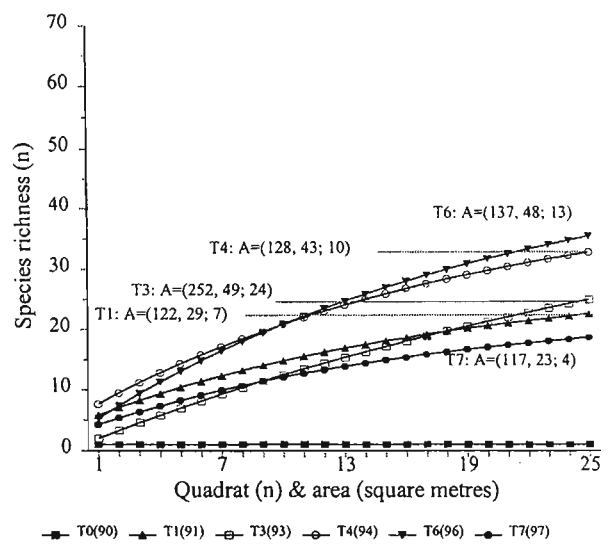
(b) Site 2b: curvature (R) $P = 0.003$, $r^2 = 1 \pm 0.01$



(c) Site 3b: curvature (R) $P > 0.05$, $r^2 = 0.99 \pm 0.01$



(d) Site 4a: curvature (R) $P < 0.001$, $r^2 = 0.99 \pm 0.01$



(e) Site 4b: curvature (R) $P = 0.06$, $r^2 = 0.99 \pm 0.01$

Figure 4.4: The relation between species richness (S) and time (T) with increasing area at five localities. Individual curves show increasing species richness with increasing number and area of quadrats. P-values are given for changes in curvature (R) over time. Correlation coefficients (r^2) are also provided. Monospecific infestations are horizontal straight lines. Species-area curves fluctuated over time, either increasing or decreasing, depending on site condition. Asymptotes (A) are given for each curve (x, y intercepts; difference in richness of A - 25 m).

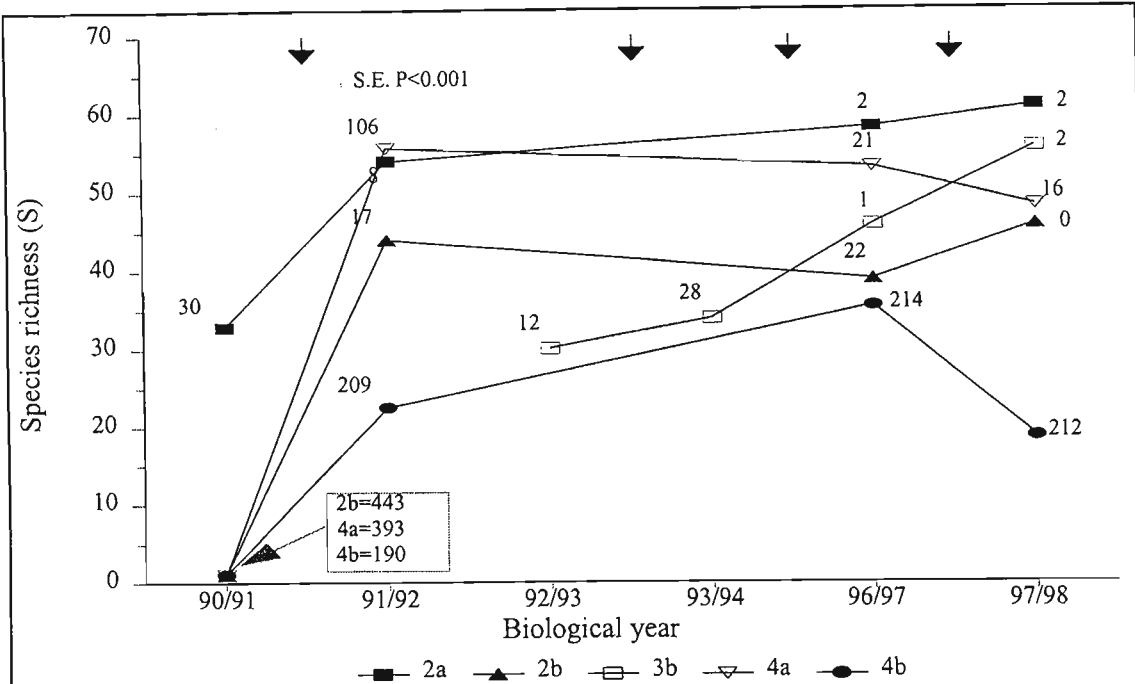


Figure 4.5: Summary of exponential curve fitting analyses of species-by-area data comparing species richness (S) and location (sites) in permanent transects of 25 m² over the study period. The 1994/95 and 1995/96 seasons were not analysed. Significant differences in species richness are depicted by the error bar (I). Arrows denote burning events during the study period. Numbers next to markers cite populations of *Chromolaena odorata*. Monospecific stands of *C. odorata* occurred at sites 2b, 4a and 4b in 1990/91.

Table 4.2 Percentage of asymptotes¹ contained within fixed-belt-transects (25 m²) at five coastal grassland sites

Site	Biological year								Mean
	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	
2a	97	92	-	-	-	-	79	85	88.3±7.9
2b	-	86	-	-	-	-	95	85	88.7±5.5
3b	-	-	86	85	83	-	87	85	85.2±1.5
4a	-	90	-	79	74	-	66	91	80.0±10.7
4b	-	76	-	51	77	-	73	83	72.0±12.3

¹ Figure 4.4

4.3.3. Scale

4.3.3.1 Individual species responses

Sites 2a and 3b are presented as case studies (Appendix D). The tables can be divided into three sections covering the changes in species local frequencies at numerous scales over four biological years. To conserve space only five scales are displayed, namely 1, 3, 6, 13 and 25 m². Change profiles display the difference between species presence values from earlier and later surveys at the scales specified.

Species were noted to respond in several ways. Species with local frequencies of 100% could not increase further. Directional changes in local frequencies of dominant species were, nonetheless, detected at a range of scales. The maximum amount of change was detected at 25 m² between the first and the final observation in 1990/91 and 1997/98 at Site 2a and 1992/93 and 1997/98 at 3b. One quadrat is equal to 4% frequency ($\frac{1}{25} \times 100$).

At Site 2a the dominant grasses that increased were *Alloteropsis semialata* (+8, = 8 quadrats or 32%), *Panicum aequinerve* (+1) and *P. dregeanum* (+3) (Table D1 of Appendix D). Dominant grasses that decreased were *Aristida junciformis* (-17), *Ischaemum fasciculatum* (-2) and *Setaria sphacelata* (-4). *Chromolaena odorata* (-11) was unable to maintain its dominance under the prevailing burning conditions set during this investigation. Examples of species that were short-lived in Site 2a were *Lobelia caerulea* and *Senecio chrysocoma* (1991-1990 profile), and *Aristea woodii* and *Tephrosia elongata* (1997-1996). *Rumex dregeanus* and *Selago trinervia* are species that established towards the end of the study.

Site 3b which was more severely invaded by chromolaena emulated species' responses that either increased, decreased or did not change. At Site 3b grass species between 1992/93 and 1997/98 either increased or remained unchanged at scales of 25 m², no grasses showed declines in local frequency (Table D2 of Appendix D). *Hyparrhenia tamba* increased local frequency by 21 quadrats (84%), *Sporobolus africanus* (+12), *Cymbopogon validus* (+12) and *Eragrostis curvula* (+10). *Aristida junciformis* did not change along with the herbs *Dicoma speciosa* and *Senecio deltoideus*. *Chromolaena odorata* (-21 or 84%) also declined under conditions of annual burning along with the herb *Melhania didyma*. Species that established

for a short while were ruderal species such as *Phyllanthus meyerianus* and *Sida dregei*. Species that only established later were *Chaetacanthus burchellii* and *Chamaecrista capensis*, both of which were components disclimax grassland at Site 2a.

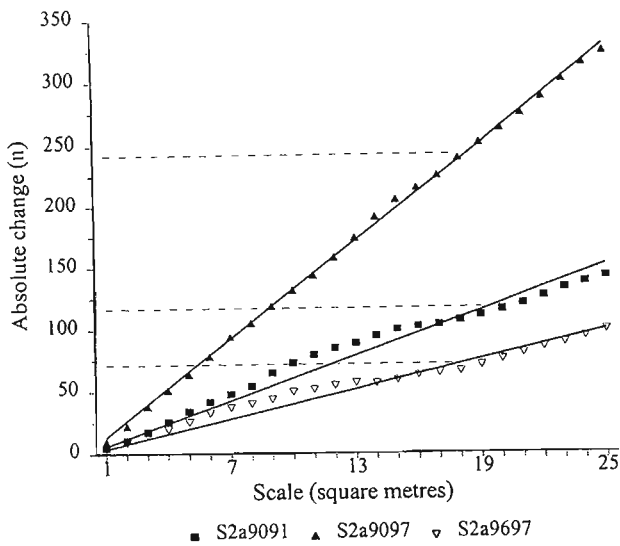
General turnover patterns indicated increases, decreases or no change in local frequency over increasing scale. Records of turnover in both directions were not detected, invalidating the application optimum scale in homogeneous quadrats. Summarised statistics of sensitivity (absolute change) and blindness indicated linear and curvilinear relations to scale. The null hypothesis that scale does not affect species local frequency was falsified. Scale had major influence on the detection of individual species responses. Optimum change was unable to account for an appropriate optimum scale, changes in local frequencies varied from species to species.

4.3.3.2 Measure of absolute change (sensitivity)

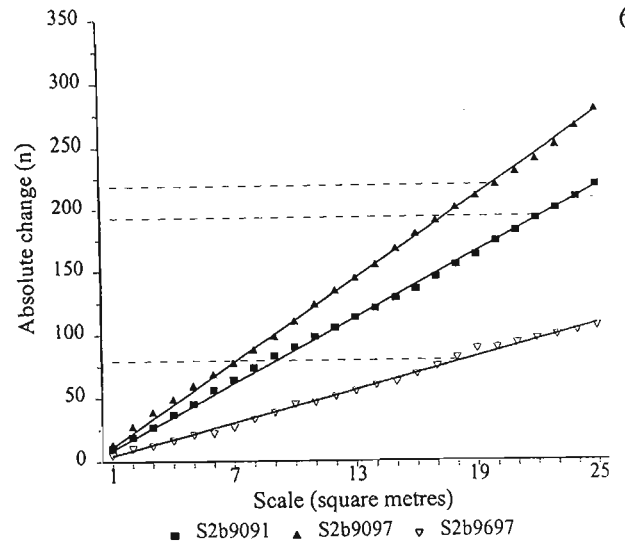
Sensitivity measures absolute change in species local frequencies between observations from 1 to 25 m². The statistical analyses of absolute change were strongly linear (Figure 4.6). Nearly all sites showed the same sequence of responses between biological years. The largest changes occurred between the first and last surveys in four out of five sites, Site 4b being the exception. The least amounts of change were found between the last two biological years at three sites. Implications are that floral richness and composition improved with time under conditions of annual burning and decreasing chomolaena (Figure 4.5).

Site 4b showed greatest change at the end of the study but these appeared only marginally greater than between the first two years. This suggests a system that did not change much florally, and changes that did occur seemed temporary. Site 4b showed signs of reverting back to its original condition with high populations of chromolaena (Figure 4.5).

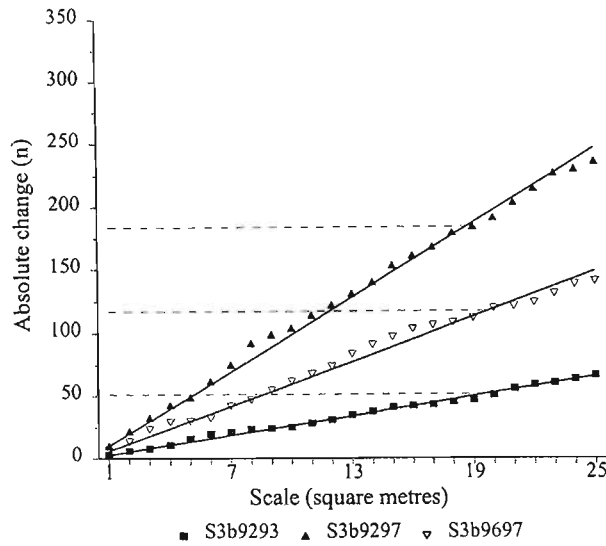
The linear effect of absolute change is evidence that scale is relative to the size of the window through which the system is being viewed. Optimum scale was less than the 25 m² scale in 14 out 15 samples (Figure 4.6) and proved meaningless in fixed-belt-transects. Implications of a relation between absolute change and scale being linear are that optimum scale lies at an unknown position beyond the transect.



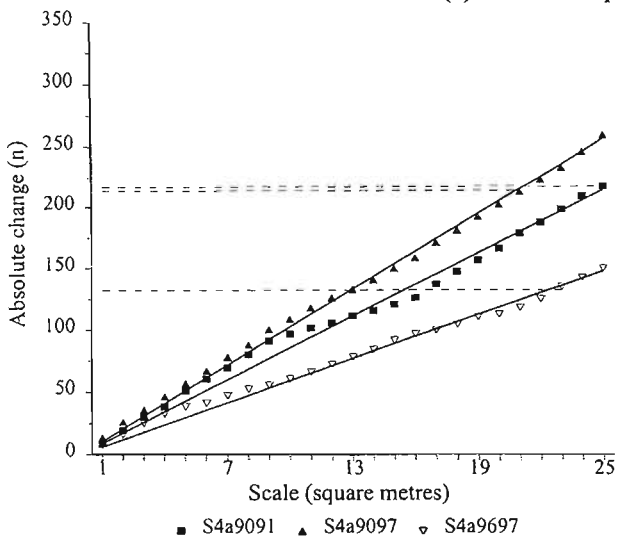
(a) Site 2a: slope $P < 0.001$, $r^2 = 0.97 \pm 0.02$



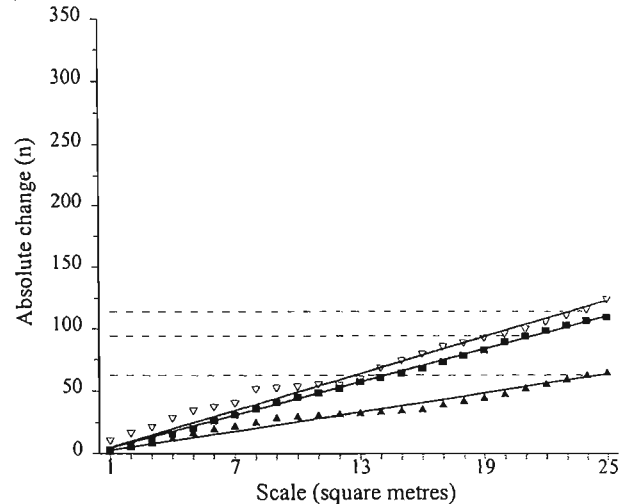
(b) Site 2b: slope $P < 0.001$, $r^2 = 0.97 \pm 0.03$



(c) Site 3b: slope $P < 0.001$, $r^2 = 0.99 \pm 0.04$



(d) Site 4a: slope $P < 0.001$, $r^2 = 0.99 \pm 0.05$



(e) Site 4b: slope $P < 0.001$, $r^2 = 0.98 \pm 0.03$

Figure 4.6: Relation between absolute change in species local frequencies and monitoring intervals. Graphs show observed values (markers) and fitted linear regressions (lines) at five localities at scales from 1 to 25 m². Markers distinguish changes between biological years, where (■) first and second, (▲) first and last and (▼) penultimate and final years. Individual lines show increasing degrees of change with increasing scale. Dotted lines show optimum change for each interval. Differences in slopes of fitted lines are given as P-values. Correlation coefficients (r^2) account for mean variation of observed values derived by regressions.

4.3.3.3 Measure of undetectable change (species blindness)

Blindness measures the total number of species whose frequencies do not change between observations. Raw data showed blindness had a curvilinear relation with scale. Exponential curve fitting proved unsuitable, 7 out of 15 time-by-location data sets ended with negative blindness values for which corresponding x-axis values could not be determined (Equation 4.2). Seven of the remaining eight samples had asymptotes that did not fall within transect boundaries.

A 'broken-stick' linear analysis (Step 1 of Equation 4.3) was done as an alternative means of determining the asymptote (Anon. 1998). Systematic correlations in the range of XY data were tested for best fit, asymptotes being the position accounting for the greatest percentage variance. After the asymptote the line becomes horizontal by adding the Z constant to the coefficient (Step 2).

Equation 4.3:

$$\begin{aligned}\text{Step 1. } Y &= a + bX \\ \text{Step 2. } Y &= a + Z\end{aligned}$$

All asymptotes from the broken-stick analysis occurred inside transects (Figure 4.7). Blindness was greatest between the penultimate and final surveys in four out of five sites, Site 3b being the exception. In other words, species with stable frequencies were greatest at the end of the study. Before/after study blindness was at its lowest between the first and last surveys, i.e. the period covering maximum effect recorded the highest differences in species local frequency. This is in keeping with the findings concerning absolute change. Site 3b showed greater blindness in the before-after study comparison and lowest blindness in both the first two and last two surveys. This suggests that alpha diversity at Site 3b did not change much over the duration of the study. The need for optimum blindness in fixed-belt-transects was not convincing. The optimum was found consistently near the larger scales and therefore contradictory in terms of its position near the midpoint. The relation between optimum blindness and scale was not clear and appeared conditional upon individual site characteristics.

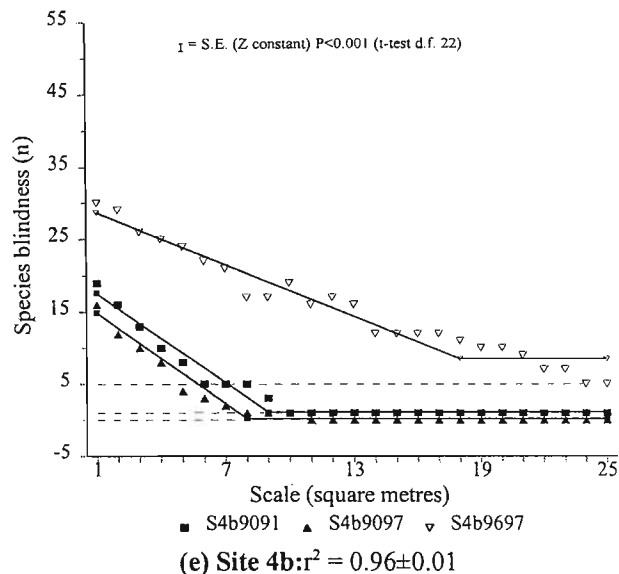
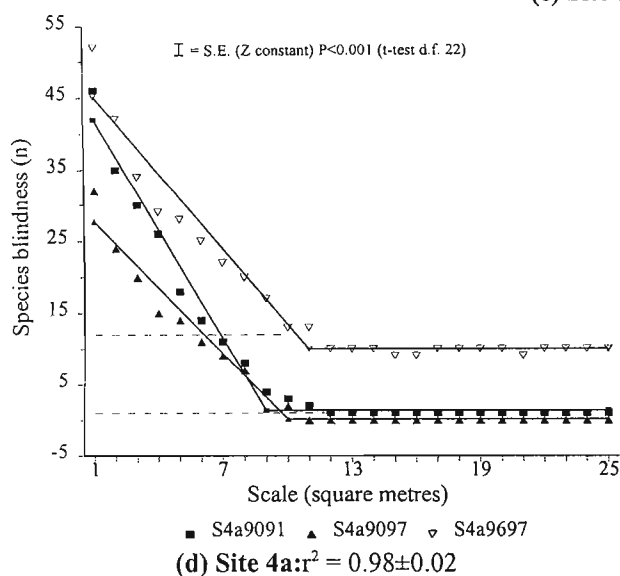
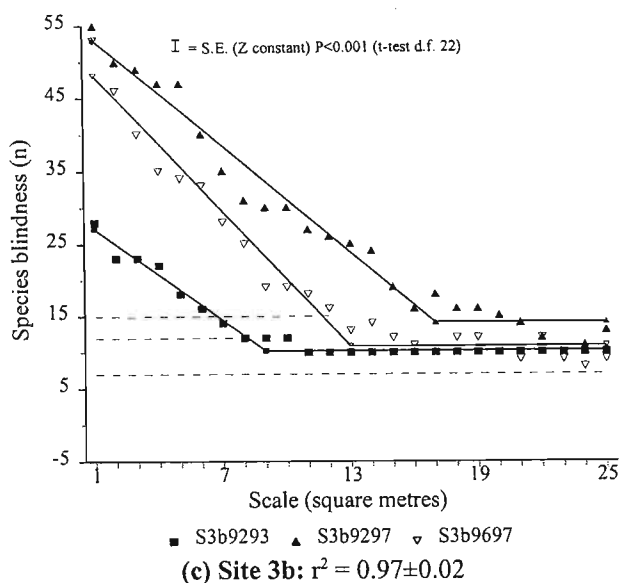
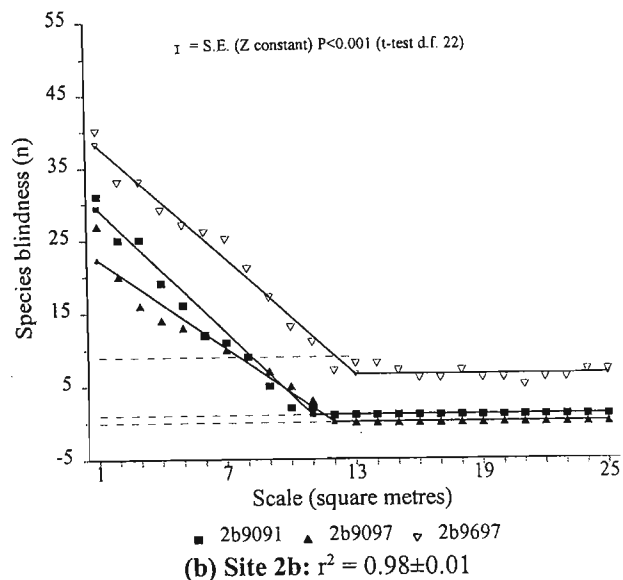
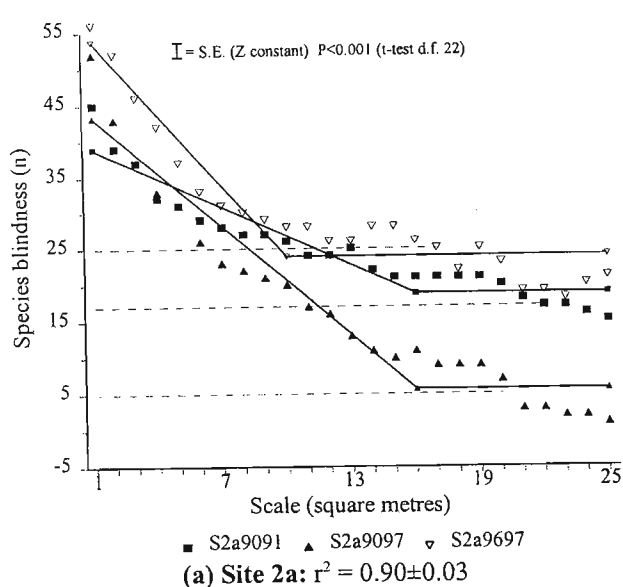


Figure 4.7: Relation between blindness (inability to detect changes) in species local frequencies and monitoring intervals.

Graphs show observed values (markers) and fitted broken-stick linear regressions (lines) at five localities at scales from 1 to 25 m². Markers distinguish changes between biological years, where (■) first and second, (▲) first and last and (▼) penultimate and final years. Individual lines show decreasing numbers of species showing no change in local frequency with increasing scale. Dotted lines show optimum blindness for each interval. Differences in horizontal regressions (Z constants) are given as P-values. Correlation coefficients (r^2) test the goodness of fit of observed values and fitted regressions.

4.4 Discussion

Sampling intensity is an important consideration in planning and executing a monitoring programme. Observers must balance accuracy and detail against objectives and available resources. A tradeoff between effort, precision and practicality is an inevitable outcome. Fixed-belt-transects of 1-by-25 m was the optimum sample size for monitoring patchy coastal grassland communities over time in a range of condition states.

Some authors have tried values ranging from 50 to 95% asymptotes of species-by-area data for sampling purposes (Greig-Smith 1983). In South Africa nonspatial methods, e.g. point techniques, for recording 'nearest plant' data have been used for determining minimal areas (77 to 99%) in grasslands (Hardy & Walker 1991; le Roux 1995). Goodall (1954 cited in Greig-Smith 1983) could not find a sample size that culminated in an asymptote using plots of increasing size. The validity of the minimal area concept as a tool for optimising monitoring strategies in plant communities was questioned. The results from this investigation concur with this opinion. Other ways of describing minimal area such as 80% of the species found at the site or alternatively 80% or less (depending on the site) of the floristic similarity (Dietvorst *et al.* 1985) would be inferior to the approach already suggested, resulting in a percentage of a percentage outcome. The sampling strategy adopted, wherein repeated measures were carried out in permanent plots, appears to have been successful, despite the failure to substantiate the value of the minimal area concept.

A weakness of the species-area curve is that all species are given equal importance, irrespective of abundance, size, life form and rates of turnover over time. Their role in describing vegetation remains limiting. Data collected on species richness in relation to area cannot be used to make assumptions about the processes responsible for inducing responses. It is not assumed that fire alone has caused species richness to increase. It is highly probable, however, that fire is operating against some of the principal determinants preventing change, e.g. sensitivity of woody species to burning, resulting in a sequential decrease in shading and competition. The only deduction about the causal issue, therefore, is the confidence that repeated responses coincided with burning interventions. Species-area curves and site histories suggest coastal grassland communities which are not grazed and invaded by chromolaena become more stable under a regime of annual burning. Species-area curves,

individual species responses and rates of change suggest that sward resilience is connected to chromolaena density more so than it is to fire.

Critchley and Poulton (1998) presented an approach using nested quadrats that could detect changes in grassland species abundances at scales less than 1 m^2 . Nested quadrats recorded species migrating from one scale to another in both directions. Belt-transects made of contiguous quadrats detected changes at scales from 1 m^2 and above. The sub-sample scale of 1 m^2 , nevertheless, proved sufficiently robust to meet sampling requirements. Species not adapted to fire and vis-a-vis species that increased under annual burning could be detected at the scale of interest. The inability of single scales to detect changes within quadrats render this sampling technique prone to incorrectly upholding a null hypothesis of no change. Single scales were incapable of detecting increases beyond the point where species exhibit 100% local frequency. Increases in density are only detectable at a range of scales smaller than the sampling unit. The same applies to species appearing static but on a smaller scale shifting within sub-sample units without leaving them. Fluctuations in species-by-area, sensitivity and blindness data show that it would be incorrect to assume that fluctuations are not taking place at smaller scales.

The measure of change in abundances of component species is more important in functional grassland ecology and management than inventories of species richness. The degree of variation within the temporal community will indicate that certain mechanisms are in place which are creating conditions suitable for improvement, degradation or stability.

Summarised statistics of these changes are useful in demonstrating trends, however, base line data (Appendix D) can reveal a great deal about the individual species, some of which are key species (Odum 1971) of underlying community structure.

Based on serial patterns of change, fragmented coastal grasslands invaded by chomolaena were observed to shift from monospecific states to species-rich communities. High beta diversity (Peet 1974) occurs between patches and between years within patches. This shows therefore that small ecosystems can sustain and regain diversity under appropriate management.

5. MONITORING SERIAL CHANGES IN WOODY SPECIES COMPOSITIONS, GRASS COVER AND YIELD

5.1 Statement of the problems

Coastal grassland sites under investigation showed woody plants increasing once the habitats became fragmented by sugarcane cultivation (Plate 1). In mid-1950 *Chromolaena odorata* was first recognised as a weed on the KZN south coast (Egberink & Pickworth 1969) and later transformed both Coastal Forest and grassland into weedy scrub or thicket-forming vegetation (Goodall & Erasmus 1996).

The role of fire in grasslands is important in the management of hemicryptophytic life forms (Rutherford & Westfall 1994). It is therefore appropriate to investigate fire as a tool for cost-effectively controlling chromolaena. The literature is ambiguous regarding the fire-tolerance of chromolaena. Several authors claim that fire is ineffective at killing adult infestations (M'Boob 1991; Wilson 1995; Mbalo & Witkowski 1997), resulting in knockdown only. Mortality of adult chromolaena under slash and burn practices is extremely variable (Uhl *et al.* 1981; Slaats 1995). Fire intensity has been reported to increase efficacy of fire for killing chromolaena (de Rouw 1993).

5.1.1 Key questions and objectives

The aims of this chapter are to describe spatio-temporal responses of native and alien woody species invading coastal grasslands to controlled winter burns. The following questions are of most interest in this investigation:

5.1.1.1 Initial chromolaena infestations

- Do density and structure of chromolaena affect grass cover?
- Is mortality of chromolaena related to grass fuel loads?
- Does efficacy of fire depend on the density and structure of infestations?

5.1.1.2 Seedling population dynamics

- Does fire prevent seedling establishment?

5.1.1.3 Chromolaena density at the end of the study

- Was the burning regime effective in controlling chromolaena and restoring grass cover?
- Are the grass yields between burns and sites significant?
- Is grass yield an indicator of key grass species?

5.1.1.4 Fire effects on other woody species

Is there a change in the density of species over time?

Is there a change in structure of species over time?

5.1.1.5 Woody plant succession

Do sample (site) compositions' change over time?

Is there a causal relation between samples and environmental variables?

It is hoped that observed responses provide insight into the invasive patterns of *chromolaena* and secondary weed establishment. The observed relation between indigenous woody species and the grass community is expected to clarify the position of coastal grasslands in succession ecology, principally by categorising them as either equilibrium or non-equilibrium communities.

5.2 Methods

5.2.1 Fire effects on *Chromolaena odorata*, grass cover and yield

Fire intensity was qualitatively evaluated in the field after the burn using ordinal values. The degree of burn was rated on a scale of 0 to 5, where 5 was a hot fire (grass tufts black, no stubble), 2-3 was a cool burn (tufts not completely burnt) and 0 was no-burn or did not burn. Population counts of *chromolaena*, grass cover and grass phytomass in fixed-belt-transects between sites were analysed using One-way ANOVA (Sokal & Rohlf 1969).

5.2.2 Fire effects on other woody species

Trees and shrubs measured in permanent plots on either side of fixed-belt-transects were grouped into four height classes, ≤ 1 , $1 < 3$, $3 \leq 5$ and > 5 m, to reduce zero values in the analyses. Woody species at each site are presented as summary statistics in Appendix C (C1 to C4). Each table of summary statistics is summarised further using the Gini index of uniformity (Dixon 1993) and Euclidean distance dissimilarity measure. The Gini measure or G , (Equation 5.1) is used in plant population biology to summarise the distribution of plant sizes. Zero represents exact equality when all plants are the same size. Values approach a maximum of 1 (+/-) when dominance occurs at the largest or smallest height spectrum (Dixon 1993).

Equation 5.1

$$G = \frac{\sum_{i=1}^n (2i - n - 1) X_i}{(n - 1) \sum_{i=1}^n X_i}$$

where: n = number of individuals

X_i = size of the i^{th} plant

Euclidean distance or ED, (Equation 5.2) was used to estimate the temporal dissimilarities of dominant species within samples.

Equation 5.2

$$ED = \frac{1}{p} \sum \frac{(x_{ik} - x_{jk})^2}{r_k^2}$$

where: p = quantitative variables x_k ($k = 1, \dots, p$)

i and j refer to units (species or sites)

r_k is the normaliser, i.e. range of the k^{th} variable

Measures of uniformity and dissimilarity were applied to species and sites. Uniformity compares evenness in structure at each time interval whereas dissimilarity compares abundances between times.

5.2.3 Woody plant succession

Multivariate data sets of samples, species, covariables and environmental variables were analysed using CANOCO 4 (ter Braak & Šmilauer 1998) using unconstrained and constrained ordinations. Before analyses, woody species abundances were multiplied by their respective height classes to single values representing each species' total height (m) in each sample.

Woody vegetation was measured in permanent plots on either side of belt-transects before burning, i.e. plots are serially dependent. The effects of autocorrelation were eliminated from ordinations by including covariables of site identities. Detrended Correspondence Analysis (DCA) was applied to detect if species responses were linear or unimodal. The maximum gradient length was < 3 SD suggesting a weak unimodal response (ter Braak & Prentice 1988). Main trends in the species data were determined by partial Principal Components Analysis (PCA adjusted for covariables). Ordination scores were scaled using correlation

biplot by selecting inter-species correlations and dividing species scores by their standard deviation. Species were centred. To prevent skewed distribution of species abundances by which a few high scoring species unduly influence the ordination, data were transformed on a log scale.

The effects environmental gradients on species and samples assemblages were analysed by partial Redundancy Analysis (RDA adjusted for covariables). Gradients included: 1 soil texture (percentage sand), 2 accrued number of fires, 3 grass production (g m^{-2} DM), 4 fire index (Equation 5.3), 5 transition gradient (1 = open grassland, 10 = secondary thicket), 6 trees >5 m (Appendix C), 7 shrubs $>1 \leq 5$ m (Appendix C), 8 coppice <1 m (Appendix C), and 9 last management intervention (years). Rare species were excluded from samples. Ordination scores were also scaled by correlation biplot. Species data were log-transformed and centred. Forward selection was carried out for detecting autocorrelation and the statistical significance of remaining variables were judged by a Monte-Carlo permutations test.

Equation 5.3

$$Fi = \sum_{n=1}^0 (DM_{ps} \times \alpha)$$

where: Fi = fire index

DM_{ps} = previous season's dry matter yield (g m^{-2})

α = fire intensity scale 0 - 5, 0 = no burn, 5 = hot fire (clean burn)

0 = number of fires (= years) at each site

Rainfall was not included as sites occurred on the same farm and the records of seasonal rainfall apply to all sites (Section 3.4). Variable topography and soil porosity, however, means that sites on flatter, sandier areas, receive higher effective rainfall, than nearby sites on clays, with drier aspects and steeper slopes. Herbaceous vegetation was analysed separately (Chapter 6).

5.2.4 Soil fertility, particle size, organic carbon, nitrogen and sulphur tests

An oversight in monitoring was the failure not to include annual soil sampling. This was done on the assumption that soil fertility would be relatively stable for the duration of the

study. This could not be determined so the temporal patterns in soil fertility remain to be investigated. Soil sampling was only carried out at the end of the study and because data could only be interpreted over a short period, the analysis is at the end of this chapter. Soil cores were augered from the top 150 mm every fifth quadrat in each transect. The samples were submitted to the KZN Department of Agriculture's Fertilizer Advisory Service for routine analyses. Rapid procedures described by Hunter (1975) and Farina (1981) were used for Ambic-2-extractable P, K and Zn, KCl-extractable Ca, Mg, acidity and pH (KCl).

5.3 Results

5.3.1 Fire effects on *Chromolaena odorata*, grass cover and yield

5.3.1.1 Initial infestation

Parent populations fell into three density groups (Table 5.1), namely sparse (Site 2a), moderate (Site 3b) and dense (sites 2b, 4a and 4b). Density was associated with height, the exception being Site 2 supporting free-standing populations growing in the open. Plants at all sites were multi-stemmed shrubs. Initial chromolaena density and height reduced grass production. Dense stands taller than 1.5 m had no herbaceous layer. Grass dry matter yields improved with decreasing chromolaena density. Dry matter production was related to cover at each location because a simplified dry-weight-ranking technique was used ('t Mannetje & Haydock 1963).

Table 5.1 Effects of an initial burning treatment on *Chromolaena odorata* infestations, seedling recruitment, grass cover and dry matter (DM) yields, by One-Way ANOVA. Assessments were done before sites were burnt in August 1991 and again six months after treatment (MAT)

Site Qdts.		Parent infestation				Seedlings	Grass Cover		Grass DM	
	Hgt.	'before'	6 MAT ³	Mortality	6 MAT ³	'before'	6 MAT ³	'before'	6 MAT ³	
(n)	(m)	(plants m ⁻²)	(plants m ⁻²) ⁴	(%)	(plants m ⁻²) ⁴	(%)	(%)	g m ⁻²	g m ⁻²	
2a	25	1	1.2±1.9 a	0.2±0.7 a	89.7±21.0	0.3±0.8 a	76.8±5.6 a	79.6±2.0 a	1317±95 a	384±10 a
2b	25	1.5	17.7±8.5 d	6.2±4.5 b	64.0±29.4	7.0±4.9 a	3.0±7.8 b	65.8±7.2 b	31±80 b	540±72 b
3b ¹	25	2.5	5.2±4.2 bc	0.1±0.4 a	95.3±20.8	0.1±0.6 a	27.8±7.2 d	43.2±5.8 d	268±70 d	417±56 ac
4a ²	25	3	15.7±6.7 d	0.9±1.8 a	93.7±13.9	42.5±29.7 b	0.0±0.0 b	5.4± 12.6 e	0±0 b	21±55 f
4b ²	25	3	7.6±5.4 c	1.2±1.5 a	80.6±24.1	83.8±42.6 c	0.0±0.0 b	0.0±0.0 f	0±0 b	0±0 f

Numbers with same letters are not significantly different ($P>0.05$) using LSD

¹Site 3b was burnt in January 1993 by a wild fire during the height of the 1992-1994 drought

²Sites 4a and 4b were slashed and burnt, ³MAT = months after treatment, ⁴coppice < 1 m

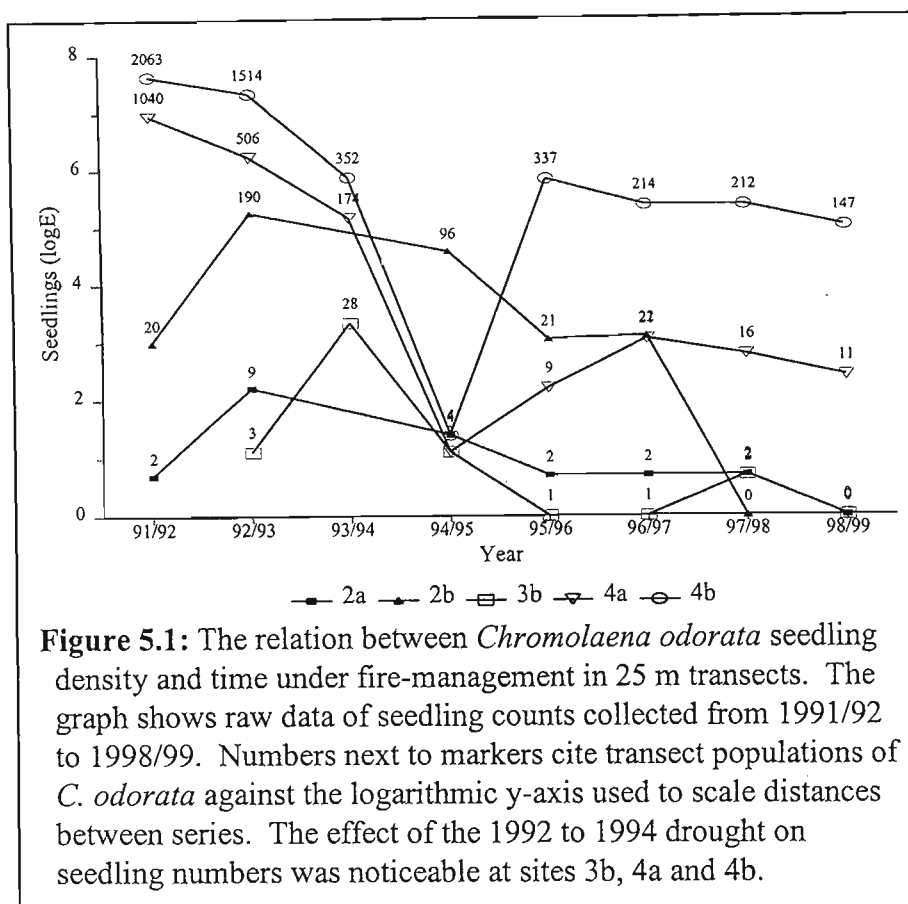
Chromolaena was sensitive to fire. The initial fires caused high mortalities at all sites, despite chromolaena density and height, slashed or burnt in its natural state. The minimum grass dry

mass for controlling standing chromolaena was between 2.7 t ha⁻¹ (Site 3b) and 0.3 t ha⁻¹ (Site 2b), where average mortality was 64%. Sites 4a and 4b did not burn in their natural state, even when forced to burn by spreading and igniting hay beneath the infestations. This showed that starting fires inside chromolaena thicket infestations (3 m high, >7 stumps m⁻²) was difficult due to the lack of fine fuels needed to ignite living material, or preheat it, into a combustible state. The two sites were then slashed and air dried *in situ* before burning in comparison to the other sites which were burnt without pre-treatment. Chromolaena coppices profusely (Erasmus & van Staden 1986, 1987; Slaats 1995), yet mortalities were not significantly different on the whole, showing that slashing had little effect in increasing the susceptibility of chromolaena to fires.

5.3.1.2 Seedling and shrub population dynamics

Seedling populations at sites 2a, 2b and 3b declined steadily under annual burns (Figure 5.1). Infestations of sparse (2a), moderate (3b) and dense (2b) chromolaena were eradicated over eight years by repeatedly burning plants in their natural state. Copious numbers of chromolaena seedlings emerged at Site 4 after parent populations were slashed and burnt. Drought conditions from 1992 to 1994 (Figs. 3.1 to 3.3) affected chromolaena seedling populations. Once above average rainfall conditions had returned seedling populations at sites 4a and 4b increased. Seedlings were hand-removed at Site 4a in 1991/92 while seedlings at 4b were left. Site 4b was exposed to the same fires as Site 4a but only two fires entered the site. Prolific seedling establishment occurred in 4b with the resumption of normal rainfall patterns in 1995/96. Seedlings became shrubs in 1996/97 and the decline in shrub numbers was due to self-thinning. Site 4b in 1998/99 was again dominated by chromolaena.

Drought and fire both suppressed chromolaena seedlings. Judging from the rates of decline at sites 4a and 4b during the drought years, the influence of drought on seedling survival appears temporarily much stronger than that of recurring fire. Individual fires killed seedlings that emerged during the preceding growing season in sites 2a, 2b and 3b, but annual fires collectively caused gradual declines in chromolaena seedling resurgence.



5.3.1.3 Infestations at the end of the study

Annual fires prevented chromolaena reestablishing in four out of five sites between 1991 and 1999 (Table 5.2). Site 4b reverted to dense thicket due to prolific seedling regeneration. Seedling dominance after the drought (Figure 5.1) continued to prevent grass establishment. Insufficient fine fuels contributed to the inability of fire penetrating thicket infestations.

Table 5.2 Final (1997/98) outcomes of annual burning treatments on *Chromolaena odorata* populations, grass covers and dry matter (DM) yields by One-Way ANOVA

Site	Qdts.	Final infestation density & structure				Grass		Grass end-start differences	
		Total	Hgt. <1 m	Hgt. 1-2 m	Hgt. 2-3 m	Cover	Dry Matter	Cover	Dry Matter
	(n)	(plants m ⁻²)	(plants m ⁻²)	(plants m ⁻²)	(plants m ⁻²)	(%)	(g m ⁻²)	(%)	(g m ⁻²)
2a ¹	25	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	94.4±10.2 a	632±69 a	17.6±9.3 a	-685±90 a
2b ¹	25	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	100.0±0.0 a	1480±0 b	97.0±7.8 b	1449±80 b
3b ²	25	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	0.0±0.0 a	88.4±9.8 a	857±95 d	60.6±11.8 d	589±114 c
4a ^{1,3}	25	0.4±1.4 a	0.4±1.4 a	0.0±0.0 a	0.0±0.0 a	80.6±22.7 c	758±213 df	80.6±22.7 e	758±213 f
4b ^{1,4}	25	8.5±8.1 b	5.5±6.5 b	0.0±0.0 a	3.0±3.3 b	15.1±19.0 d	39±49 g	15.1±19.0 a	39±49 g

Numbers with same letters are not significantly different ($P>0.05$) using LSD

¹ & ² Accumulated number of burns = 6 & 5, ^{3/4} slash & burn & ³ hand pull seedlings in the first year

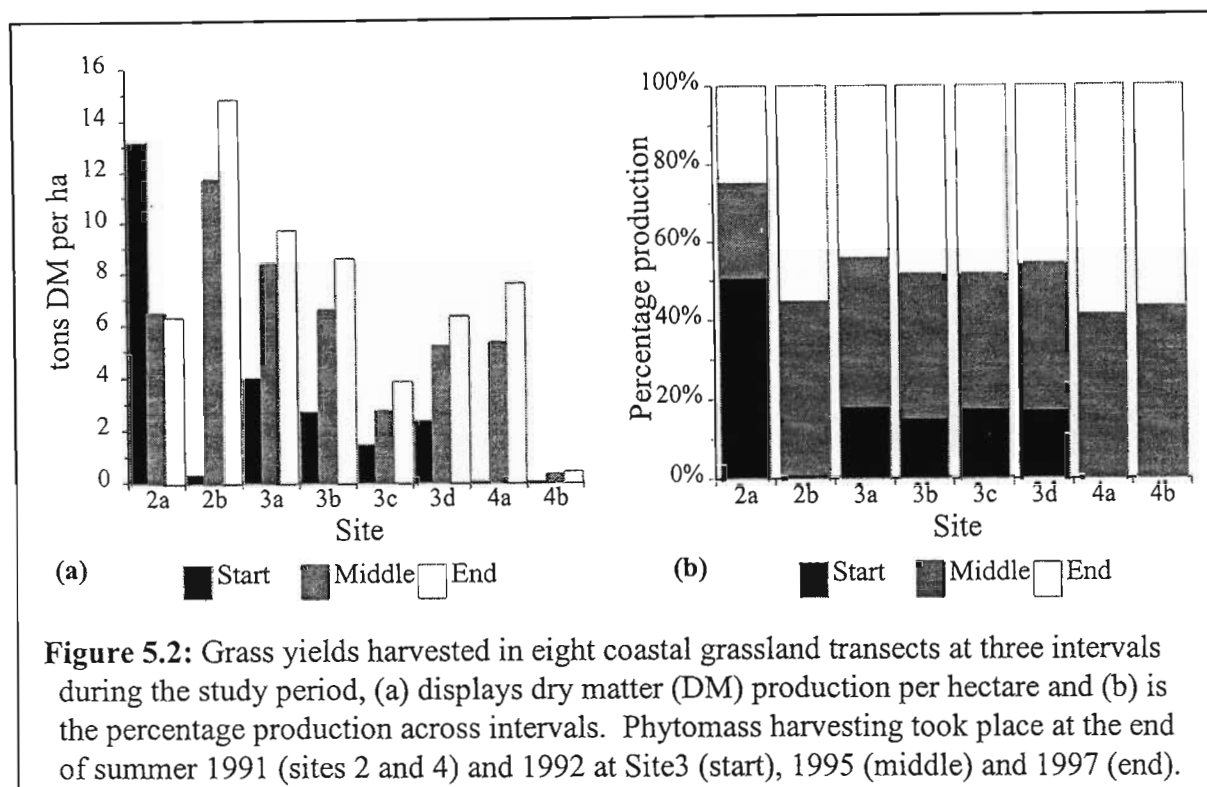
Grass cover and yield improved at all sites. The exception was site 2a, moribund in 1990/91, dropped from 13 t ha⁻¹ in 1990/91 to 6 t ha⁻¹ in 1997/98 (Table 5.2, Figure 5.2). The most striking recovery was at Site 2b. Although the efficacy of fire on chromolaena mortality was below average after the initial burning treatment (Table 5.1), grass yield went from 0.3 t ha⁻¹ to more than 5 t ha⁻¹. At the end of the study Site 2b recorded 100% grass cover in every quadrat and dry matter production amounted to nearly 15 t ha⁻¹. The differences between before and after cover at 2a and 4b were not significant. Site 2a had almost full grass cover initially, while at 4b grasses were absent. Site 4b failed to rehabilitate and maintained low grass cover and high chromolaena populations. The divergence between 4a and 4b from 1990 to 1998 was due to a single operation removing seedlings in 4a in the same season as the initial burning treatment, promoting the establishment of grass at 4a only (Table 5.1).

Differences in dry matter yields occurred over time and location (Tables 5.1 and 5.2).

Dominant grasses at Site 2a (Table 5.3) characterised the veld as short-tufted (≤ 1 m).

Indicator species remained unchanged for the duration of the study, except *Aristida junciformis* which was replaced by *Panicum dregeanum*. Annual grass production after the initial burn had removed moribund material remained constant at 6 t ha⁻¹ (Figure 5.2a).

In 1990 2b was dominated by 1.5 m chromolaena thickets that suppressed grass cover and yield (Table 5.1, Figure 5.2a). Site 2b occurred in a natural drainage line where soils are loamy-sands. *Setaria sphacelata*, *Ischaemum fasciculatum* and *Themeda triandra* remained the dominant grasses throughout the study. The species in question may be resilient under short, dense chromolaena in sandy soils that are not moisture-stressed. Species compositions are shifting towards a grass-sedge community (Figure 6.7). The sedges *Fuirena pubescens*, *Mariscus solidus*, *Pycreus macranthus* and *Scleria melanomphala* were as abundant as grass, possibly accounting for half the biomass. This helps to explain why site 2b, having similar indicator grasses as 2a (Table 5.3), produced more than double the phytomass (Figure 5.2a).



Hyparrhenia tamba at Site 3 on Glenrosa soils characterised the veld as tall-tufted (2 m). In the slash and burn plots Site 4a improved from zero grass cover in 1990 to 7.5 t ha^{-1} in the 1997/98 growing season. *Oplismenus hirtellus* and *Panicum maximum* established in the partially wooded area after the burn in 1990 but were rapidly replaced by the ruderal grasses *Eragrostis curvula*, *H. tamba* and *S. sphacelata* with increasing numbers of fires. Site 4a was classed as an intermediate-tufted (1-1.5 m) ruderal grassland community. Site 4b on other hand was unable to produce significant quantities of fine fuel due to the persistence of chromolaena. Here *Oplismenus hirtellus* was the dominant grass at the end of the study.

Although fires cannot easily be started in dense chromolaena infestations, because of the lack of fine fuels (grasses and herbs), under certain conditions chromolaena was highly flammable. Observations on infestations outside the study area at sites 3 and 4 suggested that when grass head fires converged on thickets they burned with intense heat. Dense infestations lacking grass cover were most combustible when burning occurred when rainfall over the past 30 days was less than 8% of the previous 12 months accumulated rainfall.

Table 5.3 Temporal matrix of indicator grasses in order of importance, in five coastal grassland communities affected by *Chromolaena odorata*

Site	START (1990/91)		MIDDLE (1994/95)		END (1997/98)	
	Species	Freq. %	Species	Freq. %	Species	Freq. %
2a	<i>Ischaemum fasciculatum</i>	100	<i>I. fasciculatum</i>	92	<i>I. fasciculatum</i>	92
	<i>Aristida junciformis</i>	92	<i>Panicum dregeanum</i>	88	<i>P. dregeanum</i>	76
	<i>Setaria sphacelata</i>	76	<i>S. sphacelata</i>	80	<i>S. sphacelata</i>	60
2b	<i>I. fasciculatum</i>	88	<i>S. sphacelata</i>	100	<i>S. sphacelata</i>	100
	<i>S. sphacelata</i>	76	<i>Themeda triandra</i>	84	<i>I. fasciculatum</i>	88
	<i>T. triandra</i>	64	<i>I. fasciculatum</i>	80	<i>T. triandra</i>	60
3b	<i>S. sphacelata</i>	64	<i>E. curvula</i>	80	<i>H. tamba</i>	100
	<i>E. curvula</i>	44	<i>H. tamba</i>	72	<i>E. curvula</i>	84
	<i>H. tamba</i>	16	<i>S. sphacelata</i>	60	<i>S. sphacelata</i>	64
4a	<i>Oplismenus hirtellus</i>	12	<i>E. curvula</i>	80	<i>E. curvula</i>	100
	<i>Panicum maximum</i>	12	<i>H. tamba</i>	72	<i>H. tamba</i>	96
	<i>E. curvula</i>	12	<i>S. sphacelata</i>	60	<i>S. sphacelata</i>	40
4b	-	-	<i>P. maximum</i>	52	<i>O. hirtellus</i>	44
	-	-	<i>E. curvula</i>	32	<i>E. curvula</i>	44
	-	-	<i>O. hirtellus</i>	20	<i>H. tamba</i>	12

5.3.2 Fire effects on other woody species

Baseline data in 1990 (1992 at 3b) describe plant successions over a 24-26 year period since previous fire at five coastal grassland sites (Appendix C1 to C4). At the beginning of the study, uniformities in the structure of indigenous species at most sites were skewed in the direction of dominance at smaller height classes. An exception to this was site 4b that displayed a normal distribution of height classes. *Chromolaena* was the dominant species at all sites. Sites 3 and 4 were visibly different in 1990 compared with the same area in 1966, but less so between 1966 and 1937 (Plate 1, f to h). Site 2, however, was mowed in 1988, the previous disturbance prior to this was a fire that occurred in 1960. The sites on glacial deposits (Glenrosa soil form) were strongly seral to forest in the absence of fire. Sites on marine deposits (regic sands) remained open grassland with *chromolaena*.

Site 2a (regic sands) had only three indigenous woody species, *Albizia adianthifolia*, *Brachylaena discolor* and *Syzygium cordatum*, all less than one metre in height (Appendix C1). Site 2b had no indigenous species. Although *chromolaena* showed variation in density it never grew above 1.5 m tall. This may be because of mowing in 1988. The general area become more woody between 1937 and 1990 (Plate 1, c to e), yet the immediate vicinity of 2a and 2b remained open.

Sites 3 and 4 (on tillite soils) were adjacent communities on the same hill slope. Both sites

were colonised by a variety of indigenous woody species with Site 4 in a more advanced successional state. At Site 3b 12 indigenous species were recorded comprising 91 individuals. Canopy height was 3-5 m with, in order of dominance, *Heteropyxis natalensis*, *Combretum molle* and *Protorhus longifolia*. The subcanopy (1-3 m) was occupied by *Dichrostachys cinerea* and *H. natalensis*. Seedling recruitment was highest for *C. molle* (Appendix C2).

Site 4a had 125 individuals from 21 indigenous species. The canopy was also recorded between 3-5 m with *C. molle* and *Trimeria grandifolia* as emergent species. Dominants in the canopy and subcanopy layers were *H. natalensis*, *D. cinerea* and *C. molle*. The most abundant seedlings were *Maytenus undata*, *P. longifolia* and *Euphorbia triangularis* with the latter species also occurring in the subcanopy (Appendix C3). Site 4b had 51 individuals from 13 species. *Combretum molle* and *D. cinerea* dominated in all layers, excepting *Maytenus undata* which dominated the seedling layer (Appendix C4).

Key species (bold print in Appendix C) showed marked differences in structure over time, as indicated by gradients in their respective uniformity indices. Although negatively skewed initially, distortion in favour of seedlings or regrowth at sites exposed to recurring fires approached the lower limit by the end of the study. Exceptions to this were *C. molle* and *H. natalensis* which displayed marginal fire resistance at sites 3b and 4a. Uniformity indices at Site 4b showed trends bordering on equality in key species in the absence of damaging fires. This is not surprising, three of the five were aliens, namely chromolaena, *Solanum mauritianum* (bugweed) and *Lantana camara* (lantana), the combined densities of which prevented fires from entering owing to the absence of fine fuel.

Uniformity was supported by dissimilarity values. Fire intensity and frequency had an obvious impact on tree heights. Fire, or suppression by alien species, both affected recruitment and growth of many indigenous species. *Psidium guajava* (guava) and *Scolopia zeyheri* in 3b and 4b where the only two species that displayed similarity throughout the study period. Fire killed guava stems but stimulated coppice that grew a metre in height between annual burns. *Scolopia zeyheri* grew in the absence of fire in Site 4b but was fire-sensitive in 4a.

Phanerophytic fire responses (Rutherford & Westfall 1994) were observed. Seedlings and saplings up to 3 m were excluded as most woody species display fire sensitivity below a critical height (Hochberg *et al.* 1994). The same abbreviations of Rutherford and Westfall (1994) were used, where: P=phanerophyte, Ch=chamaephyte, T=therophyte, hyphen separates the response variable from the control, F=fire as a determinant:

1. Fire-tolerant phanerophytes (P-FP): *C. molle*, *H. natalensis*, *S. cordatum*;
2. Semi fire-tolerant phanerophytes (P-FCh), i.e. survive as 0.5 m coppice under annual burning: *D. cinerea*, lantana, *M. undata*, *P. guajava*, bugweed;
3. Fire-intolerant phanerophytes (P-FT), i.e. plants were killed by fire and last only one season under annual burning: most species fell into this group but examples where larger species died after the first fire are chromolaena, *Canthium inerme*, *P. longifolia*.

Levels of fire-tolerance (P-FP and P-FCh) occurred in savanna species, namely *C. molle*, *D. cinerea* and *H. natalensis* which may have persisted from the open grassland/woodland period in 1966 (Plate 1). Recruitment of these species was not accounted for in heavily shaded sites (4a and 4b) at the time of the first census in 1990, confirming their requirement for more open conditions. Shading as opposed to fire appears determinantal to the persistence of savanna species in forest, whereas forest precursors, e.g. *P. longifolia*, only established in absence of fire. Savanna species are perhaps an intermediate stage between open grassland and closed canopy forest in coastal grasslands that are not burnt.

5.3.3 Woody plant succession

5.3.3.1 Indirect gradient analysis

The results of partial PCA (Figs. 5.3 and 5.4) summarises woody plant successions in five coastal grassland communities. Site 2 was analysed separately from sites 3 and 4.

Exploratory data analysis showed sites that were different compositionally were clumped together, with eigenvalues of the first axis either very high ($\lambda_1 = >0.7$), or very low ($\lambda_1 = <0.1$), depending on whether the species data were transformed or not.

Site 2 was on open grassland on regic sands where only four woody species were recorded throughout the study period (Figure 5.3). The first two principal components captured 95% of the overall variation in the species data ($\lambda_1 = 0.586$, $\lambda_2 = 0.169$). Inertia in the species data after fitting covariables was 0.797, 74% of which was explained by the first axis. Covariables

explained 20% of the total inertia ($\frac{1-0.797}{1} \times 100$).

Chromolaena dominated the ordination (Figure 5.3) while *Albizia adiantifolia* was the highest ranking species on the second axis. Site 2a was associated with tree seedlings and sparse chromolaena whilst Site 2b was monospecific in 1990. Both sites followed similar successional trajectories away from chromolaena domination between 1990 and 1998. Indigenous tree seedlings and regrowth influenced the sample trajectory of Site 2a where they persisted under prevailing conditions. Both sites did not have chromolaena at the end of the study.

Woody plant succession by partial PCA at sites 3 and 4 (Figure 5.4) on Glenrosa soils accounted for 42.8% of the overall variation in the species data on the first principal component ($\lambda_1 = 0.267$). The second axis provided 15.3% of the remaining variation ($\lambda_2 = 0.096$). Covariables explained 37.5% of the total inertia in the species data. In 1966 sites 3 and 4 were both open grassland (Plate 1). In 1990 the sites had moderate (Site 3) and dense (sites 4a and 4b) stands of chromolaena with a mixture of savanna and forest tree species. *Protorhus longifolia* and *Solanum mauritianum* were the two dominant species on the first axis. Sites responded differently to internal factors between 1990 and 1998.

Tree and shrub encroachment at Site 3b in 1992 was less advanced than Site 4a in 1990, although both sites had many species in common. More open conditions were maintained at Site 3 throughout the study. *Combretum molle*, *D. cinerea* and *H. natalensis* remained the dominant indigenous species but their structural dynamics were altered over time. The population of plants less than 3 m tall dropped from 1 359 to 97 between 1992 and 1998 (Appendix C2). Populations larger than 3 m went from 22 to 7 over the same period. The successional trajectory (Figure 5.4) shows the diminishing influence of woody species between 1992 and 1998. Succulents (*Aloe arborescens*, *A. maculata*), half-woody shrubs (*Athrixia phyllicoides*, *Lippia javanica*), assorted tree coppice and the lack of chromolaena characterised the differences between start and end times. Large populations of earlier dominants persisted at heights less than 1 m. Larger specimens were widely spaced in the permanent plot at the end of the study. Alien woody species had a little impact at Site 3b after 1995. *Psidium guajava* occurred as a single plant that produced vigorous coppice after fire.

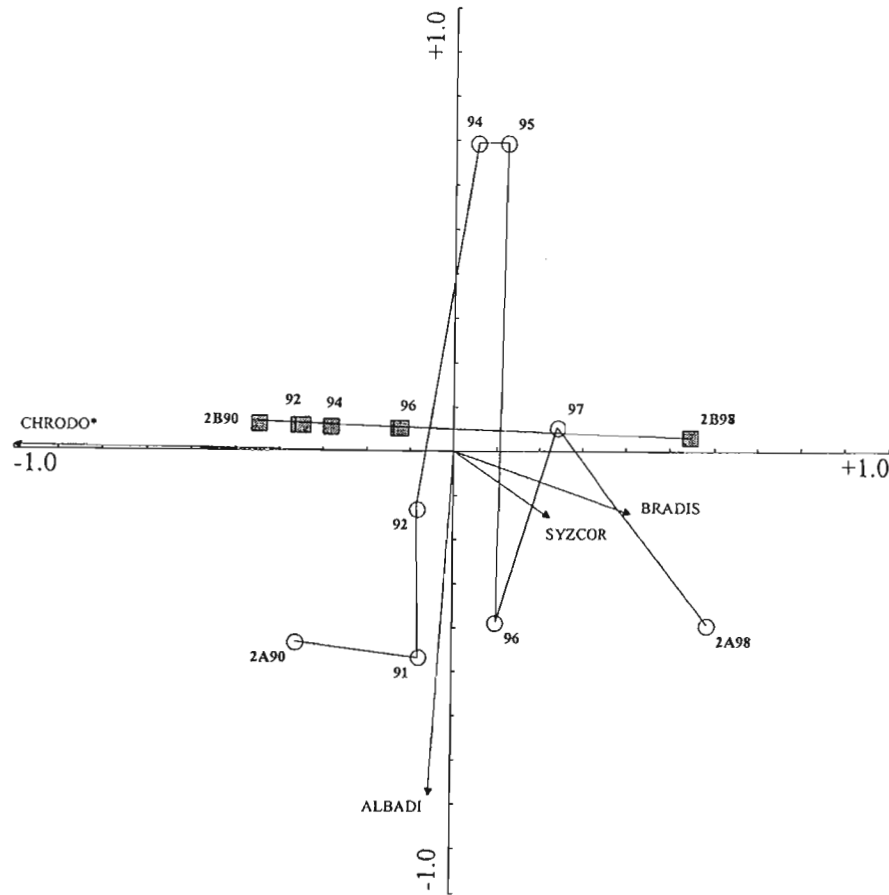


Figure 5.3: Correlation biplot based on partial Principal Components Analysis of serial woody plant dynamics in coastal grasslands on regic sands. Samples are presented as a number followed by a letter, e.g. 2A = Site 2A, followed by a two digit number representing the biological year in which the site was sampled, e.g. 90 = 1990. The ordination shows successional trajectories (lines) of samples in dense (■) and sparse (○) *Chromolaena odorata* infestations responding to underlying environmental gradients along the first principal component. Arrows indicate the direction in which species abundances increase and their rates of change. The fit for species is additional to the fit due to covariables. The alien species is denoted by an asterisk. Species accounted for: ALBADI = *Albizia adianthifolia*, BRADIS = *Brachylaena discolor*, CHRODO* = *Chromolaena odorata*, SYZCOR = *Syzygium cordatum*. Eigenvalues and residual variance in species data along the first two axes are: $\lambda_1 = 0.586$ (73.5%), $\lambda_2 = 0.169$ (94.7%). Sum of all unconstrained eigenvalues after fitting covariables amounted to 0.797.

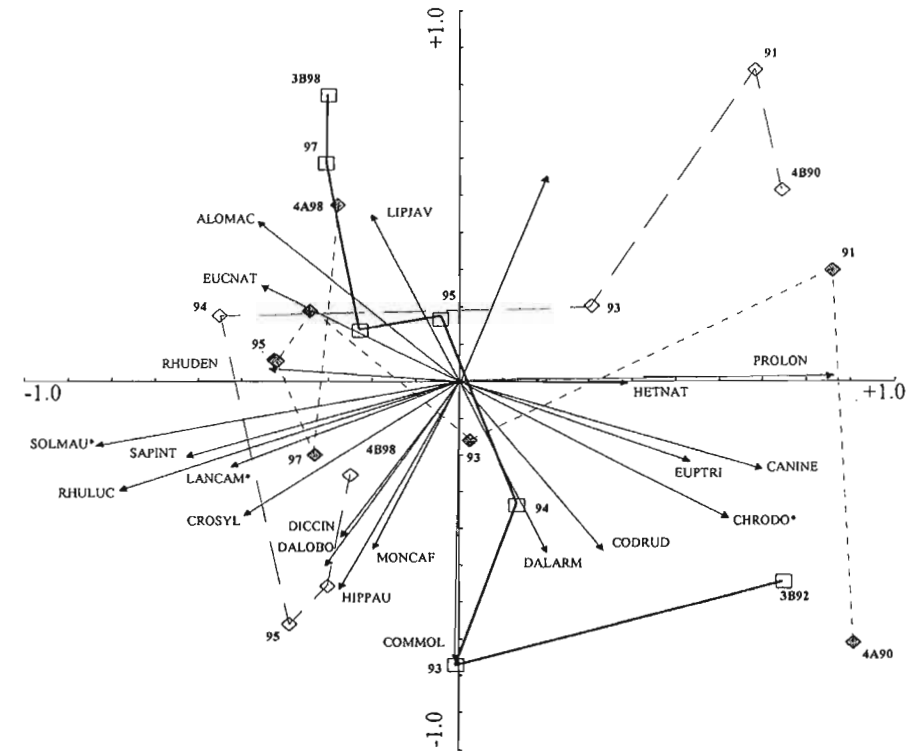


Figure 5.4: Woody plant dynamics in three coastal grassland communities on Glenrosa soils between 1990 and 1998 by partial by partial Principal Components Analysis. Samples are presented as a number followed by a letter, e.g. 4A = Site 4A, followed by a two digit number representing the biological year in which the site was sampled, e.g. 90 = 1990. The ordination shows successional trajectories (lines) of samples in dense (◆, ◇) and moderate (□) *Chromolaena odorata* infestations responding to underlying environmental gradients. Arrows indicate the direction in which species abundances increase and their rates of change. Alien species are denoted by asterisks. Species accounted for: ALOMAC = *Aloe maculata*, CANINE = *Canthium inerme*, CHRODO* = *Chromolaena odorata*, CODRUD = *Cordia rudis*, COMMOL = *Combretum molle*, CROSYL = *Croton sylvaticus*, DALARM = *Dalbergia armata*, DALOBO = *Dalbergia obovata*, DICCIN = *Dichrostachys cinerea*, EUCNAT = *Euclea natalensis* subsp. *natalensis*, EUPTRI = *Euphorbia triangularis*, HETNAT = *Heteropyxis natalensis*, HIPPO = *Hippobromus pauciflorus*, LANCAM* = *Lantana camara*, LIPJAV = *Lippia javanica*, MONCAF = *Monanthotaxis caffra*, PROTON = *Protosorus longifolia*, RHUDEN = *Rhus dentata*, RHULUC = *Rhus lucida*, SAPINT = *Sapium intergirrimum*, SOLMAU* = *Solanum mauritianum*. Eigenvalues and residual percentage variance in species data along the first two axes are $\lambda_1 = 0.267$ (42.8%) and $\lambda_2 = 0.096$ (58.1%). Sum of all unconstrained eigenvalues after fitting covariables amounted to 0.625.

In 1990 both sites 4a and 4b had thickets of chromolaena and several forest precursor species. Between 1990 and 1998 Site 4a shifted from a thicket state to a patchy community similar to Site 3b. Increasing populations of bugweed (Appendix C3) influenced sample trajectories from 1994 under conditions of diminishing chromolaena. Site 4b showed similar sample trajectories to Site 4a but was unable to advance beyond the state dominated by chromolaena, lantana and bugweed.

5.3.3.2 *Direct gradient analysis*

A partial RDA without forward selection was conducted to first ascertain how the environmental variables were plotted in relation to samples and species data (Figure 5.5). Eigenvalues of the first and second axis were 0.176 and 0.052, or 64% of the residual inertia. Samples were highly variable from the outset. Two sites occurred on regic sands (2a and 2b) and three sites occurred on Glenrosa (3b, 4a and 4b). The percentage of sand was variable across location but remained constant over time. Sand was omitted because it had negligible variance after fitting covariables. The influence of soil form on species-environmental relations could not, therefore, be detected. Secondly, woody plants other than chromolaena were rare in grasslands on regic sands. The vegetation gradient was disproportionate, sandy grasslands were open while Glenrosa samples were closed or partially closed. Species other than chromolaena were unique to location, i.e. soil form. While comparison of sites through direct ordination are insurmountable, the study of within-community change with general *post hoc* conclusions was the primary objective.

The value for trees in sample 4A90, i.e. Site 4a in 1990 (Figure 5.5), was more than three standard deviation units from the mean, i.e. an outlier. Nevertheless, it was not removed. This sample contained species data of secondary woody succession gradient that was more advanced than any other plot in the study (Appendix C). The variable 'shrubs' in sample 4B95 was also an outlier, with a leverage of >4 SD. It was dominated by dense chromolaena coppice and had 2 to 5 times the value for shrubs of all sites. Environmental variables with multiple collinearity (variance inflation factors >20) were fire, grass, transition gradient and shrubs.

The direction of increasing numbers of fires was synonymous with increasing grass. Fire index was the product of grass and fire (Equation 5.3), therefore all three variables convey the influence of the same determinant, i.e. fire. The transition gradient increasing in the direction of secondary thicket was negatively correlated with the numbers of fires, i.e. fire was also associated with open vegetation. The management variable can be viewed as a successional gradient pointing in the direction of increasing elapsed time since the last intervention (neglect). Trees and shrubs increased under periods of lengthy neglect and were associated with the transitional gradient signifying transformation from open grassland to alien vegetation. Sites on regic sands (Site 2) were positioned independently of the management gradient and tree succession throughout the study. Sites on Glenrosa soils (sites 3 and 4) were associated with shrub and tree dominance under increasing management absence. With implementation of burning regimes sites 3 and 4 followed pathways to more open conditions associated with coppice and secondary woody alien invaders.

Under forward selection, management was the only variable that contributed to the minimal model at the 5% level (Table 5.4). Fire contributed to a lesser extent ($P < 0.1$) but was included in the canonical ordination of woody plant data (Figure 5.6). Fire was quantitatively evaluated whereas management was based on visual ratings. Fire is therefore the principal determinant and being collinear with grass, indicated open conditions made up of fire resistant species.

Table 5.4 Marginal and conditional effects of environmental variables after forward selection. The statistical significance of each variable was judged by a Monte-Carlo permutation test and their significance are given in the P- and F-value columns

Marginal Effects ¹			Conditional Effects ²				
Variable	Var.N	Lambda-1	Variable	Var.N	Lambda-A	P	F
Management	9	0.16	Management	9	0.16	0.05	6.88
Fire	2	0.13	Fire	2	0.05	0.09	2.26
Thickets	5	0.13	Coppice	8	0.03	0.37	1.49
Shrubs	7	0.1	Con	5	0.02	0.14	1.27
FireI	4	0.08	Tree	6	0.02	0.29	0.93
Tree	6	0.08	FireI	4	0.02	0.76	0.76
Coppice	8	0.07	Shrubs	7	0.02	0.16	1.30
Grass	3	0.05	Grass	3	0.01	0.82	0.53

¹ Environmental variables occur in order of the variance they explain singularly (lambda-1)

² Environmental variables occur in order of their inclusion in the model, with additional variance each variable explains at the time of inclusion (lambda-A)

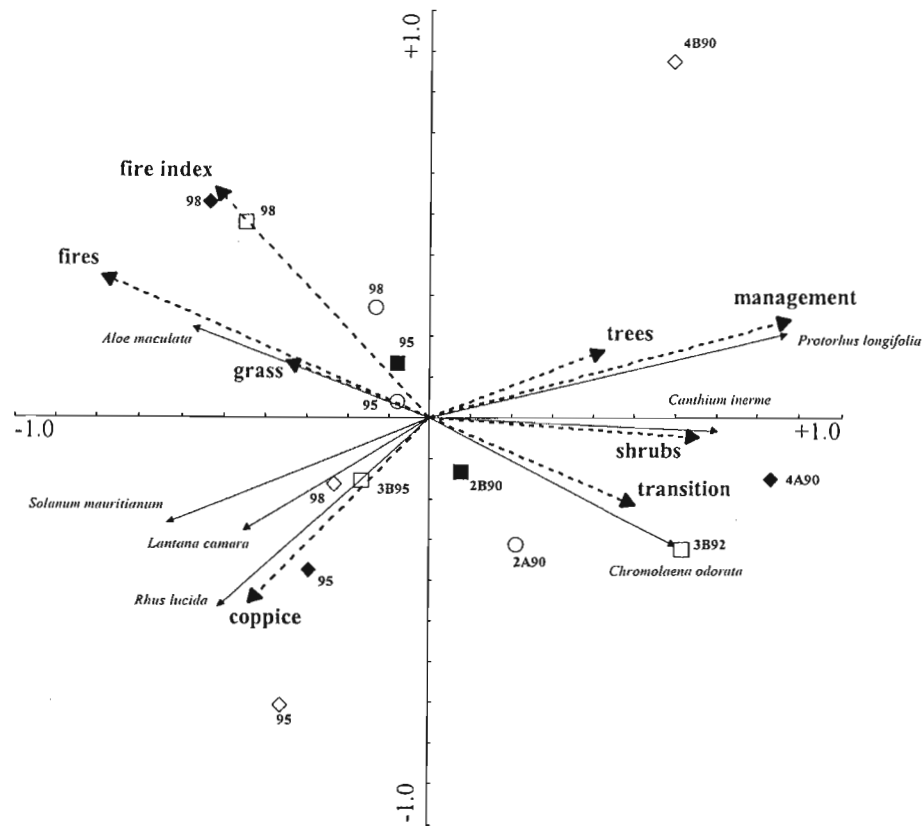


Figure 5.5: Triplot based on partial Redundancy Analysis of woody plant dynamics in relation to all measured environmental gradients in five coastal grassland sites at three intervals between 1990 and 1998. Percentage sand of regic sands (○, ■) and Glenrosa (◆, ◇, □) samples had negligible variance after fitting covariables and was ignored. Sites had initial (1990) dense (◆, ◇, ■), moderate (□) or sparse (○) *Chromolaena odorata* infestations. Arrows indicate the direction in which species and environmental variables increase and their rates of change. The fit for species is additional to the fit due of covariables. Alien species are denoted by asterisks. Trees, coppice and management were the only external variables with variance inflation factors < 20. Eigenvalues: $\lambda_1 = 0.176$, $\lambda_2 = 0.052$. Sum of all unconstrained and canonical axes amounted to 0.355 and 0.332. First axis residual inertia was 49.4% and 50.3% was explained by environmental variables.

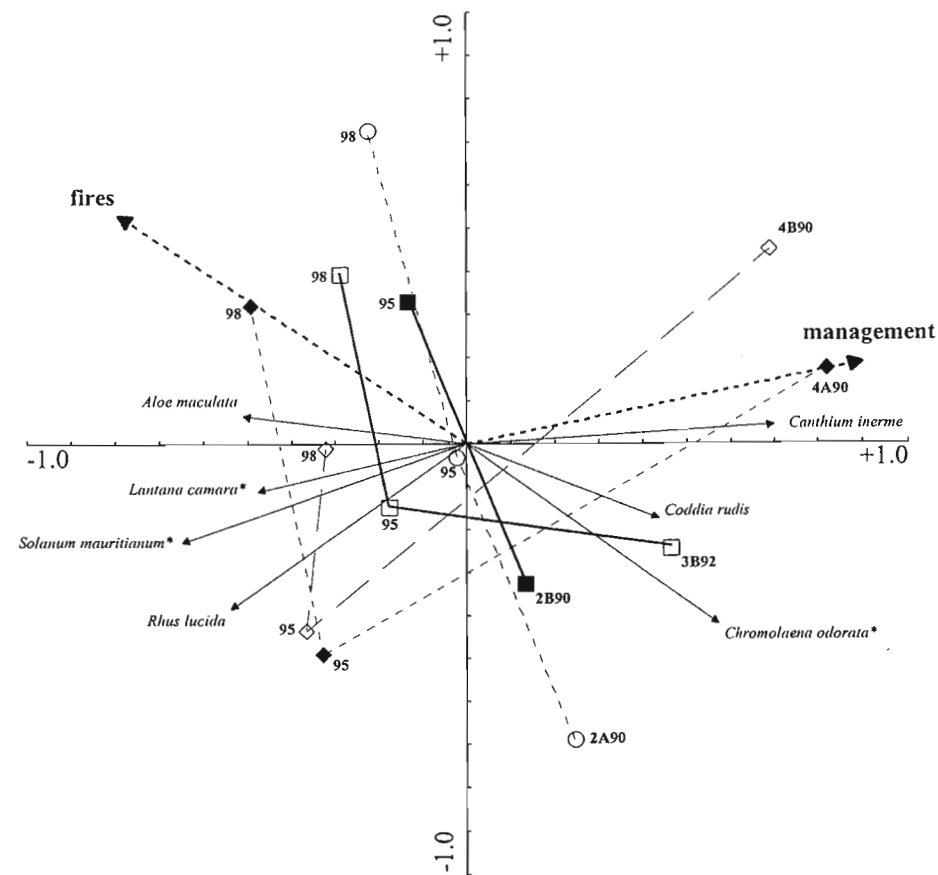


Figure 5.6: Partial Redundancy Analysis of the minimal model ($P < 0.1$) fitting period of management neglect and fire regimes to woody plant data in five coastal grassland sites at three intervals between 1990 and 1998. The ordination shows successional trajectories (broken or solid lines) of samples in dense (◆, ◇, ■), moderate (□) and sparse (○) *Chromolaena odorata* infestations. Arrows indicate the direction in which indicator species increase and their rates of change. The fit for species is additional to the fit due to covariables. Alien species are denoted by asterisks. Eigenvalues of the first two canonical axes are 0.17 and 0.041 explaining 59.4% of the residual inertia and 100% of the environmental relation in the species data. Covariables explained 0.645 (65%) of the total inertia, 0.211 is by environmental variables and 0.144 of the remaining inertia is unexplained.

The partial RDA of the minimal model (Figure 5.6) showed that covariables explained 0.645 (64.5%) of the inertia in the species data. Additional inertia explained by management absences and the number of fires was 21.1%. The remaining 14.4% is unexplained. Coastal grasslands became invaded by woody vegetation when they were not burnt, highlighted by the magnitude of the transition from open to closed canopy communities. The direction of forest succession was negatively correlated to secondary weedy communities caused by fire intervention, however, chromolaena was sensitive to fire. Forest succession caused shading that was detrimental to sward survival.

Sites on regic sands appeared more resistant to forest succession than sites on Glenrosa soils, but equally susceptible to chromolaena invasion. Under controlled burning, sites on regic sands recovered more rapidly than Glenrosa sites. Bugweed and lantana were important invaders of bare ground where the density of chromolaena had been reduced by fire. Bugweed trees were unable to coexist with increasing chromolaena populations when natural grasses failed to establish, thereby allowing fire-sensitive chromolaena to reestablish.

The potential states showed that although thickets of chromolaena established on more than one soil type, thickets on regic sands did not develop with a suite of other woody species. Scrub forest did not pass through thicket and become open grassland. Open grassland succeeding to savanna and forest on sedimentary soils showed no signs of reverting to open grassland in response to fire (Plate 4). Annual fires may not halt the persistence of savanna trees once they have established in coastal grassland communities.

Fire frequency caused mortality of forest precursor species (e.g. *P. longifolia*) and topkill of savanna species (e.g. *D. cinerea*). Grass production increased over time at sites with woody plant dominance once annual burning was carried out. The implications of failure to maintain burning means sites will revert back to weedy scrub forest dominated by chromolaena, lantana and bugweed, with chromolaena, emerging as the dominant species in the long term.

5.3.4 Soil fertility, texture, carbon and nitrogen contents at the end of the study

Soil analyses showed that Glenrosa soils had lower sample densities, i.e. higher clay contents, than regic sands (Table 5.5). Inferences about recurrent fires on the results of the soil

analyses will therefore be overshadowed by soil form. Sample density is dependent on clay content and organic matter, the latter a determinant of total nitrogen (Table 5.6). The relation between clay and organic matter to sample density of coastal grassland soils is presented below:

$$\text{Sample density (g ml}^{-1}\text{)} = 1.277 - (0.019 \times \text{clay \%}) + (0.08 \times \text{OM \%})$$

$$\text{df } 8, F \text{ } 7.73, P < 0.02, r^2 = 0.721$$

All the sites were deficient in P (Table 5.5), a trend found in most African topsoils (Wild 1988). Phosphate levels of about 2-3 are normally found in grassland in KZN (Dr N Miles pers. comm., KZN Department of Agriculture, Private Bag X9059, Pietermaritzburg 3200). In this respect Glenrosa soils were considered normal, but regic sands were below normal.

Cation exchange levels were also higher in Glenrosa (tillite) soils than regic sands, although all sites had adequate levels of K, Ca and Mg. Total cations or CEC were lower on sandy sites than the tillite soils despite pH being equal across sites. Exchangeable acidity showed sands had higher levels of aluminium, confirmed by the acid saturation levels

$\left(\frac{\text{exchangeable acidity}}{\text{total cations}} \times \frac{100}{1} \right)$. Sites 2a, 2b and 3b, however, were the only sites that were significantly different in H^+ and Al^+ , while 1a, 2a and 2b were different as regarding acid saturation percentages (see Figure 5.7). Manganese in acid soils is often found at levels that are toxic to plants ($>50 \text{ mg l}^{-1}$), however, Ma in coastal grassland sites were well within these limits.

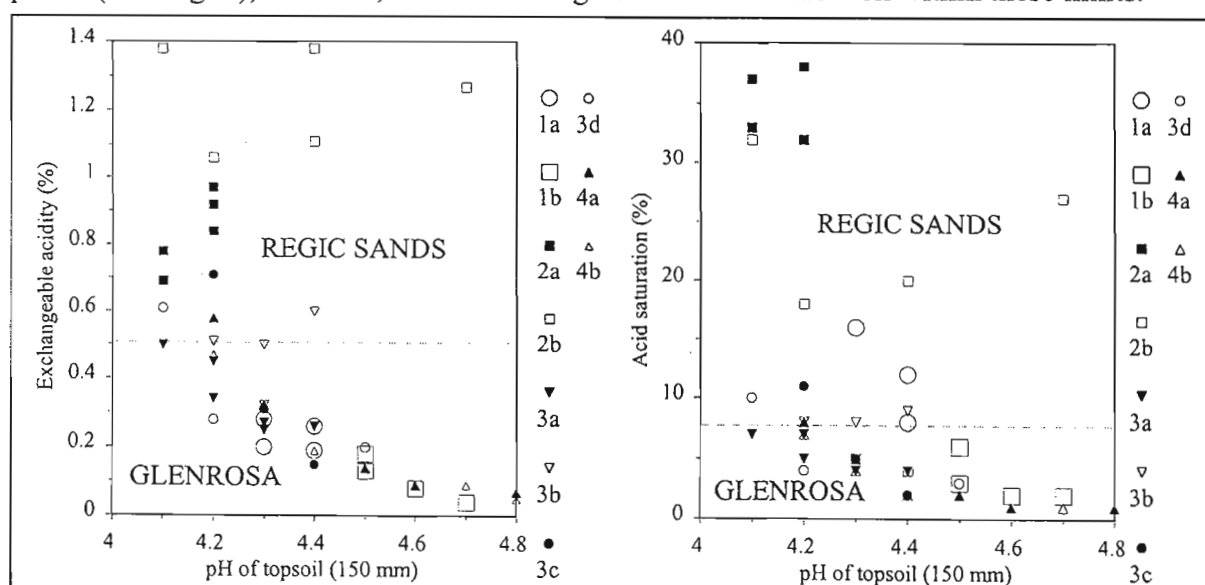


Figure 5.7 Exchangeable acidity (H^+ & Al^+) and acid saturation as a proportion of the total cations (CEC) in relation to pH levels in the topsoil of coastal grasslands sites (1a to 4b) studied. Dashed line indicates mean range of y-axis values of the Glenrosa samples.

Table 5.5 Results of soil fertility tests from the coastal grasslands studied. Soil samples were taken at the end of the study period from every fifth quadrat along the transect profile. Means were compared using One-way ANOVA

Site	Soil Form	Sample density ¹ g ml ⁻¹	P ¹ mg l ⁻¹	K ¹ mg l ⁻¹	Ca ¹ mg l ⁻¹	Mg ¹ mg l ⁻¹	Exch. Acid ¹ cmol _c l ⁻¹	Total Cations ¹ cmol _c l ⁻¹	Acid Sat. ¹ %	pH ¹ KCL	Zn ¹ mg l ⁻¹	Mn ¹ mg l ⁻¹
Site 1a	regic sand	1.25±0.02 _g	1±0 _{ab}	62±8 _a	151±35 _{ab}	100±16 _a	0.20±0.05 _a	1.92±0.28 _a	12±3 _b	4.41±0.09 _a	0.4±0.0 _a	4±1 _{ab}
Site 1b	regic sand	1.12±0.02 _e	0±0 _a	90±6 _a	280±39 _{bc}	197±34 _b	0.15±0.03 _a	3.39±0.45 _b	5±1 _a	4.48±0.05 _a	0.6±0.1 _a	2±0 _a
Site 2a	regic sand	1.17±0.02 _f	2±0 _{bc}	48±8 _a	132±16 _a	102±9 _a	0.84±0.05 _c	2.46±0.17 _{ab}	34±1 _d	4.18±0.02 _a	0.9±0.1 _a	5±1 _{ab}
Site 2b	regic sand	1.05±0.01 _c	2±0 _{abc}	58±11 _a	290±57 _c	244±28 _b	1.24±0.07 _d	4.85±0.37 _c	27±3 _c	4.35±0.11 _a	0.9±0.1 _a	19±3 _d
Site 3a	Glenrosa	1.02±0.01 _b	5±1 _{de}	255±21 _{bc}	533±20 _d	351±16 _c	0.35±0.04 _{ab}	6.54±0.16 _d	5±1 _a	4.26±0.04 _a	1.1±0.1 _a	8±2 _{bc}
Site 3b	Glenrosa	0.98±0.01 _a	3±0 _{bc}	191±11 _b	580±33 _d	357±8 _c	0.45±0.06 _b	6.77±0.15 _d	7±1 _{ab}	4.28±0.03 _a	1.3±0.6 _a	5±0 _{ab}
Site 3c	Glenrosa	0.96±0.01 _a	3±1 _{cd}	245±35 _{bc}	580±63 _d	373±15 _c	0.33±0.13 _{ab}	6.92±0.25 _{de}	5±2 _a	4.33±0.06 _a	1.0±0.2 _a	8±3 _{abc}
Site 3d	Glenrosa	0.97±0.01 _a	3±2 _{bcd}	279±58 _{bc}	577±55 _d	353±23 _c	0.36±0.13 _{ab}	6.86±0.43 _{de}	6±2 _{ab}	4.26±0.12 _a	0.5±0.1 _a	12±5 _c
Site 4a	Glenrosa	1.08±0.01 _{cd}	5±1 _{de}	277±37 _c	749±70 _e	385±22 _c	0.24±0.10 _a	7.85±0.52 _e	3±1 _a	4.48±0.12 _a	1.1±0.2 _a	6±1 _{abc}
Site 4b	Glenrosa	1.11±0.01 _{de}	6±1 _e	267±49 _{bc}	732±48 _e	352±38 _c	0.21±0.07 _a	7.45±0.52 _{de}	3±1 _a	4.46±0.12 _a	1.4±0.2 _a	11±2 _c

Means with same letter are not significantly different (P<0.05) LSD

¹ Ambic-2-extractable P, K and Zn, KCl-extractable Ca, Mg, acidity and pH (Kcl) procedures described by Hunter (1975) and Farina (1981).

Table 5.6 Results of Particle Size and CNS analyses from the topsoil (150 mm) of coastal grasslands at the end of the study period

Site	PARTICLE SIZE ¹			CNS ²						
	Clay	Silt	Sand	Total C	Total N	C:N	³ N kg ⁻¹ ha ⁻¹	⁴ max. avail. N kg ⁻¹ ha ⁻¹	Total S	N:S
	%	%	%	%	%				%	
1a	8	5	86	0.93	0.1	11.3	1025	51	0.01	7.45
1b	15	11	74	1.36	0.1	13	1300	65	0.02	6.93
2a	9	6	85	1.02	0.1	11.3	1125	56	0.01	6.92
2b	19	6	75	2.05	0.16	12.9	1987.5	99	0.03	6.36
3a	23	21	56	2.34	0.19	12.5	2337.5	117	0.02	8.13
3b	23	21	56	1.95	0.16	11.9	2037.5	102	0.02	9.06
3c	22	21	57	1.66	0.14	11.8	1762.5	88	0.02	7.83
3d	23	22	55	2.43	0.19	12.5	2425	121	0.02	8.08
4a	22	22	56	1.98	0.17	11.6	2137.5	107	0.03	6.84
4b	21	20	58	2.4	0.21	11.5	2612.5	131	0.03	8.36

¹ Determined by pipette method (MacVicar 1991). Texture classes: clay <0.002, silt 0.02-0.002 and sand 2.0-0.02

² Total C, N and S are analysed by the Automated Dumas dry combustion method using a LECO CNS 2000 (Leco Corporation, Michigan, USA).

³ N kg⁻¹ ha⁻¹ = (Sample density × 10⁶) × N % (MacVicar *et al.* 1991)

⁴ Maximum available N kg⁻¹ ha⁻¹ = N ha⁻¹ × 0.05 (Wild 1988)

Permanent grassland in temperate regions contain 2 to 6 t N ha⁻¹ (Wild 1988). In comparison, coastal grasslands corresponded to the lower N limit (Table 5.6). Approximately 5% (or less) of the N content is available to plants as nitrate and ammonium ions. Glenrosa samples (sites 3 and 4) had higher N levels than regic sands. Site 2b on regic sands and all sites on Glenrosa soils had reasonable levels of 'available' N, despite being burnt annually. Carbon to N ratios for all sites were within the limits between 10 and 14, a phenomena of most soils throughout the world. The N:S ratios were also in keeping within worldwide trends of between seven and eight.

5.4 Discussion

Chromolaena was sensitive to fire at any height. Chromolaena density had a negative impact on grass production. Six to seven years of annual burning increased grass production and

effectively controlled moderate and dense infestations of chromolaena. Eighty percent mortality is acceptable for registering herbicides for the control of specific species in South Africa (E Wolmarans pers. comm., Registrar: Act No. 36 (1983), Private Bag X343, Pretoria 0001) and the results here are comparable. From the point of cost-effectiveness fire is free, and if mortality exceeds reinfestation rates, then the method is effective, no matter how low the degree of fire-induced mortality. Infestations with grass yields of less than 1 t ha^{-1} can be used effectively to reduce chromolaena, provided the weed is burnt when it is most vulnerable at the height of the dry season.

Mortality in dense infestations after slashing and burning chromolaena was better than other cultural control experiments in fallow-cropping systems where the incidence of regrowth after fire was quite high (Slaats 1995). Chromolaena has a high seed production potential and survival is favoured by rapid growth, rapid net assimilation and allocation of many resources to the shoot system (Ramakrishnan & Vitousek 1989). Chromolaena is a C_3 species with large biomass contributions to secondary successional communities. The short agricultural cycles in fallow-cropping systems presents unique difficulties for suppressing chromolaena under conditions that attract early successional species monopolised by C_3 exotics. In systems where clearing of chromolaena is to promote long cycles or states, i.e. grassland, intense fires will impoverish the chromolaena seed bank and reduce reinfestation.

Secondary weed invasions are a problem after the removal of dense infestations. Bugweed and lantana were the most important alien species responsible for secondary invasions in coastal grasslands. Slash and burn practices must be integrated with chemical control to prevent seedling establishment in situations where chromolaena is dense and grass cover is nonexistent. Follow-up control of alien invasive species is one of the most important operations in integrated weed management (Goodall & Naudé 1998). Routine burning as a control strategy will remove chromolaena infestations from grasslands and maintain them free of the weed indefinitely, but this depends on the density of the parent population and soil texture. Dense infestations other than on sandy or sandy loam soils will require extra effort.

Depending on the ecosystem, the presence or absence of fire causes ecological disturbances promoting chromolaena invasions. The presence of chromolaena in indigenous forest poses a

fire hazard during the dry season (Macdonald 1983). Veld fires incinerate infestations growing on forest margins, causing severe damage to fire-sensitive forest species. New opportunities are created for chromolaena to invade the margin and understory of fire-damaged forests. Repeated fire will not effectively control the chromolaena, however, the forest ecosystem will be destroyed. Fire is therefore not an appropriate control method in indigenous forests. Coastal grasslands are seral to weedy scrub in the absence of fire. Implementation of burning regimes will end woody plant succession and promote the establishment of grass. Fire is therefore a disturbance event in forest but a determinant of grassland. The absence of fire in grassland is seen as a process-interruption facilitating undesirable woody plant establishment.

Regic sands appeared stable and resilient to woody invasion but the window of observation was extremely narrow. Site 2 showed strong signs of forest development over a 30 year period without fire (Plate 1, c and d). Bush clumps were initiated by *S. cordatum*, presumably by growing away from its dwarf shrub habit under irregular burning regimes. The bush clump in Site 2 (Plate 5) in 1990 contained large *Bridelia micrantha* trees killed by fire in 1991, leaving a community of fire resistant species (*S. cordatum*, *Phoenix reclinata* and *Strelitzia nicolai*). These findings concur with von Maltitz *et al.* (1996) who showed that sandy *Themeda/Aristida* coastal grasslands are seral to forest. In addition, forest occurs almost continuously along the KZN coastal sand dunes (Tinley 1985) where it has not been interrupted by cane or timber plantations.

Routine fires in coastal grasslands on Glenrosa soils killed forest precursor species but did not kill savanna species. Studies on tree survival strategies in West African savannas show that bark thickness is the main explanation for survival in intense fires (Gignoux *et al.* 1997; Hochberg *et al.* 1994). Tree recruitment rather than adult survival, stem profile and growth rate of young trees between successive fires were the main reasons for survival in systems with annual but low intensity fires.

Simulated savanna tree dynamics in control and burn plots showed a doubling rate of tree populations every six years under fire exclusion (Hochberg *et al.* 1994). Annual fires merely prolonged doubling to around 30 years. Mortalities from fire had no impact on equilibrium

density. Tree survival strategies in the form of fire resistance (bark properties), or the ability to rebuild aboveground structures quickly, provided windows of opportunity for trees to shade-out and displace grass. The probability of annual fires occurring in fragmented coastal grasslands are remote. This study showed that once savanna trees established in grassland, fire alone was unable to restore the former state. Fire favoured the development of grassland vegetation but trees and shrubs that established during fire-free windows suppressed grass (cf. Trollope 1984).

Authors in the past have intuitively argued about the role chromolaena plays in woody succession in KZN, some advocating facilitation (Cooper 1977; le Roux & le Roux 1991), while others suggest inhibition (Wilson 1995; Goodall & Erasmus 1996). Facilitation requires that chromolaena dies out once its niche is replaced by higher life forms, i.e. tree species (Connell & Slatyer 1977). Seedlings and saplings of indigenous species growing with chromolaena (Appendix C) did not prove that the alien weed promoted succession to forest. Chromolaena was persistent in 30 year successions without being replaced by other species.

Inhibitor species under the Connell and Slatyer (1977) model tolerate individuals of other species that have lower competitive thresholds. Competitive exclusion would have caused mortalities of indigenous species of similar size but this was not observed prior to the first burn. Self-thinning was only observed in chromolaena. The inhibition model does not work either because native species were well represented at seedling and adult stages in 1990 (Appendix C2 - C4). Seedlings were skewed in the direction of juveniles but this may be more a factor of young woody successions in unburnt grassland than a process of inhibition. Earlier hypotheses that the chromolaena inhibits forest regeneration (Goodall & Erasmus 1996) are possibly incorrect.

The divergence model (Huston & Smith 1987) manifests the arrival of a 'super-species' in multispecies succession. In this model competitive abilities are equal in early stand development when resources are not scarce. This phase is followed by one species displaying a competitive advantage for many reasons, e.g. regenerative ability, growth rate, size,

morphology, resistance to herbivory by insects and other invertebrates. The super-species in this case is *chromolaena*.

Huston and Smith (1987) simulations on the removal of an earlier colonist in a successional sequence showed that species replacements are different had the colonist not been removed. The trend was observed in sites 4a and 4b when seedlings of *chromolaena* were removed by hand in Site 4a and left in Site 4b. This single action, in combination with fires prescribed to both sites, resulted in 4a becoming open woodland while 4b reverted to alien thicket.

The response in Site 4a was also conditional on the form of the next dominant. In the simulations of Huston and Smith (1987), removal of the earlier dominant caused dramatic increases in the next dominant. In weed ecology this model predicts the arrival of another alien 'super-species'. In Site 4a bugweed emerged as the second dominant that was more resistant to fire than *chromolaena*. In Site 4b *lantana*, more resistant to fire than both bugweed and *chromolaena*, emerged as the second dominant after the initial treatment. In this case an interesting picture emerged, also predicted from the simulation models. Although *chromolaena* was replaced by *lantana* and bugweed, the thicket-forming process resisted fires and indirectly facilitated conditions for *chromolaena* to reestablish and become dominant again.

The role of *chromolaena* in forest establishment remains a 'chicken or egg' scenario. The entire process from the immigration of species to its hypothetical disclimax or equilibrium would have to be measured in order to do so. Control plots cannot be used to evaluate treatment effects in experiments sampled only at the end (O'Connor 1985). Baseline data cannot be used to draw conclusions about succession in long term studies that do not maintain a subset of baseline information in an untreated state.

Alien species play a pivotal role in present day ecology, particularly in the southern African eastern coastal zone. Many of these species possess abilities to invade natural vegetation and alter existing states, arresting the processes determining stability and resilience of intact ecosystems. Woody plant communities were unstable but resilient in open grassland under conditions of no burning. Savanna succession was replaced by forest species and

chromolaena. Although savanna seedlings were arrested under chromolaena thickets the domain dominated by woody vegetation persisted. Fire eliminated forest and chromolaena successions but was only partially effective with savanna species. Coastal grasslands are non-equilibrium communities that function in multiple states whether fires are excluded or are a part of vegetation management.

Often overlooked, is the impact natural enemies (insects, pathogens and viruses) have on regulating species populations and most noticeable in biological control projects in alien dominated vegetation. At some stage biological control of chromolaena may reverse the dominance of a Huston and Smith (1987) 'super-species'. The possibility of another scenario emerging is a distinct possibility, namely a 'super-species' niche may be replaced by another 'super-species' if biological control provides an advantage for competitive displacement. Displacement was observed between chromolaena and bugweed when fire was introduced as a management strategy. Fire can therefore be used as a cost-effective control option for reducing the distribution and local density of the chromolaena in open and wooded grasslands, but must be integrated with chemical control should hardier alien species become secondary invaders.

6. MONITORING SERIAL CHANGES IN HERBACEOUS SPECIES COMPOSITIONS

6.1 Statement of the problems

The fate of the herbaceous component after *Chromolaena odorata* invasion, and herbaceous species dynamics in successions during recovery, remain undescribed. This chapter aims to reveal spatial and temporal dynamics of the herbaceous communities responding to the modifying effects of fires on the woody stratum. An understanding of patterns in species diversity and turnover is fundamental in establishing resilience and non-equilibrium in coastal grassland ecosystems.

Species-centred approaches to biodiversity do not provide process-orientated information on ecosystem structure and function. The process of matching functionality to species is therefore critical. Constant awareness of environmental conditions determining vegetation pattern and successional status are important. Several steps were used for articulating herbaceous community trends based on structure, function, succession and diversity.

6.1.1 Key questions and objectives (Q. & O.)

The aims of this chapter are to describe the spatial and temporal responses of grassland communities to woody plant invasions in the absence of fire and the ensuing restoration patterns following the implementation of a burning regime. The following questions are of most interest:

- 6.1.1.1 Q. *Were spatially independent communities at the outset compositionally different?*
O. Classification of sites to reveal spatial and temporal structure.
- 6.1.1.2 Q. *Does the null hypothesis of no serially induced changes hold for grasslands with variable degrees of dominance by woody plants?*
O. Use of statistics to interpret herb-layer dynamics, e.g. trends in species richness or diversity, turnover and community level response curves.
- 6.1.1.3 Q. *Can species diversity be better presented as organisms functionally adapted to, and partitioned by, intrinsic determinants?*
O. Use of descriptive statistics and unconstrained ordinations to describe life forms and growth forms in communities with different growing conditions.

- 6.1.1.4 Q. *Does the null hypothesis of no serially induced changes hold for species compositions over a range of growing conditions?*
- O. Use of descriptive statistics to illustrate changes in grass composition.
 - O. Use of constrained ordinations to reveal underlying determinants causal to herbaceous species displacements in spatio-temporal communities, i.e. succession.

Explanations of observed responses will provide insight into the functional ecology of coastal grasslands and provide recommendations for their future management.

6.2 Methods

All sites, with the exception of 2b, had indigenous woody species recorded in the transects. Sites 1a and 1b were the only sites which did not have chromolaena. All woody species with the exception of shrublets were excluded from this analysis. Many herbs have semi-woody stems but do not grow larger than 2 m, shrublets are closer to herbs than to woody shrubs or trees. The herbaceous component of the grass layer comprises growth forms such as grasses, sedges, creeping and twining vines, ferns, geophytes (lilies, irises and orchids), herbs (forbs or dicotyledonous herbs), shrublets (dwarf woody and semi-woody herbs) and succulents. In this study the term 'herb' refers specifically to erect and procumbent broad-leaved herbs (i.e. forbs) that are not vines.

6.2.1 Classification of herbaceous communities

Herbaceous community data of a large samples-by-species matrix were subjected to Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979), to reveal underlying structure in the spatial and temporal communities. Standard default settings were used. Pseudo-species cut levels were 0, 2, 5, 10 and 20% and hierarchical division was continued to the sixth level.

6.2.2 Spatial and temporal trends in herbaceous community dynamics

6.2.2.1 Trends in species richness and diversity

In keeping with the objectives, data were not converted to index format but presented as numbers of species expressing actual community dynamics in time. Alpha diversity (α -) refers to the number of species within a community, i.e. the variety of species sharing the same place and potentially competing for the same basic resources (Cowling *et al.* 1989; Burton *et al.* 1992). Alpha diversity can be measured in several ways (Peet 1974; Whittaker

1977). Species richness (S), i.e. the number of species per unit area, is the most important and universal definition of diversity. Species richness will vary according to sample size in the same vegetation, i.e. S is dependent on sample area (A). Site 1a and 1b were 60 and 80 m long whilst the remaining sites were standardised at 25 m. Richness data were therefore adjusted for A using Equation 6.1 (Gleason 1922).

Equation 6.1

$$d = \frac{S}{\log A}$$

where: d = diversity
 S = species richness
 A = sample area (m^2)

Beta (β -) diversity is the extent of species replacement or biotic change along environmental gradients (Whittaker 1972), simply viewed as the turnover in species composition from one location to another. As with alpha diversity there are several ways of presenting species turnover in index form (e.g. Sorenson 1948; Whittaker 1960; Wilson & Shmida 1984). Indices of beta turnover were avoided, as was the case with alpha diversity, because they do not communicate actual magnitudes of change. Turnover data were determined simply as the units of variation between successive surveys, conveyed as the number of species shared, gained or lost between two biological years. Within-site and between-site turnover was compared for differences using G^2 tests (Sokal & Rohlf 1969).

The number of biannual surveys per site varied for financial reasons. The benchmark sites (sites 1a and 1b) were only monitored over one biological year (1 July 1992 to 31 June 1993) following a wild fire in autumn of the pervious year. The benchmark sites therefore had no turnover data. Within the time-frame three surveys were carried out at the benchmark sites, namely spring (October 1992), midsummer (January 1993) and early winter (June 1993). Sites 2a (sparse chromolaena) and 2b (dense chromolena) on regic sands were measured in the first and last two biological years of the study, i.e. 1990/91, 91/92, 96/97 and 97/98. Site 3b (moderate chromolaena on Glenrosa) was measured annually from 1992/93 to 97/98. Site 4a and 4b (dense chromolaena on Glenrosa) were measured from 1990/91 to 97/98, except for the years 92/93 and 95/96.

Raw data were presented descriptively in graph and table form showing trends in species richness over time. The effects of initial chromolaena density on species richness in

permanent quadrats were examined by One-way ANOVA with *post hoc* Scheffé test (Sokal & Rohlf 1969) for comparison of between-sample means. Changes in levels of species richness over time in response to fire were inferred from *post hoc* Friedman ANOVA.

Two-way ANOVA was used for determining differences phytomass dry weights of both herbs and grasses in randomised and replicated 0.25 m² quadrats sampled at the benchmark site. Thirty random samples were cut on each aspect (east, crest and west) at the end of the previous season (May 1992) and again at three intervals over the next growing season, namely October, February and June 1993. Means were compared *post hoc* by Scheffé test with 0.1% probability of error.

6.2.3 Life form analysis

6.2.3.1 Nomenclature

Scientific names of species conform to Arnold and de Wet (1993). The exceptions to this were (a) *Argyrolobium rotundifolium* (Edwards 1993), a new species, (b) *Buchnera simplex* an unpublished species (Dr T Edwards pers. comm., University of Natal, Private Bag X01, Scottsville 3209) and (c) *Gerbera kraussii*, reinstated as being a separate species from *G. ambigua* (Retief *in lit*). Attention is drawn to the alien *Solanum viarum*, misidentified as *S. acanthoideum* (Goat Apple), a half-woody shrublet invading planted pastures in the KZN midlands. Records at National Botanical Institute (NBI) no longer list the species as *S. acanthoideum* and the species is now unofficially called *S. viarum* until the work is published (Henderson *in lit*). The species was referred to as *S. acanthoideum* in this study. Life forms incorporated Raunkiaer (1934) and Rutherford and Westfall (1994).

6.2.3.2 Procedure for categorising life forms

The grassland communities studied were comprised of a great number of herbaceous species. Multivariate analyses of these sites will result in large summarisation of this diversity. The properties of species as functional components of the ecosystem may, to a large extent, be lost in ordination space. Prior to the analyses of the species component, deductive logic using published works were applied to the 214 herbaceous species recorded between 1991 and 1998. The purpose was an attempt to group species according to functional and niche-adapted types comprising life-form trajectories.

Each life form uses a double-barrelled code, namely Raunkiaer (1934) - Rutherford and Westfall (1994) classifications, describing the fate of herbaceous species in environments subjected to fire. The purpose of using such a code was to provide a holistic concept of the life form dynamic in systems that are fire-driven to accommodate the scenario "with and without fire". Exposure to fire and not climate determines whether the plants live or die in this subjective categorisation, i.e. fire becomes the principal determinant. The life-forms chosen nevertheless were based on Raunkiaer (1934), in which climate becomes a predetermined variable. No woody species were included, apart from shrublets. Country of origin (i.e. indigenous or exotic) was used as one of the criterion for splitting life forms. Herbarium specimens collected in the field were compared alongside specimens from the Bews Herbarium collection to determine the position of the renewable bud.

Life form abbreviations are as follows:

- (*) asterisk = denotes alien life forms,
- (Ch) chamaephytes = perennial woody plants with buds below 0.7 m above ground,
- (F) fire = not a life form but a deterministic process replacing unfavourable season,
- (G) geophytes = shoot-forming buds are below ground on bulbs, tubers or rhizomes,
- (H) hemicryptophytes = plants with renewable buds near the soil surface, most often applies to grass and sedge species, but in rare cases includes perennial herbs with annual stems,
- (P) phanerophytes = woody plants with buds at 0.7 m above ground,
- (Ph) herbaceous phanerophytes = perennial herbaceous plants,
- (Pht) herbaceous biennial phanerophytes = biennial herbaceous plants
- (Pn) nanophanerophytes = semi-woody plants which grow less than 2 m high,
- (Ps) phanerophytic succulents = herbaceous or semi-woody plants which conserve water by storing it in large parenchyma cells in swollen stems or leaves,
- (T) therophytes = plants which complete their life cycles in a year, i.e. annuals.

6.2.3.3 Analysis

The fates of species in each transect were determined from monitoring persistence in the form of presence data, converted to percentage frequency, as a measure of local abundance.

Descriptive statistics were used to compare life forms against growth forms to examine the effectiveness of the approach in assigning functionality to the visible attributes of species.

Data in a samples-by-life form matrix were analysed using Principal Components Analysis (PCA). Detrended Correspondence Analysis indicated that species responses to underlying

variables were linear, as the length of the gradient on the first axis was less than 3 SD.

6.2.4 Herbaceous species composition and succession

Grassland community data were subjected to indirect gradient analysis by Detrended Correspondence Analysis (DCA) using CANOCO 4 (ter Braak & Šmilauer 1998). The effects of serial dependency (repeated measures) were partialled out by including covariables identifying sites with time series data (samples). Method of detrending was by segments and species local frequencies were not transformed. Biplot scaling focussed on inter-species distances.

Direct gradient analysis was by Canonical Correspondence Analysis (CCA) focussing on inter-species distances using biplot scaling. Species frequency data were not transformed but rare species were down-weighted. Samples from the benchmark site (Site 1) were deleted because they were only measured over one season and relevant only to indirect gradient analysis. Samples that did not have any herbaceous species, i.e. monospecific *chromolaena* stands, were made supplementary (weight = 0.00). Most of the environmental variables were determined from the absolute density of woody plants in height classes. Alien species were separated from indigenous woody species. Height classes were bushes (≤ 2 m), shrubs ($> 2 \leq 5$ m) and trees (> 5 m). Woody variables were given quantitative values by multiplying abundance by the respective height classes. Multiplication factors used for adjusting height classes were: ≤ 2 m (x1), $> 2 \leq 5$ m (x3), > 5 m (x5). Other environmental variables were bare ground (%) and fire frequency, expressed as cumulative numbers of burns at each site. Percentage bare ground was calculated from by subtracting grass cover from 100 (%).

Canodraw 3.1 (Šmilauer 1992) was used to displaying the results of gradient analyses. Sites and species were classified for better interpretation of ordination diagrams. The grassland sites investigated were made into site classes, each made up of sets of community composition data from surveys carried out between 1990/91 and 1997/98. Species were classed into growth forms based on Appendix B, namely alien, geophytes, vines and sedges. Successional attributes were given to grasses and herbs (after Trollope *et al.* 1990). Grasses were summarised into decreaser or increaser species using various sources (e.g. Tainton *et al.* 1976; van Oudtshoorn 1992). Herbaceous species were summarised into species dominant in

disturbed communities (ruderal herbs) or species associated with disclimax grassland (climax herbs). The separation of herbs into these two classes was achieved partially by their presence at sites along a successional profile (Appendix B), and by looking at shoot and root morphology of specimens in the Bews Herbarium (Dr T Edwards pers. comm., University of Natal). Site and species classes were given unique symbols identifiable from legends.

Herbaceous plant indicators were chosen using *a priori* restrictions in Canodraw 3.1. Area of purity was set 0.01 with a minimum species weight (visibility threshold) of 35/100. Only the names of species having major influence on the ordination were listed but symbols without labels added clarity as to what type of species were scattered in the dimensional space allotted to the first and second axes.

6.3 Results

6.3.1 Classification - structure in herbaceous community data

The TWINSPLAN classification of the herbaceous samples-by-species matrix (Figure 6.2) based on the first axis of a Correspondence Analysis (Figure 6.1) revealed differences between cluster positions. The major difference was the separation of sites 1 and 2 on regic sand from 3 and 4 on Glenrosa, on the first level dichotomy (Group 0 and Group 1). Pseudo-species were characterised by *Vernonia oligocephala*, a grassland herb, in Group 0, and in Group 1, pioneer species *Eragrostis curvula* and *Melhania didyma*.

The herbaceous communities within the two groups were significantly different, but this was only partly due to soil type. The differential species on the right side of the classification are associated with disturbed and shady conditions. At level two there is a clear gradient from the uninvaded bench mark sites at Group 00 to the dense infestation at site 4b (Group 11), with sparse and moderate infestations at groups 01 and 10 respectively. No differential species were selected for Group 00 although the crude indicators from the first axis ordination (CA) (not shown) were the herbs *Pentanisia prunelloides*, *Indigofera hiliaris*, *Graderia scabra* and *Argyrolobium humile*, not recorded in transects at other sites. *Desmodium dregeanum*, a leguminous creeping herb, was identified as the indicator species for both sites 2a and 2b.

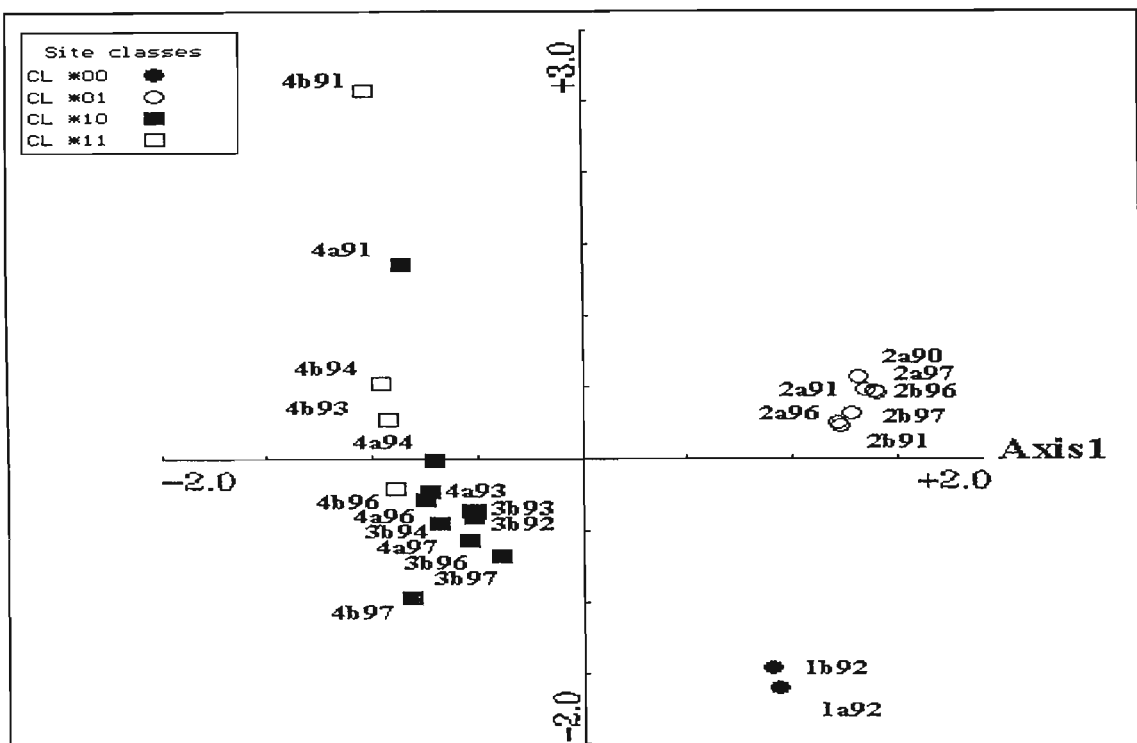


Figure 6.1: The division of the first ordination axis using Correspondence Analysis (CA) of the same samples-by-species matrix used in the TWINSPLAN classification. Location of sites are identified by a number followed by a letter, e.g. 2a. Temporal dimensions of sites are denoted by a two digit suffix, e.g. 90 = 1991. Eigenvalue for $\lambda_1 = 0.840$ (23.2%), total inertia = 3.619.

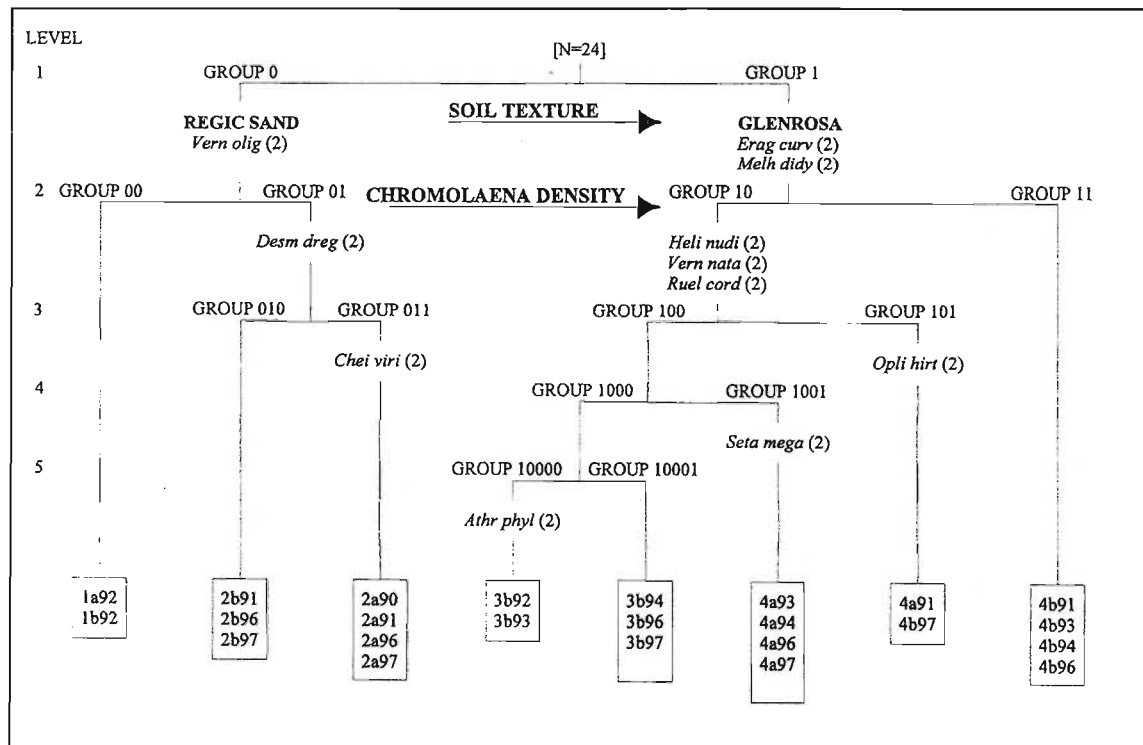


Figure 6.2: Dendrogram of the TWINSPLAN classification of seven coastal grassland communities measured between 1990 and 1998. Explanatory variables have been included. Species names for acronyms can be found in Appendix B. Location of sites are identified by a number followed by a letter, e.g. 2a. Temporal dimensions of sites are denoted by a two digit suffix, e.g. 90 = 1991.

Greater variation occurred on the right side of the dendrogram. A profile of the groups 11, 101, 1001, 10001-10000 shows a sequential successional gradient from moderate chromolaena. The sixth level portrays very high turnover patterns in the first two years of the moderate and dense infestations and apparently very little change in the sparser infestations. The reasons for the discriminations in the herb layer of Glenrosa sites was possibly conditional upon on density of alien and indigenous woody species. Sites associated by thickets and infrequent fires, namely Site 4 (see Figure 5.6) were characterised by the presence of shade-tolerant grasses, whilst open woodland (Site 3) was identified with having ruderal herbs.

6.3.2 Spatial and temporal trends in herbaceous community dynamics

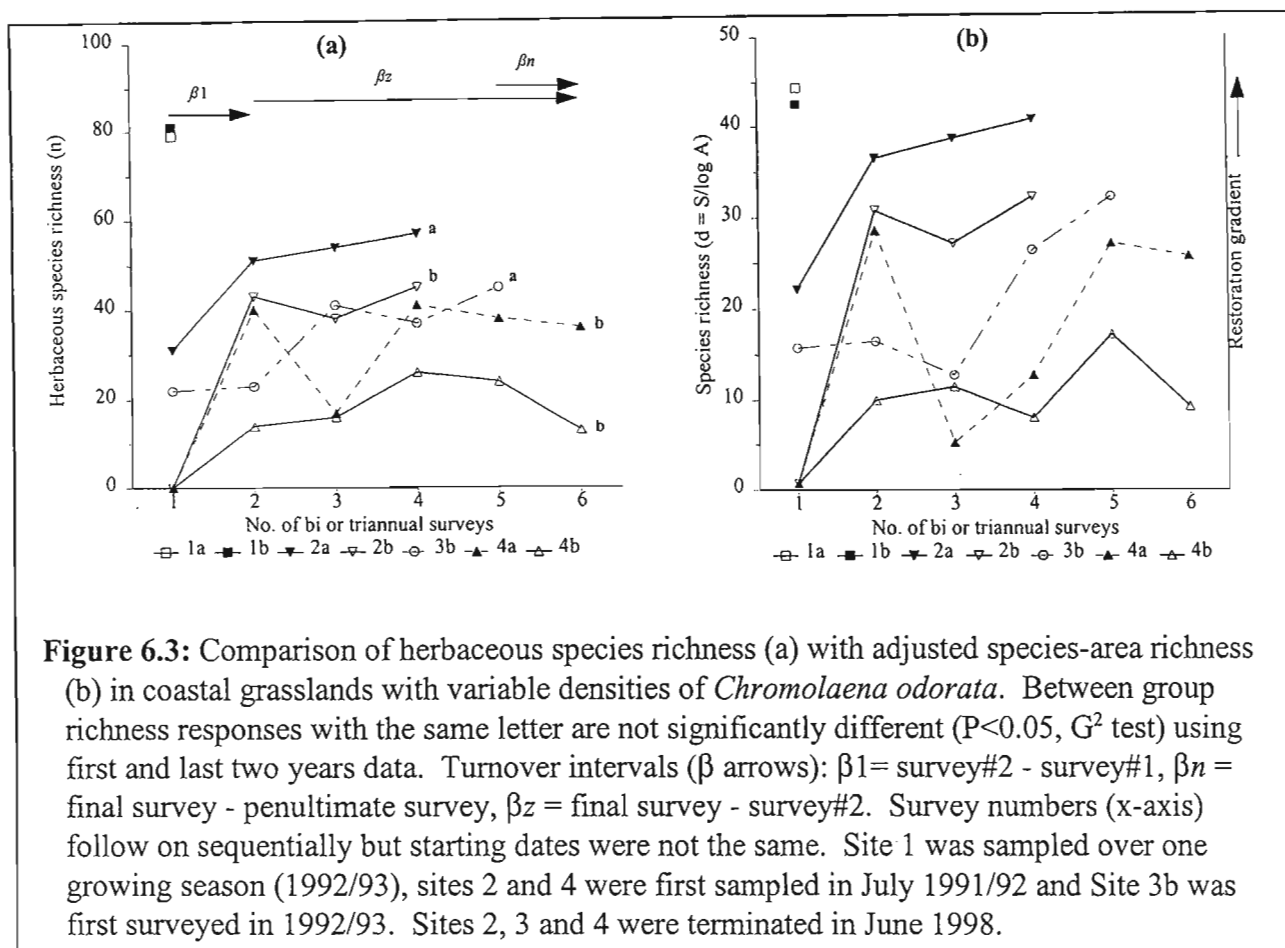
6.3.2.1 Trends in species richness and diversity

Initial chromolaena density had an impact on species richness (Figure 6.3). Sparse and moderate infestations (sites 2a and 3b) had more herbaceous species than sites with dense infestations (2a, 4a and 4b). Invaded sites did not recover in equal proportions and by the end of the study species richness, adjusted for sample size (Figure 6.3b), was still greater at the benchmark sites (1a and 1b).

Spatial and temporal differences in the capacity of sites to support numbers of species were evident. Trends in richness show that the communities were not static. Variable recruitments of species were measured in the second survey, i.e. turnover interval β_1 (Figure 6.3a and Table 6.1), of species gained since the baseline survey. Site 3b only recorded one extra species due to drought conditions. The KZN coastal belt experienced a two-year drought from 1991, indicated by an extended period of low annual rainfall (< 700 mm), as illustrated in Figure 3.1. Contrary to Tilman and El Haddi (1992), local extinction due to drought was not observed at any of the sites, although stochastic aridity appeared to have had a temporary effect on richness in sites 3 and 4. Site 4a showed a significant decline in numbers in 1992 (survey #3 in Figure 6.3) but recovered strongly once the drought had passed.

Turnover between the first two years (β_1) was significantly different to turnover between the last two biological years (β_n). Fires at the start exerted a stronger influence in initiating change than the later burns. All sites were therefore responding to the efficacy of the first fire

on woody plant suppression, although 2a was affected by moribund conditions more so than by *chromolaena* density.



Initial turnover (β_1) was not different to β_z turnover (final survey - sample #2) in 2a and 4b (Table 6.1), that is, the outcomes of the first and last fires were similar. Site 2a approached a plateau (Figure 6.3a and 6.3b) at the end of the study. The response line in 4b fluctuated, but the fact that sample diversity in survey #6 is almost identical to #2 identified the system was in stress and experiencing negative change. The remaining sites fluctuated throughout the study period, with exception of β_n vs β_z turnover at site 3b which had similar aggregates (Table 6.1). Moribund conditions in 2a appear not to have had any long term effect on species dynamics.

Table 6.1 Turnover of herbaceous species in sites of equal area using contingency tables (G^2 test)

Site	Variable	* β_1	* β_n	* β_z	G test: β_1 vs β_n		G test: β_1 vs β_z		G test: β_n vs β_z	
		$^aT_2 - ^bT_1$	$^cT_n - ^dT_{n-1}$	$^eT_n - ^aT_2$	$G_{adj.}$	χ^2	$G_{adj.}$	χ^2	$G_{adj.}$	χ^2
2a	shared	31	50	40	6.14	<.05	0.05	ns	8.28	<.005
	gained	20	7	17						
	lost	0	4	11						
	turnover	20	11	28						
	aggregate	51	61	68						
2b	shared	0	35	26	63.89	<.005	32.35	<.005	10.63	<.005
	gained	43	10	19						
	lost	0	3	17						
	turnover	43	13	36						
	aggregate	43	48	62						
3b	shared	22	30	21	12.99	<.005	19.96	<.005	1.65	ns
	gained	1	15	24						
	lost	0	7	2						
	turnover	1	22	26						
	aggregate	23	52	47						
4a	shared	0	28	20	45.84	<.005	24.43	<.005	6.38	<.05
	gained	40	8	16						
	lost	0	10	20						
	turnover	40	18	36						
	aggregate	40	46	56						
4b	shared	0	10	3	9.25	<.005	2.36	ns	4.05	<.05
	gained	14	3	10						
	lost	0	14	11						
	turnover	14	17	21						
	aggregate	14	27	24						

* β = turnover intervals: β_1 = survey#2^a - survey#1^b (initial turnover),
 β_n = final survey^c - penultimate survey^d, β_z = final survey^c - survey#2^a

The spatial and temporal trends in species richness using the species-area curves (Figures 4.4 and 4.5) conclusively supports the notion that these sites differed over time within sites and between sites. Species-area curves measure the rate of species accumulation in relation to sampling intensity. In Section 4.3.2 the data included both woody and herbaceous species, richness being a function of asymptote position. The asymptotes were significantly different ($P < 0.001$) between and across sites. The asymptotes in all cases lay beyond the scale of interest. Asymptote profiles were plotted on an XY graph but trends were no different to richness data (Figure 6.3). Both were unable to contribute to the effects of turnover on plant community composition. The effect of fire in promoting restoration of grassland was only partially revealed. Richness data excludes local frequency, which measures abundances of individuals, and does not measure gross changes in underlying structure.

6.3.2.2 Subsample or quadrat diversity in relation to *Chromolaena odorata* density

The effect of chromolaena on mean species richness per quadrat is presented in Table 6.2. Chromolaena density reduced species diversity significantly. Initially, sites 2b, 4a and 4b were comprised of monospecific stands, whilst sparse and moderate infestations (2a and 3b) were also inhibited to lesser degree. Small scale diversity patterns support the findings presented in 6.3.2.1.

Table 6.2 Mean initial *Chromolaena odorata* density and annual burning on herbaceous species richness in permanent contiguous 1 m² quadrats by One-way ANOVA

Site	<i>C. odorata</i> plants m ⁻²	Total species richness (S m ⁻²) in initial and final monitoring surveys			
		Initial	Second	Penultimate	Final
1a ¹	0 ± 0 a	23.1 ± 3.4 a ²	23.1 ± 3.4 a ²	23.1 ± 3.4 a ²	23.1 ± 3.4 a ²
1b ¹	0 ± 0 a	19.2 ± 3.3 b	19.3 ± 3.3 b	19.3 ± 3.3 b	19.3 ± 3.3 b
2a	1.2 ± 1.9 b	9.9 ± 1.8 c _α	15.2 ± 2.9 c _β	15.7 ± 2.5 c _β	15.3 ± 2.5 c _β
2b	17.7 ± 8.5 c	0 ± 0 d _α	8.6 ± 1.8 d _β	9.8 ± 2.0 d _β	10.3 ± 2.1 d _β
3b	5.2 ± 5.2 d	5.5 ± 2.8 e _α ³	7.2 ± 2.6 de _{αβ} ³	8.4 ± 1.4 e _β ³	10.7 ± 2.6 d _γ ³
4b	15.7 ± 6.7 c	0 ± 0 d _α	5.6 ± 2.3 e _β	7.4 ± 2.1 e _β	8.1 ± 2.0 e _γ
4b	7.6 ± 5.4 d	0 ± 0 d _α	2.6 ± 1.5 f _β	4.5 ± 1.6 f _β	1.8 ± 1.1 f _β

¹ Benchmark sites 1a and 1b measured over one season only but compared against all sites across the temporal spectrum

² Between group (independent) samples with same letters are not significantly different ($P > 0.05$), Scheffé test for unequal sample sizes

³ Within group (serially dependent) samples with same Greek subscripts not significantly different ($P > 0.05$) using Friedman ANOVA (after Dzwonko & Loster 1998). Site 1 was not tested

Chromolaena, from the initial density presented in Table 6.2, appears to have exerted a residual effect on suppressing diversity. All infested sites failed to recover to the level of species richness recorded at the benchmark sites. This is primarily attributed to the effects of initial density on species eliminations recorded in the baseline data and the influence of chromolaena seedling survival in preventing the establishment of herbaceous vegetation (Section 5.3.1.3).

Between group variation was more meaningful than within group variation. Fire treatments between initial and second surveys was responsible for the most dramatic changes (see also Section 6.3.2.1). The changes occurring in sites over time after the second year was variable. Site 2a showed minimal fluctuation indicating that the site reached equilibrium richness after one fire (Plate 2, d). Initial richness increased by 53%, yet remained stable from the second year. The additional accumulation of grassland species may be a slow sequential process

because environmental resources are more limited in this system of diverse functional groups. Site 2b showed an increase over time but these differences were not significant from the change between the first and second surveys. It is possible this site was not a monospecific thicket of chromolaena at the beginning of the study (Appendices A and B; Table 6.2). Although no species other than chromolaena was recorded, indigenous species may have been present but severely suppressed so as to pass unnoticed in baseline surveys. Site 2b had similar community structure as Site 2a (Figure 6.2). Chromolaena density coincided with species eliminations, but an unknown period of dominance on regic sands is required before this process is complete.

Site 3b showed a significant increase in richness over time, at the end of the study diversity was numerically the same as site 2b (Table 6.2, Figure 6.3b). Site 4a likewise followed a similar trend. Site 4b followed the same trend initially but the inability of fire to prevent reinfestation resulted in species eliminations once again.

The analyses of species richness and diversity only partially contributed towards interpreting ecosystem function. Species richness only satisfied the statistical comparison of species numbers and the rate at which these amounts changed. The explanation of trends at this stage was biased by the author's historical knowledge of the sites monitored. Diversity measures on their own could not divulge characteristics of individual species as biological indicators of ecosystem condition. Richness data, therefore, could not explain what serial communities were made up of, why the communities changed, how they changed and what determinants caused them to change. Trends in the herb layer were highly dynamic. The null hypothesis of no serial changes in herb layer under chromolaena of variable density was refuted.

6.3.3 Herb and grass production at the benchmark site

The effect of aspect and life form on phytomass (grasses vs herbs) were highly significant ($P < 0.01$) (Table 6.3). The ratio of between-group variability (Mean Square Effect) with within-group variance (true random error or Mean Square Error) was significantly greater than 1, $F = 42.5$. Herb dry matter production at Site 1 in May 1992 was not significantly different to the herb production in June 1993 on eastern, crest and western aspects. Aspect differences in herb phytomass between years were also not significant ($P > 0.05$). Trends in

annual herb phytomass production after dry season burns showed that herbs reach optimal yields early in the growing season (October). There was, however, an indication of peak herb production in midsummer with rapid increase leading up to, followed by rapid decline after midsummer, with increasing grass phytomass.

Grass production between crest and western aspects were similar in May 1992 and June 1993, but within aspect differences between years were significant (Table 6.3). The KZN coastal region was stricken by drought from 1991/92 until 1993/94 (Lionnet 1993) (Figs. 3.1 to 3.3). Total rainfall in 1991/92, i.e. the beginning of the drought, was 729 mm, 30% less than the 10 year average of 1048 mm. Total rainfall over the harvesting period (1992/93) was 628 mm, 40% below average. It would appear that drought had an impact on grass production on the crest and western slopes, but the effect was less apparent on the eastern aspect. Grass production was significantly lower than the previous season's production on the crest and western aspects.

Herbs were less affected by drought than grass. On the eastern aspect herb and grass phytomass in May 1992 and June 1993 were not significantly different, although means suggest that grass contributed between 73 and 80% towards the aspect's dry matter. In May 1992 grass phytomass was significantly greater than herb phytomass on crest and west-facing slopes. The effect of drought on phytomass at the end of the study resulted in life forms across aspects being not significantly different. The contribution of aspect to total phytomass in May 1992 was 17, 46 and 37% for eastern, crest and western aspects respectively. Totals of mean phytomass of all aspects went from 1 196 g m⁻² in May 1992 to 542 g m⁻² in June 1996, of which 36, 38 and 26% was accounted for by east, crest and western aspects.

It is conceded, however, that 30 random 0.25 m² quadrats were insufficient a sample size (Section 6.2.2). Mean coefficient of variance was 83% (min. = 34%, max = 205%). Reducing CVs to between 10 and 20% meant 78 random replicates (Sokal & Rohlf 1969) on each aspect at each interval. This was beyond available project resources. Despite sampling deficiency, significant differences were extracted at very low alpha levels. The implications of this are that aspect has a major influence on life form biomass which may translate in differences in species composition and beta level diversity.

Table 6.3 Herb (including geophytes, vines and ferns) and grass (including sedges) phytomass from three aspects at a coastal grassland benchmark site (Site 1) using a Two-way ANOVA. Means with same letters are not significantly different ($P>0.01$) by *post hoc* Scheffé test. Wild fire burnt the site at the end of May 1992

Aspect	Growth form	Mean yield expressed as dry matter (DM g m ⁻²) ¹			
		May '92	Oct. '92	Feb. '93	June '93 ²
East	herbs	41.3 _{ab}	34.4 _{ab}	150.4 _{abc}	53.3 _{ab}
	grasses	161.9 _{abc}	8.3 _a	142.8 _{abc}	143.8 _{abc}
Crest	herbs	58.2 _{ab}	30.8 _{ab}	77.1 _{ab}	41.0 _{ab}
	grasses	491.6 _e	12.0 _a	271.0 _{cd}	165.8 _{bc}
West	herbs	24.0 _{ab}	9.0 _a	39.3 _{ab}	17.8 _a
	grasses	419.2 _{de}	16.8 _a	177.3 _{bc}	120.3 _{ab}

¹ All effects (site, life form): MS Effect 254 492 (df 11), MS Error 5994 (df 636), $F=42.5$, $P<0.001$
Site effect: MS Effect 309 171 (df 11), MS Error 5994 (df 636), $F=51.6$, $P<0.001$
Life form effect: MS Effect 2 678 086 (df 1), MS Error 254 492 (df 11), $F=10.5$, $P<0.008$

6.3.4 Herbaceous life form composition

6.3.4.1 Efficiency of life forms at summarising herbaceous plant community data

Table 6.4 illustrates the effectiveness of the integrated life form approach at converting quantitative and descriptive information about species into process-driven configurations. The divergent codes assisted in determining fire-survival strategies of herbaceous species recorded in transects by distinguishing (a) perennial and annual species, and (b) surviving-bud positions on fire-tolerant perennials. Eight herbaceous growth forms were transformed into 18 life form codes summarising 214 species. The relation between life form (Raunkiaer 1934) and fire life form (Rutherford & Westfall 1994) is presented in the first column. Each life form contains a record (row) of plant growth forms. The number of ‘hits’ per record infers the level of congruence, but one hit is equal to synonymity. The maximum value in a record indicates the most common description for said life form.

Hemicryptophytes (H-FH) were dominated by grasses and sedges. Three perennial herbs with annual stems constituted 6.7% of the H-FH class, namely *Hibiscus pusillus*, *Indigofera hilaris* and *Oxalis smithiana*. Notable deviations in life forms existed which defined the fate of species (Appendix B). Herbaceous phanerophytic fire chamaephytes (fire-tolerant herbs) comprised 92.9% of the life form Ph-FCh and 36% of all the species recorded in the grass layer. Herbaceous phanerophytic fire therophytes, i.e. fire-intolerant perennial herbs, were dominated by species associated with forest, ecoctones or disturbed areas (ruderal herbs).

Table 6.4 Growth form by life form congruity matrix

4 Growth form by life form congruency matrix										
Life form Species		Growth form (n)								
code	(n)	fern	geophyte	grass	sedge	herb	vine	shrublet	succulent	
G-FG	23		22				1			
G-FT	3		3							
H-FH	45			29	13	3				
H-FH*	1			1						
H-FT	1			1						
H-FT*	2			1		1				
P-FCh	1						1			
Ph-FCh	84					78	6			
Ph-FG	1	1								
Ph-FH	5					3	2			
Ph-FT	16					11	5			
Ph-FT*	4					4				
Pht-FT	1					1				
Pn-FCh	5							5		
Pn-FT	3							3		
Ps-FPs	1								1	
T-FT	14			2		11	1			
T-FT*	4				1	3				
Σ	18	214	1	25	34	14	115	16	8	
%		100	0.5	11.7	15.9	6.5	53.7	7.5	3.7	

Key to life forms: geophyte (G), therophyte (T), hemicryptophyte (H), phanerophyte (P), herbaceous phanerophyte (Ph), chamaephyte (Ch), nanophanerophyte (Pn), succulent phanerophyte (Ps), biennial herb (Pht). Fire (F) is a determinant. Asterisks denote alien life forms.

Nanophanerophytic fire chamaephytes (Pn-FCh) were comprised solely of shrublets, e.g. *Eugenia capensis* subsp. *capensis*. Fire sensitive shrublets (Pn-FT) were jointly forest and ecotone species. Only one succulent species, *Aloe maculata*, was found in the transects, although *Aloe arborescens* was rare in the woody plant plots (Appendix C2). Annuals (T-FT) were largely confined to herbs, but included two grasses, *Melinis repens* and *Panicum aequinerve*. Exotic species were found in hemicryptophytes, phanerophytic herbs and therophytes but only one fire resistant herbaceous alien species was recognised, namely *Paspalum dilatatum* (H-FH*).

Associated with life form richness is life form abundance, i.e. the frequency of occurrence over location and time. Richness ratios between the two dominant life forms (Ph-FCh:H-FH)

were 1:5.4 (Table 6.4), but in terms of abundance hemicryptophytes were ranked on a par with chamaephytic herbs at 1:0.97 (Table 6.5). More importantly, hemicryptophytes comprised most of the phytomass (Table 6.3). The most abundant life forms after Ph-FCh and H-FH were annuals (T-FT), geophytes (G-FG), fire-intolerant herbs (Ph-FT), alien therophytes (T-FT*) and fire-tolerant hemicryptophytic herbs (Ph-FH).

Table 6.5 Accumulated life form abundances from presence data in 25 m belt transects from seven separate coastal grassland sites between 1990 and 1998

Life form code	Frequency score	% distribution	Species examples
G-FG	979	4.5	<i>Hypoxis multiflorus</i>
G-FT	16	0.1	<i>Disa woodii</i>
H-FH	8309	38.5	<i>Acroceras macrum</i> , <i>Hibiscus pusillus</i>
H-FH*	156	0.7	<i>Paspalum dilatatum</i> *
H-FT	76	0.4	<i>Oplismenus hirtellus</i>
H-FT*	24	0.1	<i>Paspalum urvillei</i> *
P-FCh	28	0.1	<i>Protasparagus falcatus</i>
Ph-FCh	8601	39.8	<i>Graderia scabra</i>
Ph-FG	187	0.9	<i>Cheilanthes viridis</i>
Ph-FH	301	1.4	<i>Sisyranthus compactus</i>
Ph-FT	621	2.9	<i>Centella asiatica</i>
Ph-FT*	40	0.2	<i>Amaranthus deflexus</i> *
Pht-FT	32	0.1	<i>Senecio chrysocoma</i>
Pn-FCh	243	1.1	<i>Eugenia capensis subsp. capensis</i>
Pn-FT	219	1	<i>Helichrysum panduratum</i>
Ps-FPs	112	0.5	<i>Aloe macropoda</i>
T-FT	1148	5.3	<i>Senecio madascariensis</i>
T-FT*	508	2.4	<i>Ageratum houstonianum</i> *

Key to life forms: geophyte (G), therophyte (T), hemicryptophyte (H), phanerophyte (P), herbaceous phanerophyte (Ph), chamaephyte (Ch), nanophanerophyte (Pn), succulent phanerophyte (Ps), biennial herb (Pht). Fire (F) is a determinant. Asterisks denote alien life forms.

Life forms were only partially successful in evaluating species fire-survival strategies, namely geophytes, hemicryptophytes and therophytes. Rutherford and Westfall's (1994) domains of divergence were more appropriate for describing species with above ground renewable bud positions. Mature fire-adapted communities, i.e. sites 1 and 2 (benchmark site), experienced less severe life form aberrations, i.e. life-death trajectories (G-FT, H-FT, Ph-FT), than did

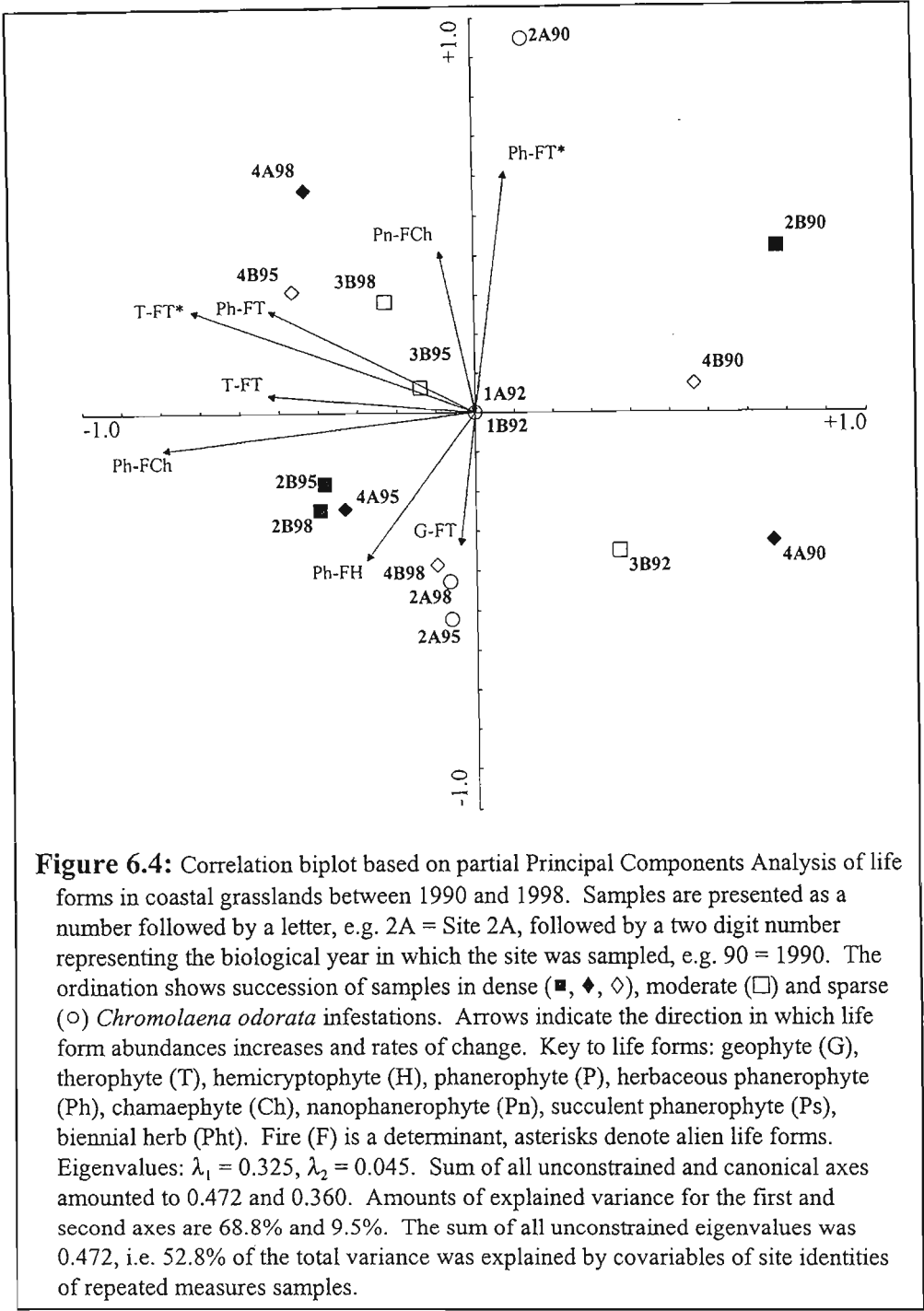
sites with ruderal herbs colonising in disturbed ground after burning dense infestations. The implication of divergent coding therefore describes the system as changing from a fire-modified state to a system controlled by principal determinants. In the case of coastal grasslands, absences of fire would result in the arrival and establishment of forest and alien phanerophytic vegetation (P) resulting in a vegetation transformation, e.g FH-P or FCh-P and so on. Coastal grasslands are herb-rich communities made up of life forms tolerant and dependent on fire.

6.3.4.2 Principal components analysis of life forms

Samples on the first axis on the right side of the partial PCA diagram (Figure 6.4) were monospecific, i.e. sites initially had zero herbaceous life forms. Over time these samples changed to positions on the left side. The partial ordination shows eight dominant life forms on the first and second axes. The importance of the first axis was 0.325, 68.8% of the total variation.

Life forms with the highest species scores were fire-tolerant herbs (Ph-FCh), grasses (H-FH), geophytes (G-FG), alien therophytes (T-FT*) and native annuals (T-FT). Herbs, grasses-sedges and geophytes were collinear and indicated by Ph-FCh in the ordination diagram. Most grassland sites were associated with the key herb-grass functional group. Ruderal communities from moderate and dense chromolaena stands, e.g. sites 3 and 4, were colonised by important ephemeral and fire-intolerant alien and native life forms.

The eigenvalue of the second axis was 0.045 (9.5%) and cumulatively accounted for 78.3% of the variance in the species data. Life forms with the highest score on the second axis were fire-intolerant alien herbs (Ph-FT*) and grassland shrublets (Pn-FCh). Site 2a was invaded by alien herbs (e.g. *Desmodium incanum* and *Oxalis* species) under moribund conditions in 1990. The benchmark sites (1a and 1b) were plotted at the origin. Overall influence of benchmark sites on the ordination of life forms was difficult to determine after fitting covariables. The bench mark sites were richer in species than the invaded sites and contained most of the native life forms found during the study.



Coastal grasslands structure was made up of primarily of native perennial grasses, sedges and fire-tolerant herbs. The principal life forms were negatively correlated to sites with thicket infestations of chromolaena, i.e. they were found only in areas that received fire. Other important components were geophytes and annuals. Ruderal grasslands had comparatively more native annuals and shrublets than relic grasslands but were also invaded by herbaceous weeds, e.g. *Bidens pilosa* and *Conyza canadensis*.

6.3.5 Herbaceous species composition

6.3.5.1 Species distribution

Herbaceous species were monitored in seven fixed-belt-transects (1a, 1b, 2a, 2b, 3b, 4a and 4b) over 4 sites (sites 1, 2, 3, 4). Sites 1 and 2 were located on regic sands and sites 3 and 4 were on Glenrosa soils. All transects were 25-by-1 m, except 1a (60 m) and 1b (80 m) and were comprised of contiguous quadrats. A total of 214 herbaceous species were recorded of which 12 species were alien. Species were grouped by location and spread (Table 6.6).

The benchmark site (Site 1) had the largest allocation of species (48%), but was also more intensively sampled than the other sites (Table 6.6). The benchmark site was sampled over one biological year compared to several years of monitoring at sites 2, 3 and 4, i.e. Site 1 does not contain species turnover data, therefore the mean number of new species per unit area was disproportionate. The incidence and type of disjunct species, i.e. species found only at specific sites, can inferred from the successional status of each site (footnote in Table 6.6). Although the benchmark site had the highest number of unique species, proportionately disjunct to common species was between 1:1.1 and 1:1.5. Site 3 was an outlier with more common species and the ratio was 1: 10.6.

Table 6.6: Distribution of species numbers in fixed-belt-transects in coastal grasslands monitored between 1990/91 and 1997/98

Site	Transect area (m ²)	Years sampled (n)	Total species (n)	New species (n m ⁻²)	Disjunct species (n)	Shared species (n)			
						Site 1	Site 2	Site 3	Site 4
1 ^a	140	1	103	0.7	49		44	21	18
2 ^b	50	4	91	1.8	38	44		20	15
3 ^c	50	5	58	1.2	5	21	20		42
4 ^d	50	6	83	1.7	33	18	15	42	
total			214		125	54	53	53	50
%			100		58.4	25.2	24.8	24.8	23.4

^a benchmark site (pristine grassland), ^b moribund grassland

^c degraded ruderal grassland, ^d succession on bare ground

The number of species shared between sites shows a high degree of spatial overlap, despite sites being fragmented by expanses of sugar cane. The number of species confined to sites on regic sands was 115 (54%), and Glenrosa soils 64 (30%). Only seven species were found at all sites, namely *Berkheya speciosa* (the only species found in all transects), *Chaetacanthus burchellii*, *Cymbopogon validus*, *Hypoxis hemerocallidea*, *Rhynchosia totta*, *Setaria sphacelata*, *Sporobolus africanus*. Thirty five species were found on both soil types.

6.3.5.2 Indirect gradient analysis

Baseline data of herbaceous species composition in permanent transects, i.e. before repeated measures were implemented, were serially and spatially independent. Species composition was highly variable. Regic sands at sites 1 and 2 and Glenrosa soils at sites 3 and 4 were important factors. Increasing levels in chromolaena density and height from Site 2 to Site 4 also increased variability in samples. Sites 2b, 4a and 4b were monospecific in 1990 due to dense chromolaena stands and base-line data for these samples were taken from 1991. Partial DCA eliminating the influence of soil type (percentage clay) was effective. Sum of all eigenvalues amounted to 2.846 ($\lambda_1 = 0.623$, $\lambda_2 = 0.107$). Species responses were significantly unimodal, gradient length of $\lambda_1 = 4.401$. The first two axes explained 32.2% of the variance in the species data. Soil form accounted for 20.4% of the residual inertia.

The benchmark site (Site 1) was rich in species and had a higher degree of species-overlap. Transects 1a and 1b occupied central positions in the ordination (Figure 6.5) relative to the other sites. Dominant species with narrow distributions were *Gerbera kraussii* (endemic), *Ischaemum fasciculatum*, *Themeda triandra* and *Vernonia oligocephala* on regic sands (sites 1 and 2). Species with broad distribution ranges were found in the positive quadrant of the ordination diagram. *Melhania didyma*, a ruderal herb was an exception and colonised bare ground at sites 3 and 4. Based on these indicators, and the strength of the first axis (59% residual variance due to species), species compositions of sites were initially different. The greatest differences in initial community composition was between Site 2 and Site 4.

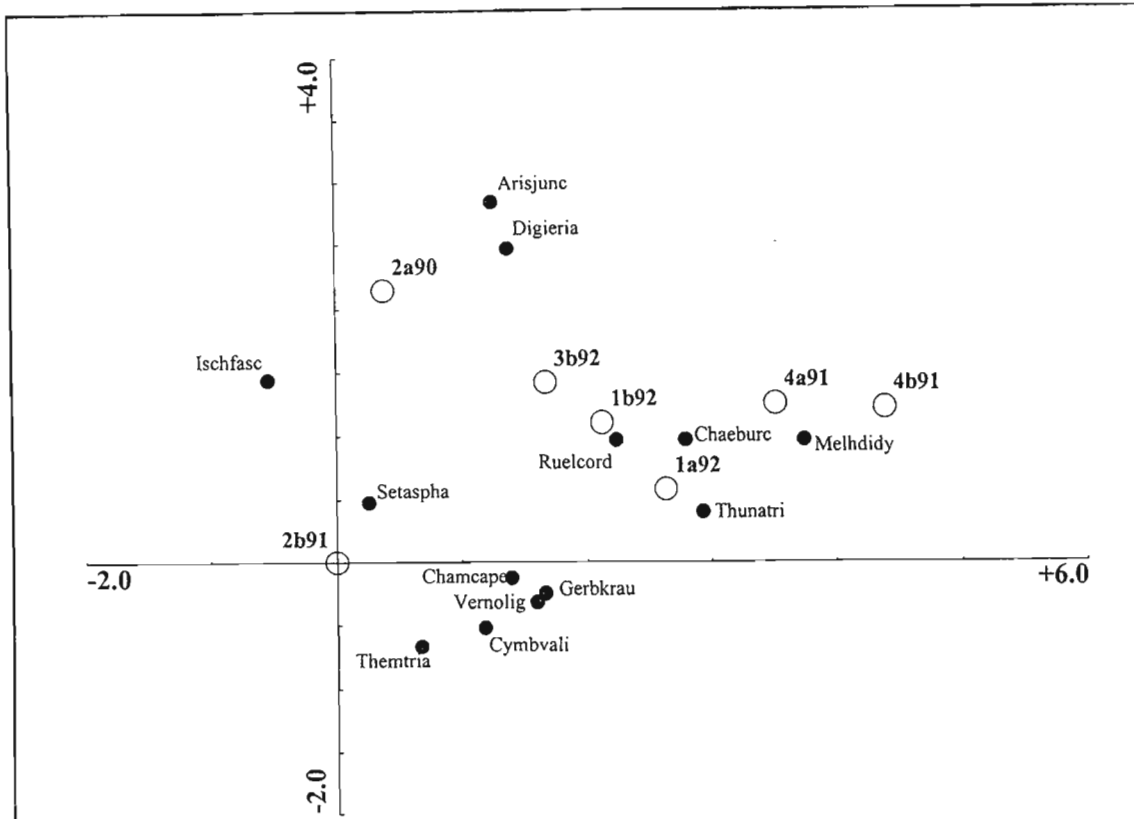


Figure 6.5: Joint plot of initial species composition after partial Detrended Correspondence Analysis along a *Chromolaena odorata* density gradient at seven coastal grassland communities. Sites are identified by a four character code, e.g. 2b91 = Site 2b in 1991. Species are displayed as the first four letters of the genus and species names, i.e. Arisjunc = *Aristida junciformis*, Chaetacanth = *Chaetacanthus burchellii*, Chamaecrista = *Chamaecrista capensis*, Cymbopogon = *Cymbopogon validus*, Digieria = *Digitaria eriantha*, Gerbkrau = *Gerbera kraussii*, Ischfasc = *Ischaemum fasciculatum*, Melhdidy = *Melhania didyma*, Ruelcord = *Ruellia cordata*, Setaspha = *Setaria sphacelata*, Themtria = *Themeda triandra*, Thunatri = *Thunbergia atriplicifolia*, Vernolig = *Vernonia oligocephala*.

Changes in species composition over time within communities was the primary aim of the study. Analysing time series data was achieved by partial DCA adjusted for covariance by including parameters identifying serially dependent samples and samples of similar soil form (Figure 6.6). Species data from 27 samples of 214 species were analysed untransformed and unweighted. Total inertia in the species data amounted to 3.810 of which 1.599 (42%) was explained by unconstrained eigenvalues. Covariables explained the remaining 58% of the variance. Eigenvalues of the first two axes were 0.378 and 0.194 with species data accounting for 36% of the cumulative segment variance. Gradient length or standard deviation units of species turnover of the first axis was 2.801.

Sites were positioned in the centre of the DCA diagram (Figure 6.6) and were located at the centroids of associated species. The benchmark site (sites 1a and 1b), occurred in the middle of the site scatter plot. Directional changes in species composition of samples over time was indicated by two major trajectories. A horizontal direction of change from right to left occurred at Site 4 compared to a vertical trajectory at Site 2 between 1990/91 and 1997/98.

Herbaceous species associated with Site 4 (both 4a and 4b) in 1991 after slashing and burning dense stands of chromolaena were ruderal herbs (*Melhania didyma*), vines (*Cyphostemma cirrhosum*) and alien species (*Solanum acanthoideum* = *S. viarum**). In 1997/98 Site 4 was typified by mixtures of ruderal and more permanent growth forms. Site 4a, however, was structurally dissimilar to 4b in both total phytomass and species composition (Figure 6.7).

Species differences in the case of vines were grassland species *Rhynchosia totta* and *Vigna vexillata* at 4a, in contrast with forest vines *Dioscorea cotinifolia*, *Protasparagus falcatus* and *Smilax anceps* at 4b. *Hyparrhenia tamba* and *Setaria sphacelata* were dominant grasses at Site 4a in 1997/98. Dry matter production at Site 4a went from zero cover in 1990 to 7.6 t ha⁻¹ in 1997. Phytomass at Site 4b was also zero in 1990 but total phytomass in 1997 was only 0.4 t ha⁻¹ with *Oplismenus hirtellus* having the highest relative frequency in the grass category.

Site 3b showed minor deviation in the ordination between 1992 and 1997 (Figure 6.6). The only species showing major reduction in local frequency was *Melhania didyma* which was lost from 17 out of 25 quadrats between start and end dates (Appendix D, Table D2). Species showing major increase in local frequency were *Hyparrhenia tamba*, *Cymbopogon validus* and *Sporobolus africanus*. *Cymbopogon validus* (solid up triangle) is positioned to the left of *Setaria sphacelata* in the ordination diagram (Figure 6.6). Total phytomass increased from 2.7 t ha⁻¹ in 1992 to 8.6 t ha⁻¹ in 1997/98 with *H. tamba* and *E. curvula* having the highest local frequencies (Figure 6.7).

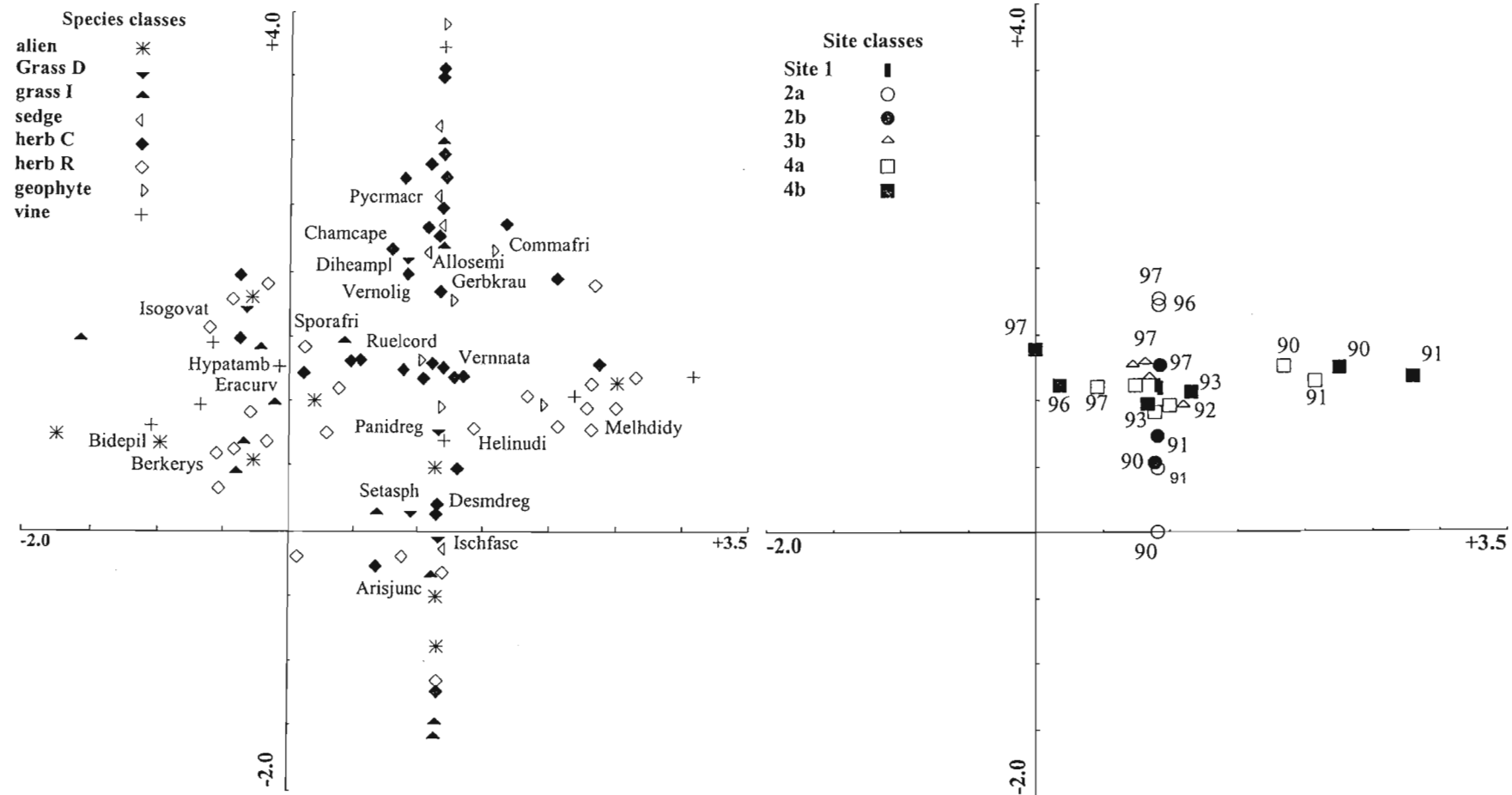


Figure 6.6: Joint plot by partial Detrended Correspondence Analysis in which species turnover along a *Chromolaena odorata* density gradient in coastal grassland communities is presented. The influence of repeated measures (serial dependency) and soil form were removed by the addition of covariables. Species composition from repeated monitoring in fixed-belt-transects contains community data from 1990/91 to 1997/98. Species and sites are displayed as separate diagrams to optimise visibility thresholds of species positions in ordination space. Species were grouped into eight growth form classes (left diagram) according to Appendix B. Classes 'alien', 'sedge', 'geophyte' and 'vine' are self explanatory. Successional classifications were accorded to grasses and herbs (Trollope *et al.* 1990), viz. decreaser grasses (grass D), increaser grass (grass I), climax herbs (herb C) and ruderal herbs (herb R). Successional status of herbs were based on species occurrences along sample condition gradients. Samples presented in the diagram on the right are identifiable from the legend of site classes. The year of monitoring is indicated next to site symbols. Plant names of dominant species are presented as the first four letters of the genus and species. Full scientific names in alphabetical order are as follows: *Alloteropsis semialata* (=Allosemi), *Aristida junciformis*, *Berkheya erysithales*, *Bidens pilosa**, *Chamaecrista capensis*, *Commelina africana*, *Desmodium dregeanum*, *Diheteropogon amplexans*, *Eragrostis curvula*, *Gerbera kraussii*, *Helichrysum nudifolium*, *Hyparrhenia tamba*, *Ischaemum fasciculatum*, *Isoglossa ovata*, *Melhanidia didyma*, *Panicum dregeanum*, *Pycneus macranthus*, *Ruellia cordata*, *Setaria sphacelata*, *Sporobolus africanus*, *Vernonia natalensis*, *V. oligocephala*.

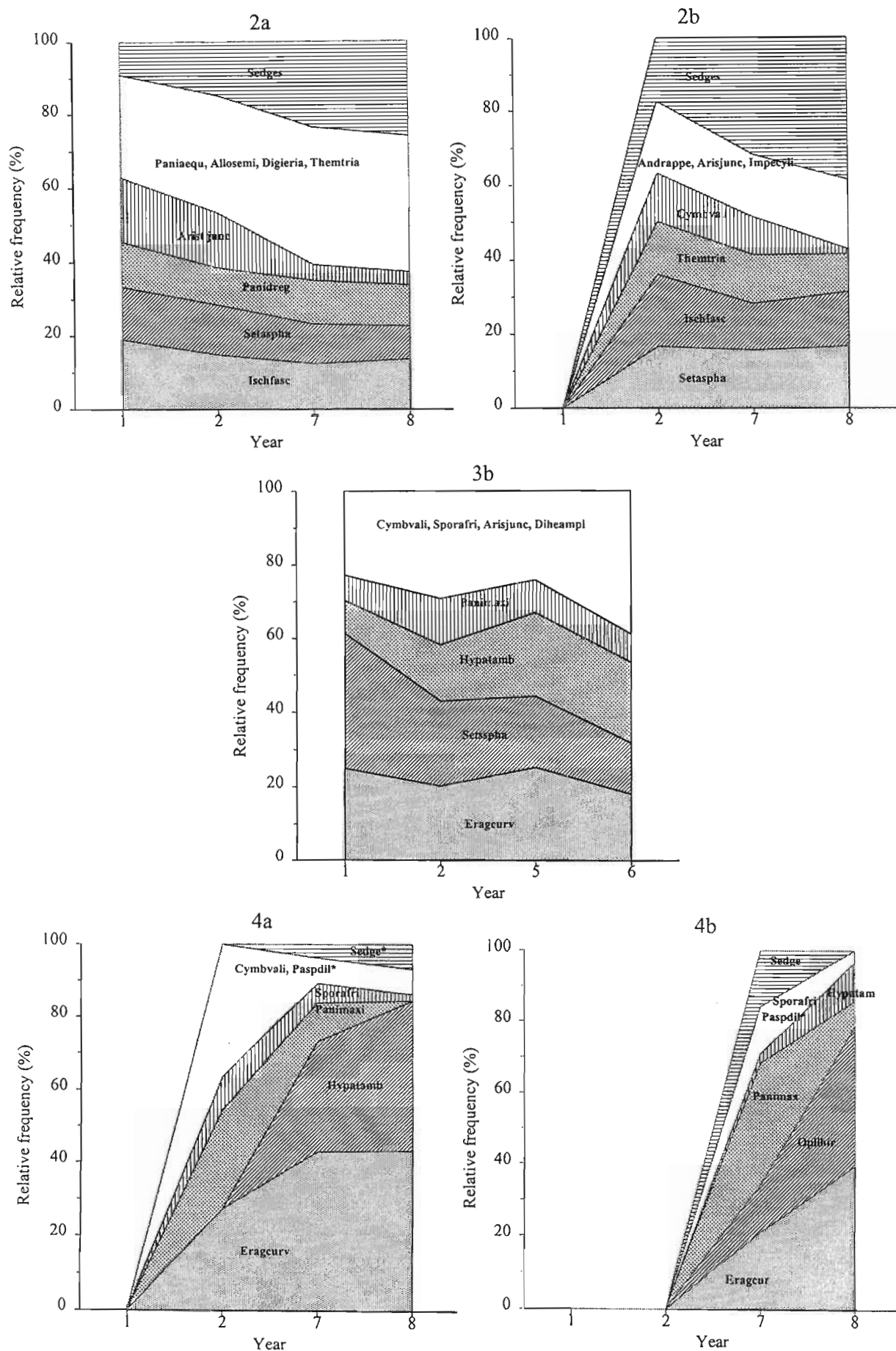


Figure 6.7: Changes in the relative frequency of dominant species found in degraded coastal grassland sites over the study period. Asterisks denotes alien species. Species names for acronyms are found in Appendix B.

The second major trajectory of change distinguishable by a vertical shift in sample position, occurred at Site 2. Species temporarily associated with the unutilised moribund community in 1990 to 1992 were increaser grasses (*Aristida junciformis*, *Cymbopogon validus*, *Eragrostis plana*), atypical indigenous grassland herbs (*Asystasia gangetica*, *Helichrysum panduratum*) and alien species (*Desmodium incanum*). In 1997 species turnover was reflected by the presence of a large suite of grassland herbs (*Chamaecrista capensis*, *Vernonia oligocephala*), sedges (*Pycreus macranthus*) and geophytes (*Commelina africana*). Graminoid species were dominated by sedges (Figure 6.7) by the end of the study. The most notable change in relative frequency was the reduction in *Aristida junciformis*. The three dominant grasses were decreaser species, namely *I. fasciculatum*, *Panicum dregeanum* and *Setaria sphacelata*. Turnover in grass species were also significant with suites of unpalatable species of 1990 being replaced by suites of other unpalatable increaser species (e.g *Alloteropsis semialata*, *Imperata cylindrica*, *Tristachya leucothrix*).

Species in the centre of the DCA diagram were associated with the benchmark site (Site 1) and Site 2 throughout the study period. Site 2 was therefore associated with palatable and unpalatable species. In order of species position vertically from bottom to top, *Digitaria eriantha*, *Ischaemum fasciculatum*, *Panicum dregeanum*, *Themeda triandra* and *Diheteropogon amplexans* were important desirable species throughout the study.

6.3.5.3 Direct gradient analysis

Exploratory data analysis by CCA was carried out on all environmental variables to ascertain their interrelation (Table 6.7). Species and environmental sample scores of the first two ordination axes were uncorrelated after adjusting for covariables. The first and second axes of the species-environment inter-set were correlated (shaded area). Intra-set correlations between environmental variables and samples scores showed that chromolaena was highly correlated to scores on the first axis. Lantana was also correlated with the first axis, but the effect was weaker than that of chromolaena. Fire frequency was moderately correlated to scores on the second axis. The remaining environmental variables did not show strong relations with sample scores.

Table 6.7: Weighted partial correlation matrix (weight = sample total) among environmental variables of the first and second ordination axes of a Canonical Correspondence Analysis without forward selection

	SPEC AX1	SPEC AX2	ENVI AX1	ENVI AX2
SPEC AX1	1.00			
SPEC AX2	0.00	1.00		
ENVI AX1	0.98	0.00	1.00	
ENVI AX2	0.00	0.95	0.00	1.00
fire	-0.37	0.67	-0.38	0.70
chromolaena	0.92	0.11	0.94	0.12
lantana	-0.67	0.16	-0.68	0.17
bugweed	-0.43	-0.20	-0.44	-0.22
guava	-0.19	0.20	-0.20	0.21
bushes	-0.18	-0.37	-0.18	-0.39
shrubs	0.10	0.12	0.10	0.13
trees	0.00	0.08	0.00	0.08
bare ground	0.59	-0.29	0.61	-0.31

The amount of bare ground was negatively correlated with fire frequency (Table 6.8). Bare ground was calculated by subtracting aerial grass (= plant or quadrat) cover from 100%. Grass cover, from prior analysis (not shown), was collinear with fire frequency. Chromolaena abundance was also correlated with bare ground, i.e. grass cover was negatively associated with increasing chromolaena density. The remaining environmental variables showed modest correlations, range -0.51 to 0.42.

Table 6.8: Correlation matrix among environmental variables used in the Canonical Correspondence Analysis of the herb data from coastal grassland communities degraded by alien and indigenous woody vegetation. Correlation coefficients are adjusted for covariables

	fire	chromolaena	lantana	bugweed	guava	bushes	shrubs	trees
fire	1.00							
chromolaena	-0.37	1.00						
lantana	0.22	-0.49	1.00					
bugweed	0.28	-0.40	0.42	1.00				
guava	0.15	-0.16	-0.02	-0.50	1.00			
bushes	-0.11	-0.41	-0.01	0.16	-0.38	1.00		
shrubs	-0.11	0.34	0.08	0.28	-0.16	-0.51	1.00	
trees	0.00	0.11	0.40	0.10	-0.51	-0.10	0.06	1.00
bare ground	-0.84	0.66	-0.20	-0.32	-0.32	-0.10	0.36	0.19

Guava and bare ground had excessive VIF values (Table 6.9). Bare ground showed multiple collinearity with fire frequency and chromolaena (Table 6.8). Variance Inflation factors are dependent on, among other variables, the number of samples. Only one guava specimen was recorded in the study which persisted at Site 3, thus recording the lowest weighed mean of all the environmental variables (0.25) with a CV of 175%. This is compared to the weighted means of chromolaena (103), bushes (70) and bugweed (20). The remaining VIFs were within accepted limits (< 20).

An unrestricted global permutation test concluded the exploratory analysis. The test was run using 199 random permutations under the reduced model. The eigenvalue of the first canonical axis was 0.316 and F-ratio statistic 2.267 ($P = 0.08$). Based on all nine environmental variables the first canonical axis was not significant. The sum of all canonical eigenvalues (trace) was significant (1.043), F-ratio = 2.39 ($P < 0.01$). Although the relation between species and the environmental variables was significant across all canonical axes, interpretations were based on the first two axes only, hence the need for a minimal model.

Table 6.9: Variance inflation factors (VIF) of environmental variables used in the Canonical Correspondence Analysis of coastal grassland data

Variable name	Variable No.	Variance Inflation Factor
fire frequency	1	10.8
chromolaena	2	5.3
lantana	3	12.1
bugweed	4	15.5
guava	5	56.9*
bushes	6	13.6
shrubs	7	12.7
trees	8	14.9
bare ground	9	55.5*

The environmental variables best explaining the variance in the species data were determined through a process of elimination by forward selection, with *post hoc* significance testing by the Monte Carlo permutation method (Table 6.10).

Table 6.10: Ranking environmental variables by their marginal (individual = λ_1) and conditional (combined = λ_a) effects on herbaceous species composition by forward selection. Cumulative total eigenvalues (cum λ_a) of significant effects were obtained by Monte Carlo permutation test under the reduced model of 199 random permutations. Variation attributed to autocorrelation were partialled out by taking site class variables as covariables

Marginal Effects			Conditional Effects					
Variable	Var. N	λ_1	Variable	Var. N	λ_a	P	F	cum (λ_a)
chromolaena	2	0.29	chromolaena	2	0.29	0.01	4.1	0.29
bare ground	9	0.2	fire frequency	1	0.16	0.005	2.4	0.45
lantana	3	0.2	lantana	3	0.11	0.035	2	0.56
fire frequency	1	0.18	guava	5	0.12	0.07	2	-
bugweed	4	0.15	bare ground	9	0.1	0.085	1.7	-
guava	5	0.13	trees	8	0.08	0.15	1.5	-
bushes	6	0.12	bushes	6	0.07	0.175	1.5	-
trees	8	0.07	bugweed	4	0.07	0.165	1.4	-
shrubs	7	0.05	shrubs	7	0.04	0.56	0.9	-

In the first step of the forward selection procedure environmental variables were ranked on the basis the fit for each variable (λ_1 under Marginal Effects of Table 6.10). Chromolaena was ranked highest, if it was the only environmental variable the first eigenvalue would be 0.29. Variables listed after chromolaena are in order independent fit. At the end of the first step the best variable, i.e. chromolaena, was selected as the first factor under Conditional Effects (Table 6.10). The remaining variables were added on the basis of additional fit. Only fire and lantana provided extra fit that was statistically significant ($P < 0.05$).

The eigenvalues of the first two canonical axes (Figure 6.8) were 0.303 and 0.157, accounting for 15.6% of the total inertia (2.953). Covariables explained 1.523 (51.6%) of the inertia and environmental variables, after eliminating covariables, 0.563 (19.1%). Cumulative percentage variance of the species-environment relation of the first two axes was 81.8%. Unexplained inertia came to 29.3%. The sum of all unconstrained variables, 1.43, contributed 32.2% of the variance in species data of first and second axes. The relation between environmental variables and species on the first axis and across all axes were highly significant (F-ratios > 3 , $P < 0.01$).

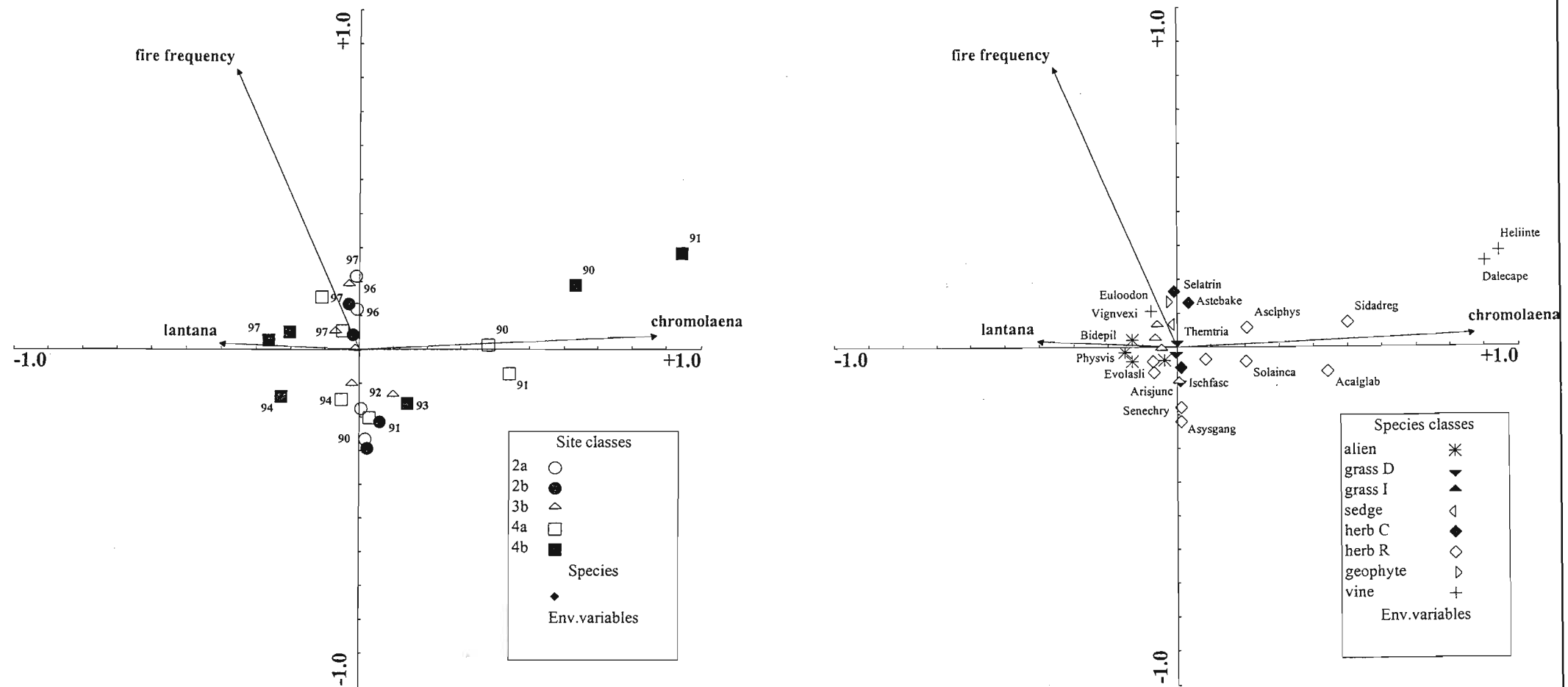


Figure 6.8: Species-conditional triplot by partial Correspondence Analysis of herbaceous coastal grassland composition with respect to woody alien invader species (*Chromolaena odorata* and *Lantana camara*) and fire frequency between 1990/91 and 1997/8. Sites are labelled in accordance with the legend and depict the year in which they were monitored. Environmental variables are indicated by arrows. Species and sites are displayed as separate diagrams to optimise visibility thresholds of species positions in ordination space. Species were grouped into eight growth forms (right diagram) according to Appendix B. Classes 'alien', 'sedge', 'geophyte' and 'vine' are self explanatory. Successional classifications were accorded to grasses and herbs (Trollope *et al.* 1990), viz. decreaser grasses (grass D), increaser grass (grass I), climax herbs (herb C) and ruderal herbs (herb R). Successional status of herbs were based on species occurrences along sample condition gradients. A total of 165 herbaceous species were analysed, comprising 12 alien species, 11 decreaser grasses, 15 increaser grasses, 10 sedges, 41 climax herbs, 43 ruderal herbs, 18 geophytes and 15 vines. Plant names are presented as the first four letters of the genus and species. Full scientific names are: *Acalypha glabrata* (=Acalglab), *Aristida junciformis*, *Asclepias physocarpa*, *Aster bakerianus*, *Asystasia gangetica*, *Dalechampia capensis*, *Evolvulus alsinoides*, *Eulophia odontoglossa*, *Helinus integrifolius*, *Ischaemum fasciculatum*, *Physalis viscosa**, *Selago trinervia*, *Senecio chrysocoma*, *Sida dregei*, *Solanum incanum*, *Themeda triandra*, *Vigna vexillata*. Scaling of species and site coordinates were 0.1525 and 1 for environmental variables was.

Most of the turnover was the effect of covariables explaining serial variances (within) of sites over time, i.e. differences in species abundance between surveys. The directional trend depicting gross changes in species compositions of sites over time in the DCA analysis (Figure 6.6), was repeated in the CCA analysis. The first axis of the CCA diagram (Figure 6.8) can be interpreted as a transition gradient from chromolaena transformed vegetation (right), through a ruderal herbaceous community (centre), to an alternative transformed vegetation dominated by lantana (left). The second axis is the restoration gradient where ruderal communities dominate below the first axis and disclimax communities occur above it.

Dense chromolaena was positively correlated with bare ground, the latter negatively correlated with fire frequency (Table 6.8). Sites associated with increasing chromolaena abundance were therefore severely degraded (sites 4a and 4b). With exposure to fire sites 4a and 4b shifted horizontally along the first canonical axis from right side of the CCA diagram (Figure 6.8) to the left side. Both sites were associated with ruderal herbs (e.g. *Sida dregei*), vines and herbaceous alien species.

Lantana was negatively correlated with chromolaena but was still associated at sites with dense chromolaena (i.e. 4a and 4b). Lantana was an important secondary alien invader of chromolaena-transformed grassland undergoing transitions towards ruderal grassland. Bugweed was also an important invader although it was not included in the conditional model. Its marginal effect (Table 6.10), $\lambda_1 = 0.15$, amounted to 11% of the sum of marginal eigenvalues, compared with chromolaena (21%) and lantana (14%). Site 4b in 1997 was dominated by chromolaena and lantana (also bugweed). Herbaceous species associated with Site 4b at the end of the study were predominantly shade tolerant ruderal herbs and alien species. This site was slashed and burnt in 1991 but chromolaena seedlings were left (Chapter 5). Fire was not able to enter the site because of low grass cover (collinear with fire). Site 4b, although showing the greatest directional change, remained infested with chromolaena. Site 4a, also slashed and burnt in 1991, did receive one follow-up treatment removing seedlings. This action encouraged some pioneer grass establishment. The net result was that Site 4a could receive the benefits of fire as was less severely affected by chromolaena, lantana and bugweed. Site 4a at the end of the study was comprised of a mixture of ruderal and climax grassland species which facilitated fires to enter and keep

chromolaena suppressed. Lantana and bugweed, however, were fire resistant and coppiced after the burn. Fire alone was unable to maintain a controlling effect on these species and the site will probably shift from ruderal grassland back to an alien dominated vegetation, this time occupied by hardier species.

Site 3b in 1990 was also invaded by chromolaena, but at lower densities compared to Site 4. It was initially comprised of both ruderal and climax grassland species. Over time the effects of fire frequency resulted in a vertical shift towards a community that was in a more advanced successional state than Site 4a. At the end of the study Site 3b was not plagued by woody alien species although lantana and guava were rare species (fire-suppressed regrowth). Site 2a and 2b showed greater magnitudes of vertical change in species composition responding to fire than Site 3. Sites 2a and 2b were both species rich communities at the end of the study.

The impact of chromolaena appears to have had a residual effect on restoration. Site 2a had the least amount of chromolaena and culminated in the greatest degree of restoration. Site 2b had more chromolaena plants per unit area initially than did Site 3b, but infestation height was lower. Site 2b did not achieve the same degree of recovery as Site 2a, and 3b was even less. Sites 4a and 4b had dense chromolaena stands and showed marginal change in the direction of restoration.

Indigenous woody vegetation was not included in the minimal model. Their conditional effects on grassland species composition were not significant (Table 6.10) compared with the conditional effects of alien species. This suggests that grassland communities are degraded at a slower rate by indigenous woody species than by chromolaena or other woody alien species.

Thirty-nine families of 214 species found in fixed-belt-transects followed a pattern perhaps typical of mesic secondary grasslands (Table 6.11). Poaceae, the second most important family, and sedges (Cyperaceae), contributed the bulk of the phytomass. Asteraceae (daisy family) and Fabaceae (pea-legume family), the largest of all the flowering plant families, were the most important 'herb families'. Herbs of the family Acanthaceae were also a recurring component of grasslands. Growth forms were not unique to sites, as already discussed in section 6.3.4.2.

Table 6.11 Contribution of families to herbaceous plant succession in fixed-belt-transects at five coastal grassland communities with condition degradation gradient ranging from pristine (Site 1) to modified (Site 4)

FAMILY	Species	Site						
	(n)	1a	1b	2a	2b	3b	4a	4b
ACANTHACEAE	7	5 ⁴	4 ⁵	3 ⁵	1	3	5 ⁵	2
ADIANTACEAE	1	1	0	1	0	0	0	0
AMARANTHACEAE	1	0	0	0	0	0	1	0
APIACEAE	3	3	2	1	1	0	0	0
ASCLEPIADACEAE	2	0	0	1	1	0	0	0
ASPARAGACEAE	1	0	0	0	0	0	0	1
ASPHODELACEAE	7	1	1	3 ⁵	2	1	2	0
ASTERACEAE	36 ¹	14 ¹	16 ²	12 ²	11 ²	11 ²	12 ¹	8 ¹
COMMELINACEAE	4	1	2	2	1	1	1	0
CONVOLVULACEAE	5	2	1	1	2	1	2	1
CUCURBITACEAE	1	1	1	0	0	0	0	0
CYPERACEAE	14 ⁴	4 ⁵	5 ⁴	7 ⁴	8 ³	0	1	1
DIOSCOREACEAE	1	0	0	0	0	0	0	1
EUPHORBIACEAE	8	2	3	0	0	3	6 ⁴	3 ⁴
FABACEAE	24 ³	12 ³	11 ³	9 ³	8	12 ¹	9 ³	1
HYACINTHACEAE	1	0	1	0	0	0	0	0
HYPOXIDACEAE	5	4	3	2	2	1	1	0
IRIDACEAE	6	2	2	3 ⁵	2	0	0	0
LAMIACEAE	4	0	0	2	1	1	2	1
LOBELIACEAE	1	1	1	1	1	0	0	0
MALVACEAE	9 ⁵	0	0	0	2	6 ⁴	6 ⁴	6 ³
MYRTACEAE	1	0	1	0	2	0	0	0
Unidentified	6	0	1	0	0	4 ⁵	2	0
ORCHIDACEAE	3	1	0	0	1	0	1	0
OXALIDACEAE	4	1	0	1	2	0	1	0
POACEAE	34 ²	13 ²	18 ¹	17 ¹	15 ¹	10 ³	11 ²	7 ²
POLYGALACEAE	3	1	1	0	1	2	2	1
POLYGONACEAE	1	0	0	1	0	0	0	0
RHAMNACEAE	1	0	0	0	0	0	0	1
RUBIACEAE	4	3	1	1	0	0	0	0
SANTALACEAE	1	0	0	1	1	0	0	0
SCROPHULARIACEAE	4	3	2	1	0	0	0	0
SELAGINACEAE	2	1	1	1	1	0	0	0
SMILACAEAE	1	1	1	0	0	0	0	1
SOLANACEAE	3	0	0	0	0	0	3	3 ⁴
STERCULIACEAE	1	0	0	0	0	1	1	1
THYMELAEACEAE	2	2	2	0	0	0	0	0
TILIACEAE	1	0	0	0	0	0	1	1
VITACEAE	1	0	0	0	0	0	1	1
39	214	79	81	71	66	57	71	41

Numbers in superscript indicate ranked order of importance

Ruderal, 'weedy' species of the families Euphorbiaceae (*Acalypha* and *Phyllanthus*), Malvaceae (*Hibiscus* and *Sida*), Sterculiaceae (*Melhania*) and Tiliaceae (*Triumfetta*) characterised the successions on sites 3b, 4a and 4b. The drought had a severe impact on these genera by significantly reducing their local abundances. During resumption of more favourable conditions in 1994, these species resumed dominance once again, suggesting that these observations were real changes and not merely an incidental factor of sampling intensity. It also suggests that succession could not proceed without these ruderal cohorts concluding their modifying role of local growing conditions on sites 3b and 4a.

Convolvulaceae (*Ipomoea* and *Evolvulus*), Cucurbitaceae (*Trochomeria*), Smilacaceae (*Smilax*) were found along a range of environmental gradients, however, shade-tolerant creepers Dioscoreaceae (*Dioscorea*) and Vitaceae (*Cyphostemma*) only occurred in 4a and 4b prior to the initial treatment and again in 4b towards the end of the study. Geophytic herbs (Asphodelaceae, Commelinaceae, Hypoxidaceae, Hyacinthaceae, Iridaceae and Orchidaceae) were more prevalent on sites least affected by woody species.

6.4 Discussion

The coastal grasslands studied were species-rich communities. Richness at the benchmark sites ranged, on average, from 19 to 23 species m⁻², similar to diversity patterns in *T. triandra* grasslands in southeastern Australia (Morgan 1998). Invading chromolaena, more so than forest succession, eliminated grassland species by forming monospecific thickets. Chromolaena established in absence of fire and increased in density. The height-density relation of rapidly expanding infestations resulted in species extinctions by intercepting light. Below optimal irradiation resulted in precipitous declines in species richness. Allelopathy through leaching of essential oils and alkaloids may have also contributed to the process of rapid degradation (Biller *et al.* 1994; Erasmus 1985).

According to D' Antonio and Vitousek (1992), chromolaena was introduced into Asia and West Africa to interrupt the native grass-fire cycle and to restore rain forest. The South African form of chromolaena also prevented woody plant succession from progressing as well as destroying grassland. Chromolaena has subsequently become a far greater threat to the West African rain forest zone than the combined influence of fire and slash and burn

agriculture (de Rouw 1991; M'Boob 1991; Gautier 1994; Slaats 1995).

Herbaceous species showed variable degrees of tolerance to chromolaena density. Although untested, soil type was important in partitioning densities of chromolaena infestations. Chromolaena thickets on regic sands were comprised of smaller and more slender bushes than thickets on Glenrosa sites. Herbaceous species colonising monospecific sites on sand resembled assemblages from disclimax grassland. Species colonising bare ground on tillite soils were made up of ruderal forms.

Patterns in turnover showed that species entering and leaving the system were phenomena of every site studied, irrespective of woody plant density. Absolute turnover (see sensitivity, Section 4.3.3.2), i.e. the gross change (=modulus of gain and loss), was higher in sites colonising bare ground. Secondary succession, i.e. the colonisation of bare soil (McCook 1994) by a cohort of ruderal indigenous and alien species, either weakly perennial or annual, typified severely degraded communities in the beginning. Pioneer grasses *E. curvula*, *S. sphacelata* and *H. tamba* persisted in communities initially affected by moderate to dense infestations of chromolaena. *Oplismenus hirtellus*, *P. maximum* and *S. megaphylla* established under shady to partly shady conditions, the former species disappearing under conditions of increasing light in response to burning.

Patterns in turnover were not analysed to the same degree as Morgan (1998) yet similarities were evident. A vast difference in species associations existed on more permanent grassland sites than did grasslands replaced by woody plant encroachment (Plates 1 to 4). Niche specialisation was an important process in sandy grasslands. Open grasslands rich in species had fewer therophytes than degraded grasslands, but those that occurred persisted, namely *P. aequinerve* and *Chamaecrista capensis*.

The results differed from Rutherford and Westfall's (1994) analysis of the dominance of life forms in the savanna biome. Firstly, broadleaved herbs were not mentioned in their study. Their definitions for life forms could have accommodated herbs as being either phanerophytes or chamaephytes, although the latter appeared more appropriate. Secondly, only one savanna region from the Northern Province lowveld was used in the breakdown of

life forms. Hemicryptophyte importance was marginally lower in coastal grasslands but geophytes, chamaephytes and therophytes were significantly higher than the Rutherford and Westfall (1994) synthesis.

Grassland texture was also different, open grasslands were characterised by a short fine sward no taller than 0.75 m, whereas ruderal grasslands were coarse and tall (1 to 2 m) with a spiny herbs, e.g. *Berkheya erysithales* and *Dicoma speciosa*. Annual fires promoted recruitment and persistence of species-rich communities, in keeping with Morgan (1998) but fires were also responsible for the elimination perennial alien species *Desmodium incanum*, *Oxalis corniculata* and *O. latifolia*. The alien grass *Paspalum dilatatum* was not affected by fire, but was unable to become dominant. Alien grasses are a growing concern throughout the world, except in Africa, because they have the potential for increasing fire frequencies and introducing fire cycles into climates where fires are rare events (D'Antonio & Vitousek 1992). Only two grass species are declared weeds in South Africa, *Nassella tenuissima* and *N. trichotoma* (Henderson 1995).

The association between *A. junciformis* and *T. triandra* is well documented yet poorly understood (O'Connor 1985; Westoby *et al.* 1989; Morris *et al.* 1992). *Aristida junciformis* declined sharply from 100% frequency to 24% in sandy soils of Site 1a under conditions of long rest (six to seven years) and annual burning. Under the same conditions *T. triandra* increased from 8% to 52%. *Aristida junciformis* was found a weak competitor in grasslands maintained by management practices that adopted (nonselective) defoliation strategies, i.e. annual burning without grazing, mowing or nonselective grazing (van Zyl 1998; Tainton 1999). *Themeda triandra*, on the other hand, benefited from conditions of zero grazing with annual burns. It is proposed that a tradeoff occurred between *A. junciformis* and *T. triandra* under prevailing conditions of high inter-specific competition created through increasing plant production and diversity. In a system of limited resources niche overlap is very small. If the overlap zone cannot supply the demand for key resources, competitive exclusion of less efficient species will result (Giller 1984). *Aristida junciformis* was a species that was unable to dominate under conditions of increasing species richness and biomass (diffuse interspecific competition), and local frequency was reduced under conditions promoting successional replacement.

Failure on the part of the farmer to maintain veld burning once sites become fragmented, resulted in indigenous woody plant successions that in time, would have replaced grassland species. The arrival of chromolaena accelerated the rate of grassland degradation. Poor grass seed dispersal and longevity of soil-seed reserves (O'Connor 1991a, 1991b; Dzwonko & Loster 1998) were probably the principle reasons why site 3b recovered faster than 4a. When invasion results in the complete removal of vegetation succession starts with phytochrome mediated germination responses of pioneer species, allowing for rapid colonisation of disturbed areas (Mbalo & Witkowski 1997). Fragmented grasslands transformed by dense infestations of chromolaena were not colonised by grass species for several years. Grass colonisation was slow and was typified with the arrival of residual pioneer species, e.g. *E. curvula*. This trend was reported by Dzwonko and Loster (1998) in abandoned limestone grasslands in Poland.

Unlike patterns of grazing where selective herbivory is responsible the elimination of certain grass species (O'Connor 1991b), woody alien invasions had the property of indiscriminate and complete suppression of grassland vegetation. The general consensus from many natural scientists are that most ecosystems are nonequilibrium systems (e.g. Tansley 1935; Shugart & West 1981; Runkle 1982; DeAngelis & Waterhouse 1987; Sprugel 1991; Whalley 1994). The effects of livestock grazing in semi-arid rangelands are known examples of non-equilibrium communities (Westoby *et al.* 1989). Although coastal grasslands are seral to forest in the absence of fire, the evidence provided in this chapter cannot support that notion that coastal grasslands are equilibrium communities and non-equilibrium dynamics are exacerbated by the arrival of woody alien species.

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 Synthesis

Chromolaena odorata invades coastal grasslands and replaces species-rich communities with monospecific thickets in a short time. The principal determinant for the establishment of chromolaena was the lack of fire. Soil type was of secondary importance in the role of supporting chromolaena infestations, but it was a major determinant of the rate and type of woody plant successions responding to fire exclusion. The processes responsible for inducing changes in species composition were not investigated. Research suggests that root competition (Slaats 1995), allelopathy (Hamilton *et al.* 1993) and shading (de Foresta & Schwartz 1991) by chromolaena are the main factors causing undesirable changes in natural vegetation.

Grass, shrubs and trees in savanna ecosystems coexist because these life forms exploit soil moisture at different depths (Scholes 1997). In coastal grasslands these factors are inconsequential in early forest or savanna succession compared with the rate of chromolaena establishment. The roots of chromolaena are superficial, feeding in upper 10 cm of the topsoil (Slaats 1995), spreading laterally with only a few roots penetrating deeper. Veld grasses can produce rooting depths up to one metre, depending on the species (Dr R Bennet pers. comm., Agricultural Research Council, PO Box 1055, Hilton 3245). The bulk (about 80%) of grass roots in natural grasslands, however, is concentrated in the top 15 to 20 cm of the soil (Dr E. Granger, University of Natal, Private Bag X01, Scottsville 3209). It is therefore feasible that chromolaena is a major competitor for soil moisture with the added advantage of growing taller than the sward and casting shade. Competition for moisture, light and the affect of allelopathic compounds in the leaves, shoots and roots (Gill *et al.* 1993; Hamilton *et al.* 1993; Biller *et al.* 1994) may be major process causing rapid structural-breakdown in herbaceous plant communities. Chromolaena is therefore a key species responsible for degradation in coastal grasslands, the rates being relative to soil type.

Infestations on regic sands were not as tall and dense as infestations on tillite soils. Fire was effective in killing chromolaena populations in a range of densities. Dense stands on tillite soils were cut down before they would burn, but stumps were killed by fire. Factors affecting chromolaena flammability were grass phytomass, fire intensity and timing of burns.

Infestations are highly flammable in August to early September if no rain falls over winter. Hot fires were most effective at reducing woody plant biomass and promoting grass establishment. Head-fires were effective at knockdown of savanna species and thicket vegetation, but even cool burns caused high mortality of chromolaena and forest species. Grass cover of 30%, or grass dry matter production of 1 t ha^{-1} , were effective at reducing chromolaena under normal veld burning conditions.

Follow-up burns were effective for controlling chromolaena seedlings. Grass production and aerial cover responded strongly to declining chromolaena populations. On tillite soils dense stands killed in slash and burn operations were replaced by dense stands of chromolaena seedlings, suppressing natural grass establishment. Minimal integration with other control methods in the first year of follow-up affected rehabilitation. One operation involving the selective removal of chromolaena seedlings resulted in sufficient grass establishment allowing fires to keep chromolaena at low densities. In situations where other alien species such as *Lantana camara* and *Solanum mauritianum* become secondary invaders, chemical control using selective broadleaf weedkillers, so as not to kill grass, must be integrated with fire. Fire did not kill the roots of lantana and bugweed and chemical control targeting the regrowth must continue if these species are a component of the vegetation.

Coastal grasslands affected by chromolaena may not return to their original composition, but to an inferior grassland dominated by undesirable species such as *Eragrostis curvula* and *Hyparrhenia tamba*. Open grasslands on tillite soils were prone to woody plant succession that fire was unable to reverse. Light infestations can be restored cheaply through the application of a burning programme. Therefore, of highest priority in coastal grassland restoration is the burning of grasslands with light infestations.

7.2 Non-equilibrium

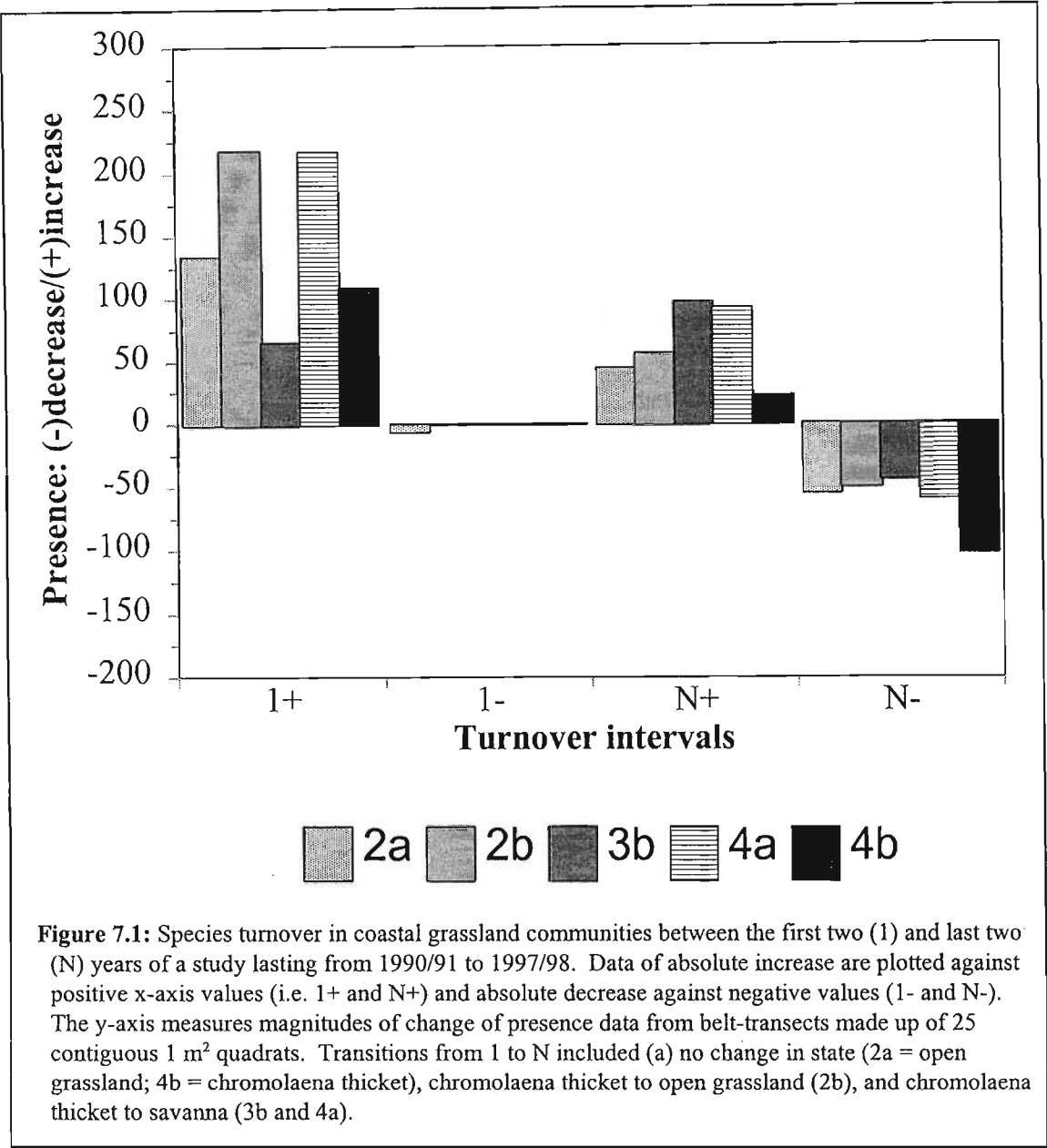
Resilience in natural communities is ability to persist by absorbing the effects of disturbance and still retaining biological structure and function (Begon *et al.* 1990). Stability is the ability and rate of communities returning to an equilibrium state after disturbances (Holling 1973). Both properties were found in coastal grasslands but in different proportions, depending on condition and soil type. The integration of properties of resilience and stability

have been used in polyclimax theory (Tansley 1935) under the notion that ecosystems can function in alternate states. In contrast monoclimax (Clements 1916) ecosystems are said to be in equilibrium with their environment, and return to the original state after disturbances.

The major forms of disturbances encountered during this study were chromolaena density and fire frequency. The effects of tree and shrub successions of both indigenous and secondary alien invasions were largely dampened by rapid chromolaena (re)establishment and the absence or inability of fire to enter systems without fine fuels. Chromolaena induced negative effects such as rapid breakdowns in community structure. Fire reduced chromolaena abundance and on regic sands the effects of structural-breakdown were reversed. On tillite soils the vegetation structure was altered by the absence of fire, but the reintroduction of burning, with follow-up control, failed to restore the original state. In cases where follow-up control integrating mechanical or chemical control with burning was not undertaken, systems reverted to chromolaena thickets. It is therefore suggested that ecological systems persist under high turnover (unstable) and zero turnover (stable). Both extremes depend on the ecological complexity (condition) of the systems in question, e.g. the number of species, population sizes, niche overlap, component life forms, functional attributes, key species and inter- and intraspecific interactions.

Serial differences in species frequencies between observations, i.e. an absolute increase opposed to absolute decrease (see sensitivity, Section 4.3.3.2), were used to illustrate stability dynamics in some degraded coastal grasslands. Species turnovers between the first two and last two years in sparse (Site 2a), moderate (Site 3b) and dense (sites 2b, 4a and 4b) chromolaena, were plotted to detect stability under different condition states (Figure 7.1).

Absolute increase in species presence values from 1990/91 to 1991/92 (1+ in Figure 7.1) were variable. Nevertheless, monospecific sites (i.e. under dense chromolaena) showed the greatest response (i.e. 2b and 4a). Most sites did not detect decreases in species local frequency (the loss of species from some or all quadrats) in the first turnover interval, except Site 2a under sparse chromolaena. Three out of the remaining four sites were monospecific and since chromolaena was present in all quadrats in the first two years, zero turnover was



recorded. At the end of the study high levels of fluctuation (gains and losses) were measured at all sites. Sites 2a and 2b (regic sands) showed marginally to balanced ratios between increase and decrease. Sites 3b and 4a (tillite) were disposed towards increasing species richness and turnover, but Site 4b was skewed by gross negative change, suggesting a system in decline.

Open grassland on regic sands (Site 2) remained as open grassland, despite being modified by dense chromolaena stands. Stability was not observed in species turnover data, despite equilibrium ratios existing between positive and negative changes (Figure 7.1). Sensitivity or absolute change is the distance between upper (+) and lower (-) turnover limits. At Site 2a

sensitivity went from 141 presence-changes per transect ($5.6 \text{ changes m}^{-2}$) during the first turnover interval (1991/92 - 1992/93) to 98 (3.9 m^{-2}) at the end of the study (1996/97 - 1997/98). Changes in frequency imply appearances or disappearances of species in contiguous quadrats. Quadrats, however, were not nested and therefore observations underestimated magnitudes of modulation by not being able to detect change within quadrats. At Site 2b turnover in a thicket went from 8.7 m^{-2} between 1991 and 1993 to 4.2 m^{-2} in open grassland between 1996/97 and 1998. Although the fluctuations in upper and lower limits became smaller over time, turnovers per quadrat did not show equilibrium. Coastal grasslands on regic sand are therefore unstable resilient ecosystems.

Non-equilibrium was detected at two sites on tillite soils. Site 3b under moderate chromolaena and patchy grassland in 1992/93 went from 2.6 turnovers m^{-2} to 5.6 m^{-2} in 1998 when it was rated as intermediately disturbed ruderal grassland. Turnover of 8.7 m^{-2} was scored at Site 4a between 1990/91 and 1991/92 after severe disturbance from slash and burn operations, dropping to 6 m^{-2} as ruderal grassland in 1997/98. Stability was only observed at Site 4b. Slash and burn in 1990/91 induced $4.4 \text{ changes m}^{-2}$, forcing a transition from a chromolaena thicket to chromolaena seedbed. At the end of the study Site 4b was again chromolaena thicket with a turnover rate of 4.9 m^{-2} between 1996/97 and 1997/98. Site 4b is a stable, equilibrium community that was resilient and functioned as a monoculture.

Grasslands on regic sands showed greater resilience to the effects of chromolaena invasions than did grasslands on tillite soils. Furthermore, stability and resilience may only be possible in a disease- and predator-free alien monoculture. This type of resilience, however, may be without ecological redundancy and the appearance of a keystone, host-specific, predators would be catastrophic, as was noted with *Azolla filiculoides* (Section 1.8.3.3). On the other hand, latent redundancy might function as another alien monoculture perpetuating the undesirable state. This happened at Site 4b when lantana and bugweed replaced chromolaena thickets during the initial stages of the study. Chromolaena resumed dominance under increasing periods without fire.

7.3 Species diversity in coastal grasslands

The appearance of grassland species as functional groups in systems that were severely degraded by chromolaena confirms resilience. Beta diversity in fragmented habitats was contrary to the notion that species losses after fragmentation are permanent (Saunders *et al.* 1991). The absence of alien vegetation eased restoration processes favouring structural and functional diversity in degraded coastal grasslands.

Near-endemism, i.e. plants confined to KZN (Arnold & de Wet 1993), was high considering seven endemic species were recorded in six transects with a total area of 240 m² (0.024 ha). Seven endemic species, four asteraceous, were found on regic sands and Glenrosa soils:

1. *Selago trinervia* (Selaginaceae) was a common species in Site 2a, appearing in late succession six years into the study. The species has been recorded in the KZN Drakensberg in montane grassland between 1600-2000 m (Scott-Shaw 1999) and as fragmented populations from the coast to 2100 m (Pooley 1998).
2. *Lobelia caerulea* var. *macularis* (Lobeliaceae) was occasional to frequent in sites on regic sands. It is a hardy species with a woody rootstock occurring in coastal grassland in the Eastern Cape and KZN. The variety *macularis* is confined to KZN coast (Arnold & de Wet 1993, Pooley 1998).
3. *Helichrysum aureum* (Asteraceae) was occasional at the benchmark site at Ifafa Beach. The species is found from the coast to the Drakensberg within KZN (Scott-Shaw 1999).
4. *Senecio dregeanus* (Asteraceae) was rare and found only at the Ifafa Beach site. It grows in mistbelt ngongoni and coastal grasslands (Scott-Shaw 1999).
5. *Senecio umgeniensis* (Asteraceae) was also rare and found only at the benchmark site. The species occurs in grassland from coast to 1 950 m (Hilliard & Burt 1987).
6. *Gerbera kraussii* (Asteraceae) was common in sites 1 and 2. It is classified as a KZN endemic in grassland from the coast to 2400 m.
7. *Dicoma speciosa* (Asteraceae) was frequent in degraded grasslands on tillite soils (sites 3 and 4). Distribution is fragmented, occurring in grasslands up to 700 m in KZN (Pooley 1998).

7.4 Threats to coastal grasslands

The benchmark site at Ifafa Beach was partially destroyed by development (Plate 2, a) sometime after monitoring ended in 1993. The remaining portion has not been burnt regularly and on a visit in 1998 was heavily moribund. Real-estate boards show that the site will be developed into holiday resort on the estuary of the Mtwalume River. The coastal lowland has been largely transformed by sugar cane and timber plantations, and urban sprawl. Most of the potential destruction has already been committed. What is very important now is the protection of relic patches occurring on farms and company estates spread along the KZN coastline. No data are available on how much coastal grassland remains in the province, their respective conditions, management and protection. The greatest threat to remaining habitats is development.

The association between threatened plants and ecosystems in KZN (Scott-Shaw 1999) shows disproportionately high representation in grassland (58%) compared with forest (16%), Drakensberg alpine tundra (11%), savanna (10%), fynbos (3%) and valley bushveld (2%). Grasslands are vulnerable to all forms of land conversion. Coastal grasslands in KZN account for 14% of the threatened species in grassland, excluding Pondoland coastal grasslands (18%) considered more protected. Uncontrolled or inappropriate ecotourism development, unsustainable agricultural expansion, exploitation of forest resources and permanent heavy grazing are threats to coastal grasslands and estuaries in the Pondoland region of the Eastern Cape (McKenzie 2000) and in KZN.

The conservation values of many (coastal) farmers need to change. Unutilised fragmented vegetation needs careful management to maintain ecosystem vigour and prevent alien plants from modifying habitats. It was shown that fragmented grasslands could be successfully maintained by regular burning. Coastal grasslands are worthy of conservation status, even if they are not used by livestock. Having rich floristic diversity, small coastal grassland patches support many rare and endangered plant species. They also act as refuges for wildlife, e.g. invertebrates, reptiles, small mammals and birds, that cannot survive in forests or in monocultures (e.g. sugar and timber).

7.5 Managing coastal grasslands

Coastal grasslands are seral to forest. Coastal land owners have the choice of managing grasslands in multiple states ranging from open grassland, savanna to forest. The short-term benefit of maintaining land in a certain condition is outweighed by the long-term cost of rehabilitation (Ash *et al.* 1994). Veld condition is therefore an overriding factor in the choice of preferred states. Fragmented grasslands are more likely to remain unutilised by farmers and become modified. Under conditions where transitions between states are unlikely to shift to an equally desirable state, e.g. from grassland dominated by palatable species to unpalatable grassland, managing the system as savanna or forest in future may be more beneficial. Decisions should be based on the costs of maintaining the vegetation in states that have structure and resilience, and non-equilibrium dynamics must be managed adaptively.

7.5.1 State-and-transition model for grasslands on regic sand (Figure 7.2)

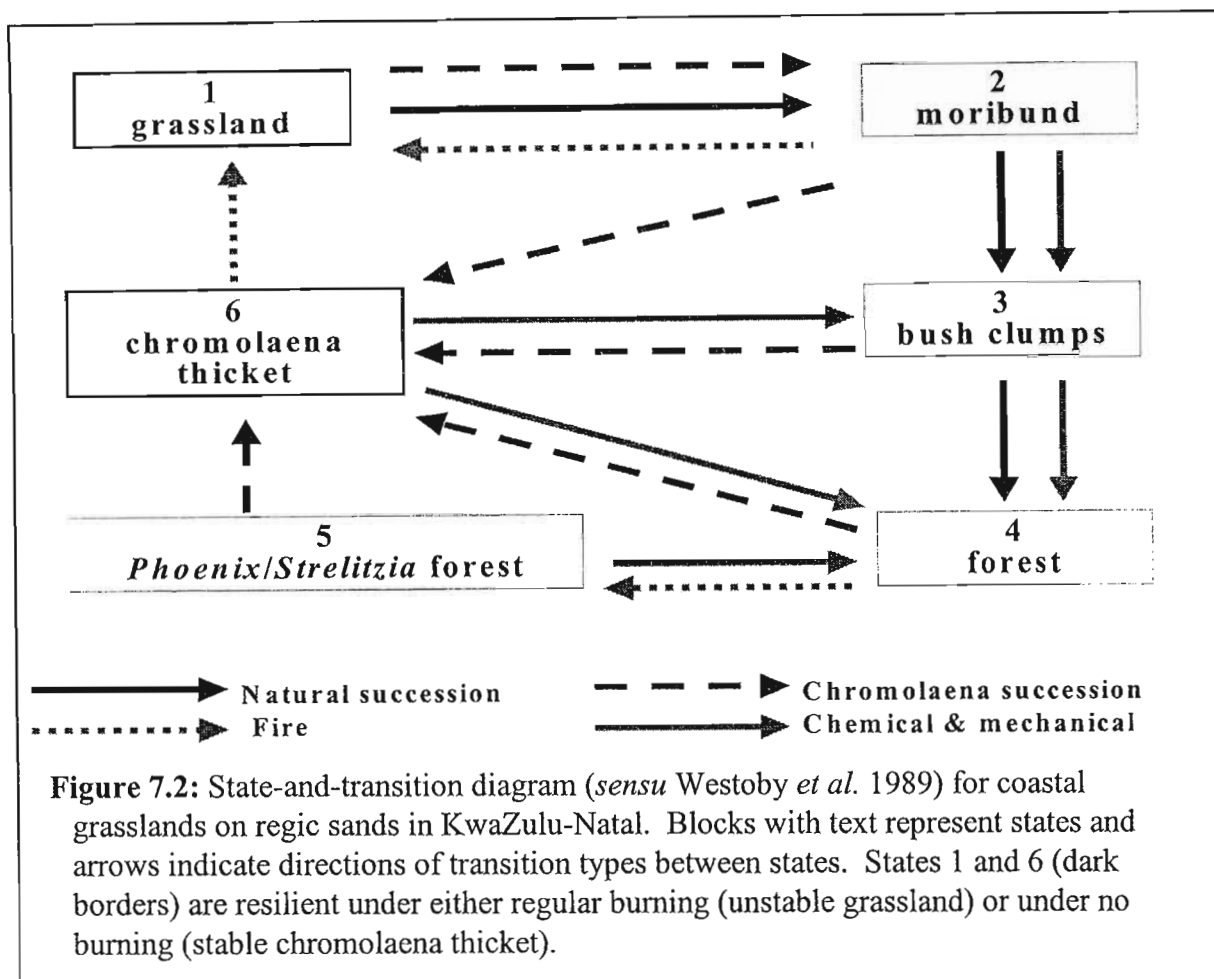
7.5.1.1. Catalogue of states

States are practical description of observed vegetation conditions over time for specific vegetation types. Its purpose is help managers identify preferred states from undesirable states.

State 1: Open perennial grassland with a short sward (0.5 m) and a preponderance of non-graminoid growth forms comprising herbs (forbs), geophytes and vines. Desirable (decreaser) grasses are more common than undesirable (increaser) grass. Grasses and sedges contribute most to biomass. Tree species, e.g. *Syzygium cordatum*, are occasional and are maintained as shrublets (0.5 m) by recurring fires. *Chromolaena odorata* does not occur.

State 2: Moribund grassland with a patchy sward (up to 2 m). Plant indicator species are *Aristida junciformis* and *Cymbopogon validus*. Non-graminoid grassland species are infrequent, smothered by grass necromass. Saplings of forest precursors (*S. cordatum*, *Phoenix reclinata*, *Strelitzia nicolai*) are occasional. *Chromolaena* occurs as scattered plants up to 1 m in height. Fire-sensitive shrublets (*Helichrysum panduratum*) and seedlings of tree species are frequent, as are herbs of the ecotone (*Asystasia gangetica*).

State 3: Bush clumps comprise mature precursor forest trees and understory shrubs (*Kraussia floribunda*). *Chromolaena* thickets occur on margins between bush clumps and surrounding grassland.



State 4: Forest develops and expands as bush clumps merge. Secondary forest develops with chromolaena and is characterised by a patchy forest canopy with a dense chromolaena understory. Chromolaena also invades forest margins and gaps left by dead trees in mature forest. In time forests become dominated by chromolaena, leaving only scattered dominant trees.

State 5: *Phoenix/Strelitzia* forest is the remains of forest patches and bushes clumps destroyed by chromolaena-facilitated wild fires (Plate 5). The soil is exposed and temporarily sterilised by the heat of the fire.

State 6: Chromolaena thicket establishes in moribund grassland and disturbed vegetation after an extended period without fire (about 5 years). Thickets are short (1.5 to 2 m) and the grass component is severely suppressed with *Cymbopogon* occurring frequently in the canopy.

7.5.1.2. *Catalogues of transitions*

Two forms of transition are presented, namely transitions showing successional direction without fire or management (black arrows) and transitions operating under fire or management or both (grey arrows).

Transition 1: Natural succession follows a sequence from grassland to forest by passing through temporary states of moribund grassland, facilitating establishment of fire-sensitive forest pioneer trees, and bush clump development. The succession is based on the theory that coastal grasslands are anthropogenically derived (Hall 1981) and are seral to forest. The succession is also applicable to the pre-World War II era when chromolaena was not yet introduced and may not be valid on the KZN coast nowadays.

Transition 2: Chromolaena succession is only possible in vegetation that is free from routine fires, therefore chromolaena only establishes in moribund grasslands and other disturbed vegetation. Chromolaena alters the direction of natural succession away from forest development towards monospecific thickets. This succession applies to the present and the future and is a key conservation threat to the future survival of coastal vegetation. Successful biocontrol may reinstate evolutionary successional pathways or indirectly ease the arrival of the next important alien.

Transition 3: Fire, either intentionally or accidentally introduced, can reverse effects created under moribund and thicket conditions by killing chromolaena and other fire-sensitive woody species. Fire destroys coastal forest, leaving a disturbed community dominated by fire-resistant pioneer trees. Conditions created by fire in forest suit the establishment of dense stands of chromolaena.

Transition 4: Chemical and mechanical control can be used to restore forest from thicket infestations, or to ensure succession from grassland to forest proceeds without chromolaena or any other alien species. Registered herbicides are listed under Section 2.1.3.4 (Tables 2.1 and 2.2).

Transition 5: Integrated control (grey arrows) are the tools managers need to use to manage vegetation as grassland or forest and includes fire, chemical control and mechanical control. Grassland states can be managed with fire only. Forests and forest successions must be managed without fire using herbicides and mechanical means to prevent chromolaena establishment.

7.5.2 State and transition model for grasslands on tillite (Glenrosa) soils (Figure 7.3)

7.5.2.1. Catalogue of states

Observed states differ from regic sands in that indigenous woody plants feature very early in the succession from grassland to forest and are typically fire-resistant.

State 1: Open grassland comprising tufted perennial grasses of both palatable (*Digitaria eriantha*) and unpalatable species (*Aristida junciformis*). Savanna trees (*Combretum molle*), shrubs (*Lippia javanica*) and regrowth (*Dichrostachys cinerea*) are widely scattered. Chromolaena does not occur.

State 2: Savanna encroachment (*D. cinerea*) occurs under irregular burning regimes. *Panicum maximum* is abundant under trees. Chromolaena is present as scattered bushes, possibly along with lantana and guava.

State 3: Forest species develop along with savanna trees under extended periods without fire (more than 30 years). In young secondary forest remnant savanna species have largely been shaded out. Grassland is replaced by an understory of dense chromolaena suppressing seedlings of forest species.

State 4: Ruderal savanna is a successional state altered by chromolaena away from forest development. The vegetation comprises of a few emergent savanna trees (*C. molle*, *D. cinerea* and *Heteropyxis natalensis*) and a monospecific chromolaena understory.

State 5: Phoenix/Strelitzia forest (see State 5, Section 7.5.1.1)

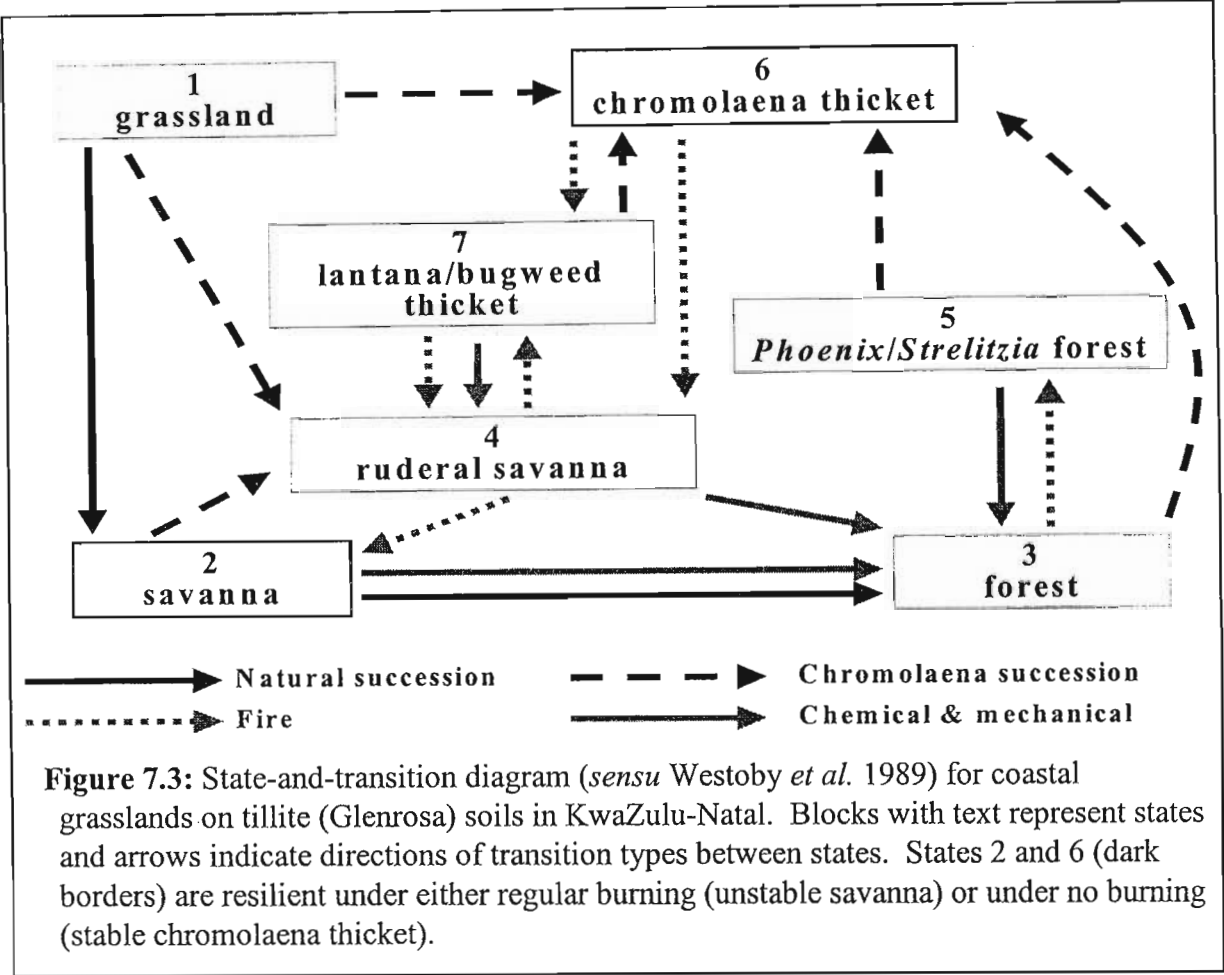
State 6: Chromolaena thickets are the final state after invading and suppressing vegetation in moribund grassland, savanna and secondary forest. It is also the final dominant in disturbed vegetation such as ruderal savanna and thickets of lantana and bugweed.

State 7: Lantana/bugweed thicket dominates for a short period after chromolaena invaded savanna is burnt.

7.5.2.2 Catalogue of transitions

Transition 1: Natural succession follows pathways from grassland to forest through savanna.

Transition 2: Chromolaena succession interferes with evolutionary succession cycles (see Transition 2, Section 7.5.1.2).



Transition 3: Fire destroys forests and chromolaena thickets but bare ground in the wake of devastating fires are conducive for the reestablishment of chromolaena, lantana and bugweed. Once grasslands are replaced by chromolaena thickets or savanna trees fire is unable to revert states to open grassland. Savanna is resistant to fire and savanna states retain resilience if fire remains a component of the tree-grass system.

Transition 4: Chemical and mechanical control is used for the control of fire-resistant aliens (lantana and bugweed) and chromolaena under certain conditions (Tables 2.1 and 2.2). If the objective is to promote forest development, burning must stop and alien vegetation must be controlled using herbicides and labour. Chemical control is also used for controlling lantana and bugweed in savanna. Chromolaena in savanna and grassland may also require chemical control on exposed ground. In situations when the objective is to restore open grassland herbicides are used to kill savanna trees and shrubs (bush control).

Transition 5: Integrated control as for regic sand (Transition 5, Section 7.5.1.2) using combinations of fire, chemical and mechanical control to achieve desired states in vegetation.

7.6 Critical review of the monitoring approach

7.6.1 Strengths

Yield, plant density and species composition were recorded annually in this study, in contrast with many medium term experiments that record botanical composition only at the beginning and end of experiments. All sites had baseline data for which serial differences could be detected. The sampling intensity made it possible to evaluate the variability of rate of change.

The objective of monitoring species composition was to analyse the raw data in ways that could help interpret the ecological importance of individual species. A primary objective of monitoring, therefore, was ensuring all species found in sample units were recorded. Surveys were carried out in spring and summer. The purpose of the spring survey was to record flowering herbs that die out as grasses assume dominance in midsummer. Annual data of species composition in each quadrat were generated by combining presence values from both surveys. Serial changes at the quadrat level are thus directly comparable between adjacent seasons. Species data were robust in that they could be analysed in many ways, namely as species, functional groups, life forms and growth forms.

7.6.2 Weaknesses

The purpose of the study was to measure species composition in relation to chromolaena density. As a long-term study it was found wanting in several respects. Control plots were not included, although baseline data of samples were recorded, and plots with variable chromolaena density were not replicated. Analysis using Repeated Measures ANOVA was not possible because of autocorrelation and pseudo-replication problems in the study design. Conclusions about species richness and sample size were based on liner and non-parametric methods.

Variation in soil type, topography and vegetation, confounded by sites that were serially dependent, meant the effects of important state variables, i.e. soil type, could not be

determined. In addition, soil samples were only collected at the end of the study. The serial effects of burning on nutrient availability and exchangeable bases could not be tested against herbaceous composition and yield. Had control plots been included, information on the progression from chromolaena thickets to alternative states would shed more light on successional dynamics.

Aerial grass cover percentages using two observers was inadequate at accounting for species dominance. Grass species were not ranked in their contribution to aerial cover or dry matter production. Presence data cannot compensate for ranking because large morphological differences exist between species, e.g. *Panicum aequinerve* (fine trailing grass) versus tufted species *Eragrostis curvula* (<1 m), *Hyparrhenia tamba* (>1 m) and *Diheteropogon amplexans* (mat-forming).

Presence data used in the calculation of abundance gives equal importance to species in uniform quadrat sizes. In retrospect, presence data are better suited to nested designs that allow for scale. Presence data can detect changes in composition if species enter or leave quadrats but overlooks change in numbers within quadrats. All species in contiguous 1 m² quadrats should preferably be counted to avoid Type 1 error in which significant changes are not detected when in fact they have occurred.

Yield was only measured at the end of the season because sites were not grazed, so compensatory production was perceived as small. Other problems with this descriptive approach were the inability to distinguish primary and ancillary determinants of states in transition. Many differences were observed between sites, including soil form, soil depth, soil texture, topography (runoff and irradiance) and vegetation (interception of light and rainfall). Rainfall of the general area was measured from one location, i.e. the same amounts of rainfall were assumed to have fallen at sites annually. The effectiveness of rainfall on soil type (regic sands vs tillite) concerning infiltration and percolation may be highly variable.

The original strategy, however, was to monitor vegetation change in samples in different condition states. The focus was therefore primarily on temporal patterns within communities. Management guidelines were developed from general observations of the various states over

time.

7.6.3 Monitoring recommendations

It is recommended that future medium-term monitoring strategies in grasslands distinguish between measuring 'diversity' and the need to detect changes in relation to management. If diversity is the objective 'all or nothing approaches' should be conducted, i.e. recording all species, in association with aspects dealing with functional redundancy. Monitoring 'biodiversity' becomes an ecologically meaningless exercise involving the monotonous cataloguing of species if the results do not convey diversity as a functional component of the vegetation.

Contiguous quadrat approaches should be used with caution in monitoring strategies that focus on recording vegetation dynamics. Nested plots measuring species distributions from the 'point scale' up to 1 m² are much more accurate at recording magnitudes of change than methods that use single scales. Furthermore, nested designs do not require very large monitoring budgets; local species frequencies are recorded simultaneously at a range of scales, negating the need for high intensity monitoring.

Sampling strategies must be randomised, replicated and include baseline, interim and final survey data to prove that changes are due to treatments and not by chance. Towards this end, controls also need to be included. Additional spatio-temporal information about intrinsic environmental parameters, i.e. geology, topography, climate and soil variables, need also be collected, the latter two regularly, to equate vegetation dynamics with environmental gradients.

7.7 Epilogue

Despite statistical limitations, this study contributes to the holistic management and conservation of coastal grasslands in southern Africa. The integration of fire and invasive plant management practices are crucial for retaining the ecological integrity of these 'fire-climax' systems. The current guidelines for managing coastal grasslands not grazed by domestic livestock include annual winter burning (August) and, depending on presence and density of alien species, the use of herbicides. The following recommendations apply to the

alien invasive woody species found in coastal grasslands.

Chromolaena odorata can be controlled in most situations with fire. Thickets of chromolaena that do not support veld grasses must be slashed and burnt and regrowth must be sprayed with triclopyr (0.375% v/v) in water in early and late summer (March). Controlled burning must continue annually until chromolaena is eliminated. Foliar sprays can be stopped once veld grasses have reasonable cover (30 - 40%). *Lantana camara* and *Solanum mauritianum* are not killed by fire and herbicides must be applied either to leaves or stumps to effect mortality. A stump treatment suitable for both species is imazapyr (2% v/v in water). Foliar applications differ, lantana must be sprayed with picloram (1% v/v) in water and bugweed with triclopyr (0.5% v/v) in water. In situations where chromolaena, lantana and bugweed occur together it is suggested that picloram (1% v/v) be sprayed to the regrowth, but this is an off-label recommendation. *Psidium guajava* is a 'hard-to-kill' species and the only registered product is imazapyr (12.5% v/v) in water on freshly-cut stumps.

The chemical control of fire-resistant alien species must continue until these species have been eliminated from affected habitats. Agricultural extension officers should be consulted before grazing animals are introduced into grasslands recovering from alien plant invasions.

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APPENDIX A: WOODY SPECIES (Nomenclature in accordance with Arnold & de Wet (1993))

SPECIES	FAMILY	ACRONYM	HABIT ¹	SIZE ¹ (m)	COASTAL HABITATS ¹	SITES
<i>Acacia karroo</i>	FABACEAE	Acackarr	small-medium tree	4-20	dune forest, forest, savanna	4a
<i>Albizia adianthifolia</i>	FABACEAE	Albiadia	large tree	15-20	forest	4a, 4b, 3b, 2a
<i>Aloe arborescens</i>	ASPHODELACEAE	Aloearbo	succulent shrub	1-4	forest, cliffs, rocky areas	3b
<i>Aloe maculata</i>	ASPHODELACEAE	Aloemacu	succulent	1	grassland	4a, 3b
<i>Baphia racemosa</i>	FABACEAE	Baphrace	shrub, small tree	3-10	riverine scrub, forest	4b
<i>Brachylaena discolor</i>	ASTERACEAE	Bracdisc	small tree	4-10	dune forest, forest	4b, 3b, 2a
<i>Canthium inerme</i>	RUBIACEAE	Cantiner	small-medium tree	4-13	dune forest, forest, savanna	4a, 4b, 3b
<i>Chaetachme aristata</i>	ULMACEAE	Chaearis	small-large tree	5-15	forest	4a
<i>Chromolaena odorata</i>	ASTERACEAE	Chroodo*	scandent shrub	4-10	disturbed areas	4a, 4b, 3b, 2a, 2b
<i>Coddia rudis</i>	ACANTHACEAE	Coddrudi	shrub	3-7	savanna, forest margins	4a, 4b, 3b
<i>Commiphora harveyi</i>	BURSERACEAE	Commharv	small-medium tree	5-15	savanna, dry forest, rocky outcrops	4a
<i>Combretum molle</i>	COMBRETACEAE	Combmol	small-medium tree	4-12	savanna	4a, 4b, 3b
<i>Croton sylvaticus</i>	EUPHORBIACEAE	Crotsylv	medium-large tree	7-20	forest	4a, 4b
<i>Dalbergia armata</i>	FABACEAE	Dalbarna	liana	10-30	forest, forest margins	4a
<i>Dalbergia obovata</i>	FABACEAE	Dalbobov	liana-small tree	2-6	forest, savanna	4a, 4b, 3b
<i>Dichrostachys cinerea</i>	FABACEAE	Dichcine	shrub-small tree	2-7	savanna, thicket	4a, 4b, 3b
<i>Diospyros lycioides</i>	EBENACEAE	Dioslyci	shrub-small tree	2-7	grassland, savanna, forest margins	4a
<i>Euclea natalensis subsp. natalensis</i>	EBENACEAE	Euclnata	small tree	4-10	forest	4a, 4b, 3b
<i>Euphorbia triangularis</i>	EUPHORBIACEAE	Euphtria	succulent tree	4-10	dry hillsides, rocky areas, coastal krantz	4a, 4b
<i>Helichrysum panduratum</i>	ASTERACEAE	Helipand	small shrub	1-2	forest margins	4b
<i>Heteropyxis natalensis</i>	MYRTACEAE	Hetenata	small tree	4-10	savanna, forest margins	4a, 4b, 3b
<i>Hibiscus fuscus</i>	MALVACEAE	Hibifusc	shrublet	1-2	disturbed areas	3a
<i>Hippobromus pauciflorus</i>	SAPINDACEAE	Hipppauc	shrub-small tree	2-9	forest margins, savanna, riverine scrub	4a, 4b, 3b
<i>Lantana camara</i>	VERBENACEAE	Lantcam*	shrub	1-4	disturbed areas	4a, 4b, 3b
<i>Lippia javanica</i>	VERBENACEAE	Lippjava	shrub	1-2	savanna	3b
<i>Maytenus heterophylla</i>	CELASTRACEAE	Maythete	shrub-small tree	2-6	savanna, forest margins	4b
<i>Maytenus undata</i>	CELASTRACEAE	Maytunda	shrub-small tree	2-15	forest, savanna, riverine scrub	4a, 4b, 3b

APPENDIX A: WOODY SPECIES (Nomenclature in accordance with Arnold & de Wet (1993))

SPECIES	FAMILY	ACRONYM	HABIT ¹	SIZE ¹ (m)	COASTAL HABITATS ¹	SITES
<i>Millettia grandis</i>	FABACEAE	Millgran	medium-large tree	10-25	forest, forest margins	4a
<i>Monanthotaxis caffra</i>	ANNONACEAE	Monacaff	liana-shrub	2-3	forest	4a, 4b
<i>Myrica serrata</i>	MYRICACEAE	Myriserr	shrub	2-6	forest, grassland	3b
<i>Phoenix reclinata</i>	ARECACEAE	Phoerecl	palm	3-10	grassland, forest	4a, 4b
<i>Protorhus longifolia</i>	ANACARDIACEAE	Protlong	medium-large tree	10-25	forest	4a, 4b, 3b
<i>Psidium guajava</i>	MYRTACEAE	Psidgua*	small tree	3-8	disturbed areas	3b
<i>Rhus chirindensis</i>	ANACARDIACEAE	Rhuschir	small-large tree	3-20	forest, forest margins	4a, 4b
<i>Rhus dentata</i>	ANACARDIACEAE	Rhusdent	shrub-small tree	1-5	forest margins, rock outcrops, riverine scrub	4a, 3b
<i>Rhus lucida</i>	ANACARDIACEAE	Rhusluci	shrub	2-5	forest, forest margins, savanna	4a, 4b, 3b
<i>Rhus pyroides</i>	ANACARDIACEAE	Rhuspyro	shrub-small tree	1-6	grassland, forest margins	4a
<i>Sapium integerrimum</i>	EUPHORBIACEAE	Sapiinte	small-medium tree	4-15	forest margins, savanna	4a, 4b, 3b
<i>Scolopia zeyheri</i>	FLACOURTIACEAE	Scolzeyh	small-medium tree	3-15	forest, forest margins, savanna	4a, 4b, 3b
<i>Scutia myrtina</i>	RHAMNACEAE	Scutmyrt	liana-shrub	2-15	forest, forest margins	4b
<i>Solanum linnaeanum</i>	SOLANACEAE	Solalinn	shrublet	1	disturbed areas	4b
<i>Solanum mauritianum</i>	SOLANACEAE	Solamau*	shrub-small tree	2-10	disturbed areas	4a, 4b, 3b
<i>Solanum panduriforme</i>	SOLANACEAE	Solapand	shrublet	1	disturbed areas	4a, 4b
<i>Syzygium cordatum</i>	MYRTACEAE	Syzycord	medium tree	5-12	grassland, forest, rivers	2a
<i>Trimeria grandifolia</i>	FLACOURTIACEAE	Trimgran	shrub-small tree	4-10	forest, forest margins	4a
<i>Uvaria caffra</i>	ANNONACEAE	Uvarcaff	liana-shrub	2-5	forest	4b
<i>Vepris lanceolata</i>	RUTACEAE	Veprlanc	small-large tree	5-20	forest, riverine scrub	4a
<i>Ziziphus mucronata</i>	RHAMNACEAE	Zizimucr	small-medium tree	3-10	savanna, forest	4a, 4b

¹ Pooley (1993)

APPENDIX B: HERBACEOUS SPECIES

SERIAL ABUNDANCES (%) OF HERBACEOUS SPECIES FROM FIXED BELT TRANSECTS IN
SITES 1A TO 4B

SPECIES ¹	ACRONYM	FAMILY ¹	DISTRIBUTION ¹	LIFE ² FORM	GROWTH ³ FORM	HABITAT ³ PREFERENCES	1a 92	1b 92	2a 90	2a 91	2a 96	2a 97	2b 90	2b 91	2b 96	2b 97	3b 92	3b 93	3b 94	3b 96	3b 97	4a 90	4a 91	4a 93	4a 94	4a 96	4a 97	4b 90	4b 91	4b 93	4b 94	4b 96	4b 97		
<i>Buchnera simplex</i>	Buchsimp	SCROPHULARIACEAE	unpublished species	Ph-FCh	herb	hyromorphic grassland							4																						
<i>Callilepis laureola</i>	Callaur	ASTERACEAE	TONCS	Ph-FCh	herb	grassland		16																											
<i>Centella asiatica</i>	Centasia	APIACEAE	TONCISLB	Ph-FT	herb	hyromorphic grassland	2	28	12	32	8	8		16	8	12																			
<i>Chaetacanthus burchellii</i>	Chaeburc	ACANTHACEAE	TONCS	Ph-FCh	herb	grassland	95	96		8	24	32							4	4					4	4	4								
<i>Chamaecrista capensis</i>	Chamcape	FABACEAE	TNC	T-FT	herb	grassland	98	28	20	68	100	96		40	56	48			16	8	32														
<i>Cheilanthes viridis</i>	Cheiviri	ADIANTACEAE	TNCISL	Ph-FG	fern	hyromorphic grassland	3		48	48	44	44																							
<i>Commelina africana</i>	Commfri	COMMELINACEAE	TONCISLB	G-FG	geophyte	grassland, savanna				68	80	80		52	12	28			4		4														
<i>Commelina benghalensis</i>	Commheng	COMMELINACEAE	TONCISLB	G-FG	geophyte	grassland, disturbed areas	1																												
<i>Commelina erecta</i>	Comumerc	COMMELINACEAE	TNCISB	G-FG	geophyte	grassland, savanna																	4			4	8	4							
<i>Conyza canadensis</i> *	Conycan*	ASTERACEAE	TONCSL	T-FT*	herb*	alien																			4							4			
<i>Crotalaria lanceolata subsp.</i>	Crotlanc	FABACEAE	TNCS	T-FT	herb	grassland															4														
<i>Cyanotis speciosa</i>	Cyanspec	COMMELINACEAE	TONCISLB	G-FG	geophyte	grassland, savanna	15	15		12	48	16																							
<i>Cynidium adonense</i>	Cyncadon	SCROPHULARIACEAE	TONCS	Ph-FH	herb	grassland	2																												
<i>Cymbopogon validus</i>	Cymbvali	POACEAE	TONCSLB	H-FH	grass	grassland, savanna	87	9	8	8				60	64	8	4	12	16	32	52					4	28	8	12						
<i>Cyperus obtusiflorus</i>	Cypeobtu	CYPERACEAE	TONCSL	H-FH	sedge	hyromorphic grassland	5	49	24	28	24	16																							
CYPERUSA	CYPERUSA	CYPERACEAE	W	H-FH	sedge	hyromorphic grassland	3																												
CYPERUSB	CYPERUSB	CYPERACEAE	W	H-FH	sedge	hyromorphic grassland	1																												
CYPERUSX	CYPERUSX	CYPERACEAE	W	H-FH	sedge	hyromorphic grassland				8																									
CYPERUSY	CYPERUSY	CYPERACEAE	W	H-FH	sedge	hyromorphic grassland										4																			
CYPERUSZ	CYPERUSZ	CYPERACEAE	W	H-FH	sedge	hyromorphic grassland										4																			
<i>Cyphostemma cirrhosum</i>	Cyphcirr	VITACEAE	TN	Ph-FT	vine	ecotones																			4								4		
<i>Dalechampia capensis</i>	Dalecape	EUPHORBIACEAE	TNCSB	Ph-FT	vine	savanna																		4							44				
<i>Desmodium dregeanum</i>	Desmdreg	FABACEAE	TNC	Ph-FCh	herb	grassland	2	3	52	52	40	64		64	80	96					4														
<i>Desmodium incanum</i> *	Desminc*	FABACEAE	TNC	Ph-FT*	herb*	alien			8	8																									
<i>Desmodium setigerum</i>	Desmseti	FABACEAE	TNCS	Ph-FCh	herb	hyromorphic grassland	2																												
<i>Dicoma speciosa</i>	Dicospec	ASTERACEAE	N provincial endemic	Ph-FCh	herb	grassland													20	20	16	24	20										4		
<i>Digitaria diagonalis</i>	Digidia	POACEAE	TNS	H-FH	grass	grassland, savanna			4	4																									
<i>Digitaria eriantha</i>	Digieria	POACEAE	TONCISLB	H-FH	grass	grassland, savanna	68	50	36	72	16	24		20	4	8																			
<i>Diheteropogon amplexans</i>	Dihcempl	POACEAE	TONCSB	H-FH	grass	grassland, savanna	10	71	4	4	12	12		4	16	20	12	12	16	16	32														
<i>Dioscorea cotinifolia</i>	Dioscoti	DIOSCOREACEAE	TNCSB	G-FG	vine	savanna																									4	4	8	20	4
<i>Disa woodii</i>	Disawood	ORCHIDACEAE	TNCS	G-FT	geophyte	hyromorphic grassland																		4											
<i>Endostemon obtusifolius</i>	Endoobtu	LAMIACEAE	TNCS	Ph-FCh	herb	grassland			4	4	4	8				8			8	4													16		
<i>Eragrostis capensis</i>	Eragcape	POACEAE	TONCSL	H-FH	grass	grassland, savanna	2							4																					

APPENDIX B: HERBACEOUS SPECIES

SERIAL ABUNDANCES (%) OF HERBACEOUS SPECIES FROM FIXED BELT TRANSECTS IN
SITES 1A TO 4B

SPECIES ¹	ACRONYM	FAMILY ¹	DISTRIBUTION ¹	LIFE ² FORM	GROWTH ³ FORM	HABITAT ³ PREFERENCES	1a 92	1b 92	2a 90	2a 91	2a 96	2a 97	2b 90	2b 91	2b 96	2b 97	3b 92	3b 93	3b 94	3b 96	3b 97	4a 90	4a 91	4a 93	4a 94	4a 96	4a 97	4b 90	4b 91	4b 93	4b 94	4b 96	4b 97
<i>Eragrostis curvula</i>	Eragcurv	POACEAE	TONCISLB	H-FH	grass	grassland, savanna											44	64	92	80	84	12	80	96	96	100			16	16	32	44	
<i>Eragrostis plana</i>	Eragplan	POACEAE	TONCSLB	H-FH	grass	grassland, savanna			4	8																							
<i>Eriosema salignum</i>	Eriosali	FABACEAE	TONCL	Ph-FCh	herb	grassland	10	20			24	24	4	4	12			4															
<i>Eriosema squarrosum</i>	Eriosqua	FABACEAE	NC	Ph-FCh	herb	grassland	2	10	20	68	80	96			4																		
ERIOSEMX	ERIOSEMX	FABACEAE	W	Ph-FCh	herb	grassland																8											
<i>Eriospermum natalense</i>	Erionata	ASPHODELACEAE	NCL	G-FG	geophyte	grassland			4	4	4		4	8	12																		
<i>Eugenia capensis sub. capensis</i>	Eugecape	MYRTACEAE	NC	Pn-FCh	shrublet	grassland		8																									
<i>Eulalia villosa</i>	Eulavill	POACEAE	TNCS	H-FH	grass	grassland, savanna							4		4																		
<i>Eulophia clavicornis var</i>	Euloclav	ORCHIDACEAE	TONCSL	G-FG	geophyte	grassland	3																										
<i>Eulophia odontoglossa</i>	Euloodon	ORCHIDACEAE	TNCS	G-FG	geophyte	hyromorphic grassland										4																	
<i>Euphorbia striata</i>	Euphstri	EUPHORBIACEAE	TONCL	Ph-FCh	herb	grassland		4																									
<i>Evolvulus alsinoides</i>	Evolalsi	CONVOLVULACEAE	TNCISB	Ph-FCh	herb	grassland, savanna											16	16	56	56					56	48	12			8	16	4	
<i>Fuirena pubescens</i>	Fuirpube	CYPERACEAE	TONCISLB	H-FH	sedge	hyromorphic grassland			4	8	8		4	28	40																		
<i>Galopina circaeoides</i>	Galocirc	RUBIACEAE	TONCS	Ph-FCh	herb	grassland	5																										
<i>Gazania linearis</i>	Gazaline	ASTERACEAE	NC	Ph-FCh	herb	grassland		4																									
<i>Gerbera ambigua</i>	Gerbambi	ASTERACEAE	TONCSL	Ph-FCh	herb	grassland, savanna													4		28	4	4			12							
<i>Gerbera kraussii</i>	Gerbkrau	ASTERACEAE	N provincial endemic	Ph-FCh	herb	grassland	80	78	4	8	8		32	28	32																		
<i>Gladiolus longicollis</i>	Gladlong	IRIDACEAE	TONCSL	G-FG	geophyte	grassland	2																										
<i>Gladiolus papilio</i>	Gladpapi	IRIDACEAE	TONCSL	G-FT	geophyte	hyromorphic grassland							4																				
<i>Gnidia anthylloides</i>	Gnidanth	THYMELAEACEAE	NC	Pn-FCh	shrublet	grassland	5	10																									
<i>Gnidia gymnostachya</i>	Gnidgymn	THYMELAEACEAE	TONCSL	Ph-FCh	herb	grassland	7	38																									
<i>Graderia scabra</i>	Gradscab	SCROPHULARIACEAE	TONCS	Ph-FCh	herb	grassland	58	46																									
<i>Helichrysum allioides</i>	Helialli	ASTERACEAE	TNC	Ph-FCh	herb	grassland	92	14									4	4			8					4							
<i>Helichrysum appendiculatum</i>	Heliappe	ASTERACEAE	TONCSL	Ph-FCh	herb	grassland			4	36	32			4	4																		
<i>Helichrysum aureum</i>	Heliaure	ASTERACEAE	N provincial endemic	Ph-FCh	herb	grassland	2	10																									
<i>Helichrysum longifolium</i>	Helilong	ASTERACEAE	NC	Ph-FCh	herb	grassland			4	4																							
<i>Helichrysum nudifolium</i>	Helinudi	ASTERACEAE	TONCSL	Ph-FCh	herb	grassland											56	64	36	36	36	28	28	28	20	32							
<i>Helichrysum pallidum</i>	Helipall	ASTERACEAE	TONCL	Ph-FCh	herb	grassland	23	21																									
<i>Helichrysum panduratum</i>	Helipand	ASTERACEAE	NC	Pn-FT	shrublet	ecotones	7		88	88	8	12	4																				
<i>Helichrysum subluteum</i>	Helisubl	ASTERACEAE	TNS	Ph-FCh	herb	grassland	8	53																									
<i>Helinus integrifolius</i>	Heliiate	RHAMNACEAE	TNCISB	Ph-FT	vine	ecotones, disturbed areas																							8				
<i>Hesperantha lactea</i>	Hesplact	IRIDACEAE	NC	G-FG	geophyte	hyromorphic grassland							4																				
<i>Heteropogon contortus</i>	Hetecont	POACEAE	TONCISLB	H-FH	grass	grassland, savanna		25																									

APPENDIX B: HERBACEOUS SPECIES

SERIAL ABUNDANCES (%) OF HERBACEOUS SPECIES FROM FIXED BELT TRANSECTS IN SITES 1A TO 4B

SPECIES ¹	ACRONYM	FAMILY ¹	DISTRIBUTION ¹	LIFE ² FORM	GROWTH ³ FORM	HABITAT ³ PREFERENCES	1a 92	1b 92	2a 90	2a 91	2a 96	2a 97	2b 90	2b 91	2b 96	2b 97	3b 92	3b 93	3b 94	3b 96	3b 97	4a 90	4a 91	4a 93	4a 94	4a 96	4a 97	4b 90	4b 91	4b 93	4b 94	4b 96	4b 97
<i>Hibiscus aethiopicus</i>	Hibiaeth	MALVACEAE	NCL	Ph-FCh	herb	grassland, ecotones													4	20	20				4	4	4					4	4
<i>Hibiscus fuscus</i>	Hibifusc	MALVACEAE	NC	Pn-FCh	shrublet	grassland, savanna												4	8	8		8			4		8			12	24		
<i>Hibiscus pusillus</i>	Hibipusi	MALVACEAE	TONCISLB	H-FH	herb	grassland, savanna													4				20		12	32	44			4		4	4
<i>Hibiscus trionum</i>	Hibitrio	MALVACEAE	TONCISLB	T-FT	herb	grassland, savanna													16				32		44	4	8		24		28		
HIBISCUSX	HIBISCUX	MALVACEAE	W	T-FT	herb	disturbed areas							4																				
<i>Hyparrhenia tamba</i>	Hypatamb	POACEAE	TONSL	H-FH	grass	grassland, savanna												16	48	56	72	100			4		68	96				4	12
<i>Hypoxis angustifolia</i>	Hypoangu	HYPOXIDACEAE	TONCSL	G-FG	geophyte	grassland		1		20	16	8		12	8										-								
<i>Hypoxis filiformis</i>	Hypofili	HYPOXIDACEAE	TONCSL	G-FG	geophyte	hyromorphic grassland	7	16								4																	
<i>Hypoxis hemerocallidea</i>	Hypoheme	HYPOXIDACEAE	TONCSLB	G-FG	geophyte	grassland, savanna	8	19		4	4	8							4	12	12		8			4	8						
<i>Hypoxis multiceps</i>	Hypomult	HYPOXIDACEAE	TONCSL	G-FG	geophyte	grassland	5																										
<i>Hypoxis rigidula</i>	Hyporigi	HYPOXIDACEAE	TONCISL	G-FG	geophyte	hyromorphic grassland	2																										
<i>Imperata cylindrica</i>	Impecyli	POACEAE	TONCISLB	H-FH	grass	hyromorphic grassland					16	16			16	28																	
<i>Indigofera hiliaris</i>	Indihila	FABACEAE	TONCS	H-FH	herb	grassland	77	83																									
<i>Indigofera tristis</i>	Inditris	FABACEAE	TONC	Ph-FCh	herb	grassland	13																	20									
<i>Indigofera trita subsp. subulata</i>	Inditrit	FABACEAE	TNISB	Ph-FCh	herb	grassland													8		4		4			12	20			16	8		
<i>Ipomoea cairica</i>	Ipomeair	CONVOLVULACEAE	TNCS	Ph-FH	vine	hyromorphic grassland	23						40	44	48																		
<i>Ipomoea crassipes</i>	Ipomeras	CONVOLVULACEAE	TONCISLB	Ph-FH	vine	grassland	35	51					4																				
<i>Ipomoea sinensis</i>	Ipomsino	CONVOLVULACEAE	TNCISB	T-FT	vine	grassland, savanna						8																					
IPOMOEAX	IPOMOEAX	CONVOLVULACEAE	W	Ph-FT	vine	disturbed areas																	4										
IRIDACEX	IRIDACEX	IRIDACEAE	W	G-FT	geophyte	grassland					8																						
<i>Ischaemum fasciculatum</i>	Ischfasc	POACEAE	TONCISLB	H-FH	grass	grassland, savanna	10	1	100	100	92	92		88	80	88																	
<i>Isoglossa ovata</i>	Isogovat	ACANTHACEAE	NC	Ph-FCh	herb	grassland	72	45											16	16	12				4					8	4	20	32
<i>Justicia betonica</i>	Justbeto	ACANTHACEAE	TNCISB	Ph-FCh	herb	grassland, savanna, ecotones	3																										
<i>Kniphofia cf. rooperi</i>	Kniproop	ASPHODELACEAE	NC	G-FG	geophyte	hyromorphic grassland	3																										
<i>Kniphofia gracilis</i>	Knipgrac	ASPHODELACEAE	NC	G-FG	geophyte	grassland			16	16	16	16																					
<i>Kohautia amatymbica</i>	Kohaumat	RUBIACEAE	TONCSL	Ph-FCh	herb	grassland, disturbed areas				4																							
<i>Ledebouria ovatifolia</i>	Ledeovat	HYACINTHACEAE	TONCSL	G-FG	geophyte	grassland, savanna	10																										
<i>Leonotis ocymifolia</i>	Leonocym	LAMIACEAE	TONCISL	Pn-FT	shrublet	forest																	4										
<i>Lobelia caerulea var. macularis</i>	Lobecner	LOBELIACEAE	N coastal endemic	Ph-FCh	herb	grassland, savanna	10	1		28			4																				
<i>Mariscus solidus</i>	Marisoli	CYPERACEAE	TNCS	H-FH	sedge	hyromorphic grassland	37	3						16	12																		
<i>Mariscus sumatrensis*</i>	Marisum*	CYPERACEAE	TNCSB	T-FT*	sedge*	disturbed areas																			12	8	16			8	36	24	
<i>Melhantia didyma</i>	Melhdidy	STERCULIACEAE	TNCS	Ph-FCh	herb	grassland, savanna, disturbed											92	100	92	72	24		72	72	72	68			72	56	84	36	
<i>Melinis repens</i>	Melirepe	POACEAE	TONCISLB	T-FT	grass	grassland, savanna, disturbed	3																							4	32		

APPENDIX B: HERBACEOUS SPECIES

SERIAL ABUNDANCES (%) OF HERBACEOUS SPECIES FROM FIXED BELT TRANSECTS IN SITES 1A TO 4B

SPECIES ¹	ACRONYM	FAMILY ¹	DISTRIBUTION ¹	LIFE ² FORM	GROWTH ³ FORM	HABITAT ³ PREFERENCES	1a 92	1b 92	2a 90	2a 91	2a 96	2a 97	2b 90	2b 91	2b 96	2b 97	3b 92	3b 93	3b 94	3b 96	3b 97	4a 90	4a 91	4a 93	4a 94	4a 96	4a 97	4b 90	4b 91	4b 93	4b 94	4b 96	4b 97
<i>Selago hyssopifolia</i>	Selabyss	SELAGINACEAE	TNCS	Ph-FCh	herb	ecotones	83	16																									
<i>Selago trinervia</i>	Selatrín	SELAGINACEAE	N provincial endemic	Ph-FCh	herb	grassland					60	72			8	4																	
<i>Senecio bupleuroides</i>	Senebupl	ASTERACEAE	TNCSL	Ph-FCh	herb	grassland	2	20			12	16			4	20					12												
<i>Senecio cf. madagascariensis</i>	Senemada	ASTERACEAE	TNCS	T-FT	herb	disturbed areas																12											
<i>Senecio cf. polyodon</i>	Sene.pol	ASTERACEAE	TONCSL	Ph-FCh	herb	hyromorphic grassland								8	8	4																	
<i>Senecio chrysocoma</i>	Senechry	ASTERACEAE	NC	Ph-FT	herb	grassland, disturbed areas				28				4																			
<i>Senecio deltoideus</i>	Senedelt	ASTERACEAE	TNCS	Ph-FCh	vine	ecotones												4	4	4		4										12	
<i>Senecio dregeanus</i>	Senedreg	ASTERACEAE	N provincial endemic	Ph-FCh	herb	grassland		1																									
<i>Senecio madagascariensis</i>	Senemada	ASTERACEAE	TNCS	T-FT	herb	disturbed areas																										4	
<i>Senecio oxyriifolius</i>	Seneoxyr	ASTERACEAE	TNCS	Ph-FCh	herb	grassland		18			16	28	20																				
<i>Senecio polyodon</i>	Senepoly	ASTERACEAE	TONCL	Ph-FCh	herb	hyromorphic grassland	10					4	4																				
<i>Senecio serratuloides</i>	Seneserr	ASTERACEAE	TNCS	Ph-FT	herb	grassland, savanna																	4										
<i>Senecio umgeniensis</i>	Seneunge	ASTERACEAE	N provincial endemic	Ph-FCh	herb	grassland	7																										
<i>Setaria megaphylla</i>	Setamega	POACEAE	TONCIS	H-FH	grass	forest, ecotones																		8	16	20	28						
<i>Setaria nigrivostis</i>	Setanigr	POACEAE	TONCSL	H-FH	grass	grassland, savanna		6																									
<i>Setaria sphacelata</i>	Setaspha	POACEAE	TONCISL	H-FH	grass	grassland, savanna	20	16	76	92	80	60		76	100	100	64	72	76	60	64		8	20	28	16	40						
<i>Sida cf. dregei</i>	Sida.dre	MALVACEAE	W	Ph-FT	herb	grassland, disturbed areas								8																			
<i>Sida dregei</i>	Sidadreg	MALVACEAE	TONCS	Ph-FT	herb	grassland, disturbed areas													8	4			56		8		8		48		4		
<i>Sida ovata</i>	Sida ovata	MALVACEAE	TONCIB	Ph-FT	herb	grassland, disturbed areas															16												
<i>Sisyranthus compactus</i>	Sisycomp	ASCLEPIADACEAE	NC	Ph-FH	herb	grassland					8	12				4																4	
<i>Smilax anceps</i>	Smilance	SMILACACEAE	TNCS	Ph-FCh	vine	grassland, forest, ecotones	35	5																									
<i>Solanum acanthoideum/viarum*</i>	Solaacan	SOLANACEAE	TNC	Ph-FT	herb*	ecotones, disturbed areas																	16							4	4	4	
<i>Solanum incanum</i>	Solainca	SOLANACEAE	TONCISLB	Ph-FT	herb	grassland, savanna																			4				4	4	4		
SPECIESB	SPECIESB	N/A	W	G-FG	geophyte	grassland															12												
SPECIESC	SPECIESC	N/A	W	T-FT	herb	grassland															8	12											
SPECIESD	SPECIESD	N/A	W	T-FT	herb	grassland															8	16											
SPECIESF	SPECIESF	N/A	W	T-FT	herb	grassland																			4								
SPECIESG	SPECIESG	N/A	W	T-FT	herb	grassland		18																									
SPECIESJ	SPECIESJ	N/A	W	G-FG	geophyte	grassland																4											
<i>Spermacoce natalensis</i>	Spernata	RUBIACEAE	TNCS	Ph-FCh	herb	grassland	3																										
<i>Sporobolus africanus</i>	Sporafri	POACEAE	TONCISL	H-FH	grass	grassland, savanna	7	26					4					4	24	52	20	52		4	12	28	12	4			4	8	8
<i>Striga bilabiata</i>	Stribila	SCROPHULARIACEAE	TONCISLB	Ph-FH	herb	grassland	18	11																									
<i>Tephrosia elongata</i>	Tephelon	FABACEAE	TNS	Ph-FCh	herb	grassland							4							8	12	20		4			4	4					

APPENDIX B: HERBACEOUS SPECIES

SERIAL ABUNDANCES (%) OF HERBACEOUS SPECIES FROM FIXED BELT TRANSECTS IN SITES 1A TO 4B

SPECIES ¹	ACRONYM	FAMILY ¹	DISTRIBUTION ¹	LIFE ² FORM	GROWTH ³ FORM	HABITAT ³ PREFERENCES	1a 92	1b 92	2a 90	2a 91	2a 96	2a 97	2b 90	2b 91	2b 96	2b 97	3b 92	3b 93	3b 94	3b 96	3b 97	4a 90	4a 91	4a 93	4a 94	4a 96	4a 97	4b 90	4b 91	4b 93	4b 94	4b 96	4b 97
<i>Tephrosia macropoda</i>	Tephmacr	FABACEAE	TNCS	Ph-FCh	herb	grassland	60	54	4	4	20	20			4				4														
<i>Themeda triandra</i>	Themtria	POACEAE	TONCISLB	H-FH	grass	grassland, savanna	52	15	8	12	52	28	64	84	60																		
<i>Thesium pallidum</i>	Thespall	SANTALACEAE	TN	Ph-FCh	herb	grassland			28	28	20	20			4																		4
<i>Thunbergia atropurpurea</i>	Tbunatri	ACANTHACEAE	TNCS	Ph-FCh	herb	grassland	98	28		4	8	4	4	4	4																		
<i>Thunbergia natalensis</i>	Thunnata	ACANTHACEAE	TNCS	Ph-FT	herb	ecotones																12											
<i>Trachyandra asperata</i>	Tracaspe	ASPHODELACEAE	TONCL	Ph-FCh	herb	grassland		18																									
<i>Trachyandra saltii</i>	Tracsalt	ASPHODELACEAE	TONIS	Ph-FCh	herb	grassland			4	8	4	4														4							
<i>Trachypogon spicatus</i>	Tracspic	POACEAE	TONCISLB	H-FH	grass	grassland, savanna		1																									
<i>Tristachya leucothrix</i>	Trisleuc	POACEAE	TONCSL	H-FH	grass	hyromorphic grassland, savanna	5			60	36																						
<i>Triumfetta pilosa</i>	Triupilo	TILIACEAE	TNCS	Ph-FCh	herb	ecotones, disturbed areas																60		8	16			24		20			
<i>Trochomeria sagittata</i>	Trocsagi	CUCURBITACEAE	NCS	Ph-FCh	vine	grassland	32	5																									
<i>Vernonia natalensis</i>	Vernnata	ASTERACEAE	TONCSL	Ph-FCh	herb	grassland											76	80	72	84	92	32	16	20	20	24							
<i>Vernonia oligocephala</i>	Vernolig	ASTERACEAE	TONCISLB	Ph-FCh	herb	grassland	85	54		40	48	48	36	36	48																		
<i>Vigna vexillata</i>	Vignvexi	FABACEAE	TONCS	Ph-FCh	vine	grassland													4	12					8	16							
<i>Watsonia densiflora</i>	Watsdens	IRIDACEAE	NC	G-FG	geophyte	grassland	85	20																									
<i>Zornia capensis</i>	Zorncape	FABACEAE	TONCS	Ph-FT	herb	grassland, savanna																4											

¹ Arnold & de Wet 1993, ² Rutherford & Westfall 1994, ³ Pooley 1998

NOTES: the term **herb** refers specifically to broad-leaved herbs (forbs)

uncertified species are present as eight digit characters in upper case (1st seven letters indicate the genus, e.g. CYPERUSX, CYPERUSY..CYPERUSB)

unidentifiable plants are presented as SPECIESB, SPECIESC..SPECIESJ

DISTRIBUTION: T=Transvaal (Mpumalanga, Gauteng, Northern & North West provinces)

O=Free State

N=KwaZulu-Natal

C=Cape (Eastern, Western & North Western Cape)

I=Namibia, S=Swaziland, L=Leshoto, B=Botswana

W=widespread, applies only to uncertified species or unidentifiable plants

APPENDIX C1: Sites 2a & 2b - number of species recorded in permanent 250 m² plots

SPECIES		HEIGHT CLASSES (m)												INDICES					
ACRONYM [†]	RANK	≤ 1			> 1 ≤ 3			> 3 ≤ 5			> 5			Uniformity ¹			Dissimilarity ²		
		90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/95	90/98	95/98
Site 2a																			
Albiadia	4	3	0	3	0	0	0	0	0	0	0	0	0	-1.00		-1.00	1.00	0.00	1.00
Bracdisc	3	0	0	1	0	0	0	0	0	0	0	0	0			-1.00	0.00	1.00	1.00
Chroodo*	1	0	20	0	300	0	0	0	0	0	0	0	0	-0.33	-1.00		0.87	1.00	0.00
Syzicord	2	6	6	5	0	0	0	0	0	0	0	0	0	-1.00	-1.00	-1.00	0.00	1.00	1.00
Total		9	26	9	300	0	0	0	0	0	0	0	0	-0.46	-1.00	-1.00	0.62	1.00	1.00
Indigenous species														-1.00	-1.00	-1.00	0.50	1.00	1.00
Site 2b																			
Chroodo*	1	0	210	0	4430	0	0	0	0	0	0	0	0	-0.33	-1.00		0.91	1.00	0.00
Total		0	210	0	4430	0	0	0	0	0	0	0	0	-0.33	-1.00		err ³	err ³	err ³

¹ Gini coefficient: index of evenness in structure within each season, 0 = homogeneous, -1 or 1 = dominance at smaller or larger heights, blank cells indicate seasons where no individuals were found in any height class

² Euclidean distance: measure of dissimilarity between seasons, values close to 0 = similarity or 1 = dissimilarity

³ Error return on community (Total) Euclidean distance index, only one woody species present

[†]Scientific names for woody species acronyms can be found in Appendix A

APPENDIX C2: Site 3b - number of species recorded in a permanent 250 m² plot

SPECIES ACRONYM †	RANK	HEIGHT CLASSES (m)												INDICES					
		≤ 1			>1 ≤ 3			> 3 ≤ 5			> 5			Uniformity ¹			Dissimilarity ²		
		92/93	95/96	98/99	92/93	95/96	98/99	92/93	95/96	98/99	92/93	95/96	98/99	92/93	95/96	98/99	92/95	92/98	95/98
<i>Albiadia</i>	23		1	1											-1	-1	1	1	0
<i>Aloearbo</i>	24			1												-1	0	1	1
<i>Aloemac</i>	10		7	10											-1	-1	0.49	1	0.09
<i>Bracdisc</i>	18				1									-0.33			1	1	0
<i>Cantiner</i>	12		1					1						0.33	-1		0	1	1
<i>Chroodor*</i>	1		10		1290									-0.33	-1		0.98	1	0
<i>Coddrudi</i>	11				1			1						0			1	1	0
<i>Comboll</i>	4	10	2	14	7	8	2	7	3	1			1	-0.42	-0.28	-0.74	1	0.30	0.21
<i>Dalbobov</i>	7		7	4	3									-0.33	-1	-1	1	0.06	0.56
<i>Dichcine</i>	3		13	29	23	9		2	1	1				-0.28	-0.68	-0.96	0.08	0.51	1
<i>Euclnata</i>	8			6	1	2	1							-0.33	-0.33	-0.90	0.03	1	0.69
<i>Hetenata</i>	2	4	4	7	16	10	6	8	5	4				-0.24	-0.30	-0.45	0.67	1	0.03
<i>Hibifusc</i>	14						2									-0.33	0	1	1
<i>Hippauc</i>	12		1		1	1								-0.33	-0.67		0.25	0.25	1
<i>Lantcama*</i>	24			1												-1	0	1	1
<i>Lippjava</i>	18						1									-0.33	0	1	1
<i>Maytunda</i>	5		5	3	1	4								-0.33	-0.70	-1	1	0.06	0.56
<i>Myriserr</i>	21		2	1											-1	-1	1	0.25	0.25
<i>Protlong</i>	6							3						0.33			1	1	0
<i>Psidguaj*</i>	16	1		1		1								-1	-0.33	-1	0	0	0
<i>Rhusdent</i>	14					2									-0.33		1	0	1
<i>Rhusluci</i>	17			1		1									-0.33	-1	1	1	0
<i>Sapiinte</i>	9			3		4									-0.33	-1	1	0.56	0.06
<i>Scolzeyh</i>	18					1									-0.33		1	0	1
<i>Solamaur*</i>	21			3												-1	0	1	1
Total		15	53	85	1344	43	12	22	9	6	0	0	1	-0.33	-0.61	-0.83	0.60	0.71	0.52
Indigenous species														-0.33	-0.57	-0.82	0.68	0.70	0.52

¹ Gini coefficient: index of evenness in structure within each season, 0 = homogeneous, -1 or 1 = dominance at smaller or larger heights, blank cells indicate seasons where no individuals were found in any height class

² Euclidean distance: measure of dissimilarity between seasons, values close to 0 = similarity or 1 = dissimilarity

Top five ranking species in bold print

†Scientific names for woody species acronyms can be found in Appendix A

APPENDIX C3: Site 4a - number of species recorded in a permanent 250 m² plot

SPECIES ACRONYM †	RANK	HEIGHT CLASSES (m)												INDICES					
		≤ 1			>1 ≤ 3			> 3 ≤ 5			> 5			Uniformity ¹			Dissimilarity ²		
		90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/95	90/98	95/98
<i>Acackarr</i>	24						1									-0.33	0	1	1
<i>Albiadia</i>	31		1												-1		1	0	1
<i>Aloemacu</i>	17		9	10											-1	-1	0.81	1	0.01
<i>Cantiner</i>	9				1			5						0.22			1	1	0
<i>Chaearis</i>	24				1									-0.33			1	1	0
<i>Chroodo*</i>	1		215	61		20	3	3925		1				0.33	-0.94	-0.95	0.91	1	0
<i>Coddrudi</i>	9		8		5			2						-0.14	-1		0.02	0.77	1
<i>Commharv</i>	28	2												-1			1	1	0
<i>Combmoll</i>	5		1	8	2	9		7	4	3	2	1	1	0.33	-0.11	-0.5	1	0.06	0.56
<i>Crotsylv</i>	26		1	2											-1	-1	0.25	1	0.25
<i>Dalbarm</i>	12							2			1	0		0.56			1	1	0
<i>Dalbobov</i>	16		7	3		1		1						0.33	-0.92	-1	1	0.08	0.51
<i>Dichcine</i>	3		66	39	7	29	2	8	1					0.02	-0.78	-0.97	1	0.10	0.46
<i>Dioslyci</i>	28	2												-1			1	1	0
<i>Euclnata</i>	11		2	4		7									-0.48	-1	1	0.20	0.31
<i>Euphtria</i>	18	7			2									-0.85			1	1	0
<i>Hetenata</i>	4		5	5	15	15	2	13	2	2				-0.02	-0.42	-0.56	0.10	1	0.47
<i>Hippauc</i>	7		22	11	5	3								-0.33	-0.92	-1	1	0.09	0.49
<i>Lantcam*</i>	31			1												-1	0	1	1
<i>Maytunda</i>	8	14	4	3	1	1	2	2						-0.80	-0.87	-0.73	1	1	0
<i>Millgran</i>	31			1												-1	0	1	1
<i>Monacaff</i>	31	1												-1			1	1	0
<i>Phoerecl</i>	20			1	1	1	1							-0.33	-0.33	-0.67	0	1	1
<i>Protlong</i>	14	8						2						-0.73			1	1	0
<i>Rhuschir</i>	13		1			1		1			1			0.67	-0.67		0	1	1
<i>Rhusdent</i>	22			2		1									-0.33	-1	0.25	1	0.25
<i>Rhusluci</i>	21					3									-0.33		1	0	1
<i>Rhuspyro</i>	28		1	1											-1	-1	1	1	0
<i>Sapiinte</i>	14		3	5	1	3								-0.33	-0.67	-1	1	0.64	0.04
<i>Scolzeyh</i>	18		3								1			1	-1		0.44	0.11	1
<i>Solamau*</i>	2		19	86		38	2		13						-0.39	-0.98	0.63	1	0.04
<i>Solapand</i>	26		1	2											-1	-1	0.25	1	0.25
<i>Trimgran</i>	6		44	20							2			1	-1	-1	1	0.18	0.33
<i>Veprlanc</i>	31		1												-1		1	0	1
<i>Zizimucr</i>	23			1		1								-0.33		-1	1	1	0
Total		34	414	266	41	133	13	3968	20	6	7	1	1	0.32	-0.79	-0.93	0.73	0.74	0.41
Indigenous species														-0.21	-0.77	-0.89	0.75	0.72	0.42

¹ Gini coefficient: index of evenness in structure within each season, 0 = homogeneous, -1 or 1 = dominance at smaller or larger heights, blank cells indicate seasons where no individuals were found in any height class

² Euclidean distance: measure of dissimilarity between seasons, values close to 0 = similarity or 1 = dissimilarity

Top five ranking species in bold print. †Scientific names for woody species acronyms can be found in Appendix A

APPENDIX C4: Site 4b - number of species recorded in a permanent 250 m² plot

SPECIES ACRONYM †	RANK	HEIGHT CLASSES (m)												INDICES					
		≤ 1			>1 ≤ 3			> 3 ≤ 5			> 5			Uniformity ¹			Dissimilarity ²		
		90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/91	95/96	98/99	90/95	90/98	95/98
<i>Albiadia</i>	15							1					1	0.33		1	1	0	1
<i>Baphrace</i>	25					1									-0.33		1	0	1
<i>Bracdisc</i>	17					1	2								-0.33	-0.33	0.25	1	0.25
<i>Cantiner</i>	7		1		2			4	1					0.11	-0.33		0.44	1	0.11
<i>Chroodo*</i>	1		968	33	1900	126	481		4	192				-0.33	-0.92	-0.18	0.45	1	0.11
<i>Coddrudi</i>	14		5		2	1	2							-0.33	-0.89	-0.33	1	0	1
<i>Combmoll</i>	4					7	4	1	3	1	2	1	3	0.78	-0.03	0.25	1	0.39	0.14
<i>Crotsylv</i>	8					11									-0.33		1	0	1
<i>Dalbobov</i>	21		7	1											-1	-1	1	0.02	0.73
<i>Dichcine</i>	3		21		4	44	10	11		6	1			0.21	-0.55	-0.08	1	0	1
<i>Euclnata</i>	12					2	2				1			1	-0.33	-0.33	1	1	0
<i>Euphtria</i>	27	1												-1			1	1	0
<i>Helipand</i>	25						1									-0.33	0	1	1
<i>Hetenata</i>	6		6	2	2	3	1	4		1				0.11	-0.78	-0.50	0.36	0.16	1
<i>Hippauc</i>	21		4				1								-1	-0.33	1	0.06	0.56
<i>Lantcam*</i>	5		1			12	2		1	9					-0.33	0.21	1	0.62	0.05
<i>Maythete</i>	27		1												-1		1	0	1
<i>Maytunda</i>	13	5	5	1		1	3							-1	-0.89	-0.50	0.25	0.25	1
<i>Monacaff</i>	23		4	2											-1	-1	1	0.25	0.25
<i>Phoerecl</i>	10			4	1	1			1				1	-0.33	0	-0.60	0.06	1	0.56
<i>Protilong</i>	9	1			1			3			1			0.11			1	1	0
<i>Rhuschir</i>	16		1			1	1	1						0.33	-0.67	-0.33	1	0	1
<i>Rhusluci</i>	19		2			1	1								-0.78	-0.33	1	0.11	0.44
<i>Sapiinte</i>	17					3									-0.33		1	0	1
<i>Scolzeyh</i>	20	1				1	1							-1	-0.33	-0.33	0	0	0
<i>Scutmyrt</i>	27		1												-1		1	0	1
<i>Solalinn</i>	27		1												-1		1	0	1
<i>Solamau*</i>	2		9	3		15	3		36	7					-0.03	-0.13	1	0.05	0.61
<i>Solapand</i>	27		1												-1		1	0	1
<i>Uvarcaff</i>	23		1	1			1								-1	-0.67	0.25	1	0.25
<i>Zizimucr</i>	11		1					1	1				1	0.33	-0.33	1	1	0	1
Total		8	1040	47	1912	231	516	26	47	216	5	1	6	-0.32	-0.83	-0.18	0.80	0.36	0.64
Indigenous species														0.03	-0.58	-0.22	0.80	0.34	0.68

¹ Gini coefficient: index of evenness in structure within each season, 0 = homogeneous, -1 or 1 = dominance at smaller or larger heights, blank cells indicate seasons where no individuals were found in any height class

² Euclidean distance: measure of dissimilarity between seasons, values close to 0 = similarity or 1 = dissimilarity

Top five ranking species in bold print

†Scientific names for woody species acronyms can be found in Appendix A

APPENDIX D: EXAMPLES OF THE EFFECTS OF SCALE ON SERIAL ABUNDANCES OF SPECIES AT TWO COASTAL GRASSLAND SITES

Table D1: Site 2a - comparison of absolute degrees of change at five scales. Sensitivity is the sum of moduli of absolute change for each scale and for optimum scale. The number of species showing no change (blindness) is the count of the species with zero absolute change.

Change in frequency Species (Site 2a)	Change Profile 1990-1997					Optimum scale Optimum frequency				Change Profile 1990-1991					Optimum scale Optimum frequency				Change Profile 1996-1997					Optimum scale Optimum frequency			
	1	3	6	13	25	Scale	1990	1997	Change	1	3	6	13	25	Scale	1990	1991	Change	1	3	6	13	25	Scale	1996	1997	Change
<i>Albizia adianthifolia</i>	0	0	0	-1	-1	13	6	5	-1	0	0	0	1	1	13	6	7	1	0	0	0	0	-1	24	6	5	-1
<i>Alloteropsis semialata</i>	0	0	1	3.5	8	19	7	12.5	5.5	0	0	1.5	3	5	24	7	12	5	0	0	-0.5	-2	-1	6	13	12.5	-0.5
<i>Argyrobolium rotundifolium</i>	0.5	-1	-1	0	0.5	1	1.5	2	0.5	0.5	0.5	0.5	1.5	1.5	13	1.5	3	1.5	0.5	0.5	0.5	0.5	1	25	1	2	1
<i>Aristea woodii</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	-0.5	-3	-5	-5	11	5	0	-5
<i>Aristida junciformis</i>	-1	-3	-5.5	-8.5	-17	9	13	6	-7	0	0	0	0	2	13	13	13	0	0	0	-2	-1.5	-2	10	8	6	-2
<i>Aster bakerianus</i>	0	1	1	1	3	25	0	3	3	0	0	0	0	0	n/a	0	0	0	0	1	1	1	3	25	0	3	3
<i>Asystasia gangetica</i>	-0.5	-2.5	-4.5	-11.5	-19	12	12	2	-10	0	0	0	0	0	13	13	13	0	0	0	0	0	0	13	2	2	0
<i>Athrixia phyllioides</i>	-0.5	-2	-2	-2	-2	3	2	0	-2	0	0	0	0	0	13	2	2	0	0	0	0	0	0	n/a	0	0	0
<i>Becium grandiflorum</i>	0	0	0	0	0	n/a	0	0	0	0	1	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0
<i>Berkheya speciosa</i>	0	0	0	0	2	22	0	2	2	0	0	0	0	1	22	0	1	1	0	0	0	0	1	22	1	2	1
<i>Buchnera simplex</i>	0	0	0.5	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0.5	1	1	13	0	1	1
<i>Centella asiatica</i>	0	-0.5	-0.5	-1	-1	13	3	2	-1	0.5	0.5	0.5	2.5	5	25	3	8	5	0	0	1	1	0	4	2	2	0
<i>Chaetacanthus burchellii</i>	0	0.5	2.5	6	8	24	0	8	8	0	0	0.5	2	2	13	0	2	2	0	0	1	0	2	9	6	8	2
<i>Chamaecrista capensis</i>	-0.5	1	3	9	19	12	5	12.5	7.5	0	0	1.5	5.5	12	16	5	13	8	-0.5	-0.5	-0.5	-0.5	-1	13	13	12.5	-0.5
<i>Cheilanthes viridis</i>	0	0	0	-1	-1	13	12	11	-1	0	0	0	0	0	13	12	12	0	0	0	0	0	0	13	11	11	0
<i>Chromolaena odorata*</i>	-0.5	-2.5	-4.5	-7	-11	18	12.5	2	-10.5	0	0	0	0	0	13	12.5	12.5	0	-0.5	-1	0	0	0	13	2	2	0
<i>Commelina africana</i>	1	2.5	3	8.5	20	18	0	13	13	0.5	1.5	4	9.5	17	20	0	13	13	0	-0.5	-2	-3	0	2	13	13	0
<i>Cyanotis speciosa</i>	0	0	1	3.5	4	14	0	4	4	0	1	2	3	3	13	0	3	3	-1	-2.5	-1.5	-5.5	-8	25	12	4	-8
<i>Cymbopogon validus</i>	0	0	0	0	-2	21	2	0	-2	0	0	0	0	0	13	2	2	0	0	0	0	0	0	n/a	0	0	0
<i>Cyperus obtusiflorus</i>	0	0	-1.5	-1.5	-4.5	18	8.5	4	-4.5	0	0	-0.5	0	-1.5	24	8.5	7	-1.5	0	0	0	-0.5	-2	23	6	4	-2
CYPERUSX	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	-2	-2	11	2	0	-2
<i>Desmodium dregeanum</i>	0	0	0	-1	3	16	12.5	12.5	0	0	0	0	0	0	13	12.5	12.5	0	0	0	1	3	6	12	10	12.5	2.5
<i>Desmodium incanum*</i>	0	0	0	-2	-2	13	2	0	-2	0	0	0	0	0	13	2	2	0	0	0	0	0	0	n/a	0	0	0
<i>Digitaria diagonalis</i>	0	0	0	0	-1	18	1	0	-1	0	0	0	0	0	13	1	1	0	0	0	0	0	0	n/a	0	0	0
<i>Digitaria eriantha</i>	0	-1	-2	-0.5	-3	21	9	6	-3	1	2	3.5	6.5	9	6	9	12.5	3.5	0	0	-1.5	1	2	23	4	6	2
<i>Diheteropogon amplexans</i>	0	0	0	0	2	21	1	3	2	0	0	0	0	0	13	1	1	0	0	0	0	-1	0	11	3	3	0
<i>Endostemon obtusifolius</i>	0	0	0	0	0.5	23	1.5	2	0.5	0	0	0	0	-0.5	24	1.5	1	-0.5	0	0	0	0	1	13	1	2	0
<i>Eragrostis plana</i>	-0.5	-0.5	-0.5	-0.5	-1	25	1	0	-1	0	0	1	1	1	13	1	2	1	0	0	0	0	0	n/a	0	0	0
<i>Eriosema salignum</i>	0	1	1	2.5	6	25	0	6	6	0	0	0	0	0	n/a	0	0	0	0	1	1	2.5	0	22	6	6	0
<i>Eriosema squarrosum</i>	1	2	5	10	19	11	5	13	8	0.5	1	3.5	6	12	17	5	13	8	0	0	0	1	4	8	13	13	0
<i>Eriosemum natalense</i>	0	0	0	1	1	13	0	1	1	0	0	0	1	1	13	0	1	1	0	0	0	0	0	13	1	1	0
<i>Eulalia villosa</i>	0	0	0	0.5	1	14	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	14	0	1	1
<i>Fuirena pubescens</i>	0	0	0	0	2	20	0	2	2	0	0	0.5	1	1	13	0	1	1	0	0	0	0	0	13	2	2	0
<i>Gerbera ambigua</i>	0	0	0	1	2	16	0	2	2	0	0	0	0	1	16	0	1	1	0	0	0	0	0	13	2	2	0
<i>Helichrysium appendiculatum</i>	0	0.5	3.5	6.5	8	21	0	8	8	0	0	0	0	1	21	0	1	1	-0.5	-0.5	-0.5	0.5	-1	25	9	8	-1
<i>Helichrysium longifolium</i>	0	0	0	-1	-1	12	1	0	-1	0	0	0	0	0	13	1	1	0	0	0	0	0	0	n/a	0	0	0
<i>Helichrysium panduratum</i>	-0.5	-2.5	-4.5	-10.5	-19	13	13	3	-10	0	0	0	0	0	13	13	13	0	0	0	0	0	1	21	2	3	1
<i>Hesperantha lactea</i>	0	0.5	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0.5	1	1	1	13	0	1	1
<i>Hypoxis angustifolia</i>	0	0	0	0	2	23	0	2	2	0	0	1	1	5	23	0	5	5	0	-0.5	-1	-2	-2	13	4	2	-2
<i>Hypoxis hemerocallidea</i>	0	0.5	2	2	2	13	0	2	2	0	0.5	1	1	1	13	0	1	1	0	0	1	1	1	13	1	2	1
<i>Imperata cylindrica</i>	0	1	2	2	4	24	0	4	4	0	0	0	0	0	n/a	0	0	0	0	-0.5	0	-1	0	6	4	4	0
<i>Ipomoea sinensis</i>	0	0	0	0	2	23	0	2	2	0	0	0	0	0	n/a	0	0	0	0	0	0	0	2	23	0	2	2

Change in frequency Species (Site 2a)	Change Profile 1990-1997					Optimum scale Optimum frequency				Change Profile 1990-1991					Optimum scale Optimum frequency				Change Profile 1996-1997					Optimum scale Optimum frequency				
	1	3	6	13	25	Scale	1990	1997	Change	1	3	6	13	25	Scale	1990	1991	Change	1	3	6	13	25	Scale	1996	1997	Change	
IRIDACEX	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	0	-2	23	2	0	-2	
<i>Ischaemum fasciculatum</i>	0	0	-0.5	-1	-2	5	13	13	0	0	0	0	0	0	13	13	13	0	0	0	0.5	1	0	9	13	13	0	
<i>Kniphofia gracilis</i>	0	-1.5	-0.5	-1.5	-1.5	13	5.5	4	-1.5	0	-0.5	-0.5	-1.5	-1.5	13	5.5	4	-1.5	0	0	0	0	0	13	4	4	0	
<i>Kohautia amatymbica</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	
<i>Lobelia caerulea</i>	0	0	0	0	0	n/a	0	0	0	0.5	2	4	7	7	13	0	7	7	0	0	0	0	0	n/a	0	0	0	
<i>Oxalis corniculata*</i>	0	0	0	0	0	n/a	0	0	0	0.5	0.5	0.5	0.5	1	25	0	1	1	0	0	0	0	0	n/a	0	0	0	
<i>Oxalis smithiana</i>	0	1	1	1	3	25	2	5	3	0.5	2	2	2	5	25	2	7	5	-0.5	-1	-1	-1	-1	25	4	5	1	
<i>Panicum aequinerve</i>	0	0	0	-0.5	1	12	13	13	0	0	0	0	0	0	13	13	13	0	0	1	1	0.5	2	14	13	13	0	
<i>Panicum dregeanum</i>	1	1	1.5	2	3	SS	13	13	0	0	0	0	0	1	13	12.5	12.5	0	0	-1	-1	-2	-3	1	13	13	0	
<i>Paspalum distichum</i>	0	0	0	0	1	21	0	1	1	0	0	0	1	1	13	0	1	1	0	0	0	0	0	13	1	1	0	
<i>Pycnus macranthus</i>	0	0	0.5	6.5	15	22	0	12.5	12.5	0	0	0	3.5	7	21	0	7	7	0	0	-1	1	5	19	10	12.5	2.5	
PYCREUSX	0	0	0	3	5	16	0	5	5	0	0	0	0	0	n/a	0	0	0	0	0	0	0	-3	24	8	5	-3	
<i>Rhynchosia totta</i>	0	1	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	13	1	1	0	
<i>Rumex dregeanus</i>	0	0	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	1	1	1	13	0	1	1	
<i>Scleria aterrima</i>	0	0	0	1.5	10	22	0	10	10	0	0	0	0	0	n/a	0	0	0	0	0	0	-1	1	17	9	10	1	
<i>Scleria melanomphala</i>	0	0	-1.5	-3	-0.5	23	8.5	8	-0.5	0	0	-0.5	-1	1.5	23	8.5	10	1.5	0	0	0	0	1	19	7	8	1	
<i>Selago trinervia</i>	1	2.5	5	11	18	15	0	13	13	0	0	0	0	0	n/a	0	0	0	0	0	1	2	3	4	13	13	0	
<i>Senecio bupleuroides</i>	0	0	0	0	4	25	0	4	4	0	0	0	0	0	n/a	0	0	0	0	0	0	0	1	23	3	4	1	
<i>Senecio chrysocoma</i>	0	0	0	0	0	n/a	0	0	0	0	1	1	4.5	7	16	0	7	7	0	0	0	0	0	n/a	0	0	0	
<i>Senecio oxyriifolius</i>	0	1.5	3	5	5	13	0	5	5	0	1	2	4	4	13	0	4	4	0	0.5	0	-1	-2	23	7	5	-2	
<i>Senecio polyodon</i>	0	0	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	13	1	1	0	
<i>Setaria sphacelata</i>	-0.5	-1	-1.5	-0.5	-4	13	13	12.5	-0.5	-0.5	0.5	3	4.5	4	1	13	12.5	-0.5	-0.5	-0.5	-1	-1.5	-5	5	13	12.5	-0.5	
<i>Sisyranthus compactus</i>	0	0	0	1.5	3	15	0	3	3	0	0	0	0	0	n/a	0	0	0	0	0	0	-1	1	15	2	3	1	
<i>Sporobolus africanus</i>	0	0	0.5	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0.5	1	1	13	0	1	1	
<i>Syzygium cordatum</i>	0	0	0	0	0	13	2	2	0	0	0	0	0	0	13	2	2	0	0	0	0	0	0	13	2	2	0	
<i>Tephrosia elongata</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	0	-1	24	1	0	-1	
<i>Tephrosia macropoda</i>	0	0	0	2.5	4	18	1	5	4	0	0	0	0	0	13	1	1	0	0	0	-0.5	-1	0	18	5	5	0	
<i>Themeda triandra</i>	0	0	0	2.5	5	18	2	7	5	0	0	0	0	1	18	2	3	1	0	0	-0.5	-2	-6	24	12.5	7	-5.5	
<i>Thesium pallidum</i>	0	-0.5	1	-2	-5	24	10	5	-5	0	-0.5	-1	-2	-3	23	10	7	-3	0	0	0	0	0	13	5	5	0	
<i>Thunbergia atriplicifolia</i>	0	0	0	0	1	22	0	1	1	0	0	0	0	1	22	0	1	1	0	0	0	0	-1	20	2	1	-1	
<i>Trachyandra saltii</i>	-1	-0.5	-0.5	-0.5	-0.5	13	1.5	1	-0.5	0	0	0	0	0.5	25	1.5	2	0.5	0	0	0	0	0	13	1	1	0	
<i>Tristachya leucothrix</i>	0	0	0.5	6.5	9	19	0	9	9	0	0	0	0	0	n/a	0	0	0	-0.5	-1.5	-2	-2	-6	19	12.5	9	-3.5	
<i>Vernonia oligocephala</i>	0	1.5	4.5	9.5	12	19	0	12	12	0	1.5	4.5	9.5	10	14	0	10	10	0	0	0	-0.5	0	14	12	12	0	
Sensitivity	10	38	78	173.5	323			242.5		5	17.5	41.5	88.5	141		0	117		4.5	15	32.5	56.5	98				71.5	
Blindness	52	37	26	13	1			5		45	37	29	25	15		0	0	17		56	46	33	26	21				25

* indicates alien species

Table D2: Site 3b - comparison absolute degrees of change at five scales. **Sensitivity** is the sum of the modulus of absolute change for each scale and for optimum scale. The number of species showing no change (blindness) is the count of the species with zero absolute change.

Change in frequency Species (Site 3b)	Change Profile 1992-1997					Optimum frequency				Change Profile 1992-1993					Optimum frequency				Change Profile 1996-1997					Optimum frequency			
	1	3	6	13	25	Scale	1992	1997	Change	1	3	6	13	25	Scale	1992	1993	Change	1	3	6	13	25	Scale	1996	1997	Change
<i>Acalypha villicaulis</i>	0	0	0	0	3	25	0	3	3	0	0	0	0	0	n/a	0	0	0	0	0.5	0.5	1	2	23	1	3	2
<i>Acroceras macrum</i>	0	0	0	3	3	13	0	3	3	0	0	0	0	0	n/a	0	0	0	0	0	0.5	1	2	6	1	1.5	0.5
<i>Albizia adianthifolia</i>	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	18	0	1	1
<i>Aloe maculata</i>	0	0	0	1	3	17	1	4	3	0	0	0	0	0	13	1	1	0	0	0	0	-1.5	-2	19	6	4	-2
<i>Argyrolobium harveyanum</i>	0	0	0	0	-2	23	2	0	-2	0	0	0	0	0	13	2	2	0	0	0	0	0	n/a	0	0	0	0
<i>Aristida junciformis</i>	0	0	0	-1	0	14	4	4	0	0.5	1.5	2.5	2.5	5	25	4	9	5	0	0.5	2	2	4	23	0	4	4
<i>Athrixia phyllicoides</i>	0	0	0	0	-2	15	6	4	-2	0	0.5	0.5	0.5	1	24	6	7	1	0	0	0	-1	-1	13	1	0	-1
<i>Berkheya erysithales</i>	0	0	1	-2	-5	17	7	2	-5	-1	0	0	0	0	13	7	7	0	0	0	0	0	1	13	2	2	0
<i>Berkheya speciosa</i>	0	0	0	4	6	17	0	6	6	0	0.5	0.5	0.5	1	25	0	1	1	0	0	0	2	2	13	0	2	2
<i>Bidens pilosa</i>	0	0	1	3	3	13	0	3	3	0	0	0	0	0	n/a	0	0	0	0	0	0	0	4	24	2	6	4
<i>Canthium inerme</i>	0	0	0	0	0	n/a	0	0	0	-0.5	0	0.5	0.5	1	21	0	1	1	0	0	0	-1	1	15	2	2	0
<i>Chaetacanthus burchellii</i>	0	0	0	0	1	21	0	1	1	0	0	0	0	0	n/a	0	0	0	0	1	1	1	0	21	1	1	0
<i>Chamaecrista capensis</i>	0	0	1	2	8	25	0	8	8	0	0	0	0	0	n/a	0	0	0	1	1	1.5	3.5	6	25	2	8	6
<i>Chromolaena odorata</i>	-1	-2	-5	-11	-21	13	13	2	-11	-0.5	0	0.5	0.5	1	5	1	1	0	0	0	0	0	1	24	1	2	1
<i>Combretum molle</i>	0	0	1	1	2	23	2	4	2	0	0.5	1	2	3	24	2	5	3	0	0	0	0	-1	15	5	4	-1
<i>Commelina/a africana</i>	0	0	0	0	1	15	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0.5	0.5	1	22	0	1	1
<i>Crotalaria lanceolata</i>	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	15	0	1	1
<i>Cymbopogon validus</i>	1	3	5	7	12	23	1	13	12	0	0	0.5	1.5	2	22	1	3	2	0	0.5	1	2	5	24	8	13	5
<i>Dalbergia obovata</i>	0	-1	-1	-1	0	15	4	4	0	0	0.5	1.5	1.5	3	25	4	7	3	0	0	0	0	0	13	4	4	0
<i>Desmodium dregeanum</i>	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	14	0	1	1
<i>Dichrostachys cinerea</i>	0	-1	0	1	6	15	10	13	3	0	1	2	3.5	7	10	10	12.5	2.5	0	0	0	0	0	15	12.5	13	0.5
<i>Dicoma speciosa</i>	0	0	0	0	0	13	5	5	0	0	0	0	0	0	13	5	5	0	0	0	0	-1	-1	13	6	5	-1
<i>Diheteropogon amplexens</i>	0	0	0	4	5	14	3	8	5	-0.5	0	0	0	0	16	3	3	0	0	0	1	2	4	21	4	8	4
<i>Endostemon obtusifolius</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	0	-1	23	1	0	-1
<i>Eragrostis curvula</i>	1	3	5	9	10	2	11	13	2	0	0	0	2.5	5	10	11	12.5	1.5	0	0.5	-0.5	1	1	12	13	13	0
<i>Evolvulus alsinoides</i>	0	0	-1	-1	-4	23	4	0	-4	-0.5	0	0	0	0	13	4	4	0	0	-1	-2	-9	-14	24	13	0	-13
<i>Gerbera ambigua</i>	0	2	3	4	7	25	0	7	7	0	0	0	0	0	n/a	0	0	0	0	0	0	4	7	23	0	7	7
<i>Helichrysum allioides</i>	0	0	0	0	1	21	1	2	1	1	0	0	0	0	13	1	1	0	0	2	2	2	2	13	0	2	2
<i>Helichrysum nudifolium</i>	0	0	-1	-4	-5	13	13	9	-4	0	0	1	1	2	4	12.5	12.5	0	-1	-2	0	0	0	13	9	9	0
<i>Heteropyxis natalensis</i>	0	0	0	0	1	14	3	4	1	0	1	2.5	2.5	5	24	3	8	5	0	0	0	0	0	13	4	4	0
<i>Hibiscus aethiopicus</i>	0	0	1	3	5	22	0	5	5	0	0	0	0	0	n/a	0	0	0	0	0	1	-1	0	14	5	5	0
<i>Hibiscus fuscus</i>	0	0	1	1	1	13	1	2	1	0	0	0	0.5	1	15	1	2	1	0	0	0	2	2	13	0	2	2
<i>Hippobromus pauciflorus</i>	0	0	0	0	0	13	1	1	0	0	0	0	0.5	1	18	1	2	1	0	0	0	0	0	13	1	1	0
<i>Hyparrhenia tamba</i>	1	3	6	13	21	9	4	13	9	0	1	3.5	4	8	25	4	12	8	0	0	0	4	7	7	13	13	0
<i>Hypoxis hemerocallidea</i>	0	0	0	0	3	24	0	3	3	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	13	3	3	0
<i>Indigofera tristis</i>	0	0	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	1	1	13	0	1	1
<i>Indigofera trita</i>	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	14	0	1	1
<i>Isoglossa ovata</i>	0	0	0	0	3	21	0	3	3	0	0	0	0	0	n/a	0	0	0	0	-1	-1	-1	-1	13	4	3	-1
<i>Maytenus undata</i>	0	0	0	-1	-1	13	3	2	-1	0	0	0.5	0.5	1	21	3	4	1	0	0	0	-0.5	-1	19	3	2	-1
<i>Melhanian didyma</i>	-1	-3	-6	-10	-17	8	13	6	-7	0	0.5	0.5	1	2	11	12.5	13	0.5	-1	-2	-1	-8	-12	12	13	6	-7
<i>Myrica serrata</i>	1	1	1	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	13	1	1	0
<i>Panicum maximum</i>	1	1	2	4	6	25	3	9	6	0	0.5	1	4	7	24	3	10	7	0.5	0.5	1	1	2	9	7	9	2
<i>Paspalum dilatatum*</i>	0	2	2	2	3	17	1	4	3	0	0	0	0.5	1	19	1	2	1	0	0.5	0.5	1.5	3	17	1	4	3

Change in frequency Species (Site 3b)	Change Profile 1992-1997					Optimum frequency				Change Profile 1992-1993					Optimum frequency				Change Profile 1996-1997					Optimum frequency			
	1	3	6	13	25	Scale	1992	1997	Change	1	3	6	13	25	Scale	1992	1993	Change	1	3	6	13	25	Scale	1996	1997	Change
<i>Phyllanthus meyerianus</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	-1	-2	17	2	0	-2
<i>Polygala hottentotta</i>	0	0	0	1	1	13	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	0	0.5	1	15	0	1	1
<i>Rhus dentata</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	-0.5	-0.5	-1	21	1	0	-1
<i>Rhus lucida</i>	0	0	0	0	-1	20	2	1	-1	0	0	0	0	0	13	2	2	0	0	-0.5	-0.5	-0.5	-1	24	1.5	0.5	-1
<i>Rhynchosia adenodes</i>	1	3	4	4	4	13	0	4	4	0	0	0	0	0	n/a	0	0	0	0	0	0	1	2	18	2	4	2
<i>Rhynchosia totta</i>	0	0	0	2	5	20	0	5	5	0	0	0	0	0	n/a	0	0	0	0.5	1	1	2	4	15	0.5	3	2.5
<i>Ruellia cordata</i>	0	0	1	5	7	12	9	13	4	-0.5	0	0.5	0.5	1	20	9	10	1	-1	-1	-1	0	1	13	13	13	0
<i>Sapium integerrimum</i>	-1	-1	-1	-1	-1	13	1	0	-1	0	0	0	0	0	13	1	1	0	0	0	0	0	0	n/a	0	0	0
<i>Senecio bupleuroides</i>	0	0	0	0	3	22	0	3	3	0	0	0	0	0	n/a	0	0	0	0	1	2	2	3	22	0	3	3
<i>Senecio deltoideus</i>	0	0	0	0	0	13	1	1	0	1	0	0	0	0	13	1	1	0	0	1	1	1	1	13	0	1	1
<i>Setaria sphacelata</i>	0	2	3	2	0	21	13	13	0	0	0	0	1	2	10	13	12.5	0	-0.5	0	0.5	0.5	1	9	12.5	12.5	0
<i>Sida dregei</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	-1	-1	13	1	0	-1
<i>Sida ovata</i>	0	0	0	1	4	22	0	4	4	0	0	0	0	0	n/a	0	0	0	1	2	3	3	4	20	0	4	4
SPECIESB	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	0	-1	-3	16	3	0	-3
SPECIESC	0	0	0	0	3	21	0	3	3	0	0	0	0	0	n/a	0	0	0	0	1	1	1	1	13	2	3	1
SPECIESD	0	0	0	0	4	22	0	4	4	0	0	0	0	0	n/a	0	0	0	0	1	1	1	2	23	2	4	2
SPECIESJ	0	0	0	0	1	23	0	1	1	0	0	0	0	0	n/a	0	0	0	0	0	1	1	1	13	0	1	1
<i>Sporobolus africanus</i>	1	3	6	9	12	24	1	13	12	0	0	0	3	5	18	1	6	5	0.5	1	1.5	4.5	8	24	5	12.5	7.5
<i>Tephrosia elongata</i>	0	0	0	4	5	22	0	5	5	0	0	0	0	0	n/a	0	0	0	0	0	0	1	2	17	3	5	2
<i>Tephrosia macropoda</i>	0	0	0	0	0	n/a	0	0	0	0	0	0	0	0	n/a	0	0	0	0	0	-0.5	-0.5	-1	20	1	0	-1
<i>Vernonia natalensis</i>	0	2	2	3	4	1	13	13	0	1	0	0.5	0.5	1	4	12.5	12.5	0	0	0	0	2	2	8	13	13	0
<i>Vigna vexillata</i>	0	0	0	0	3	22	0	3	3	0	0	0	0	0	n/a	0	0	0	0.5	1	1	1	2	25	1	3	2
Sensitivity	10	33	62	131	235				184	3	7.5	19.5	35	66			51.5		7.5	23.5	32.5	83.5	140				117
Blindness	48	42	33	18	6				7	28	23	16	10	10			12		53	46	40	35	34				15

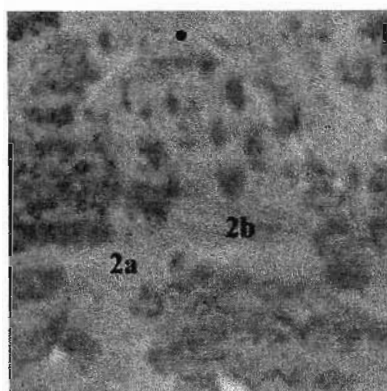
* indicates alien species



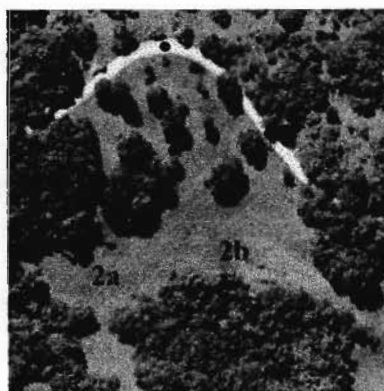
(a) View across Site 1a in June 1992



(b) View across Site 1b and crest in June 1992



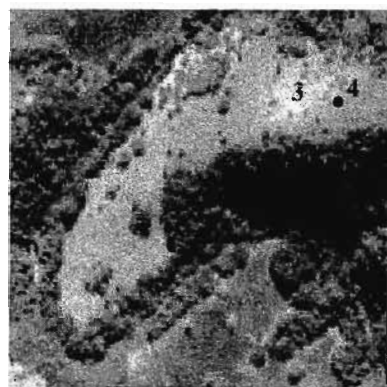
(c) Site 2a and Site 2b in 1937



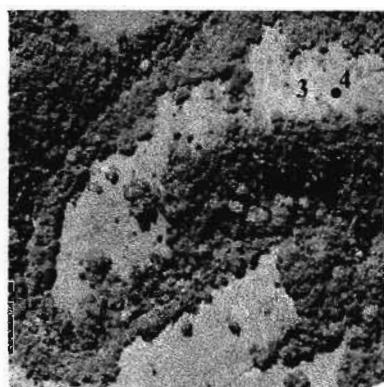
(d) Site 2a and Site 2b in 1966



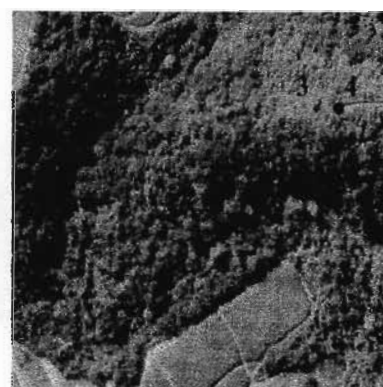
(e) Site 2a and Site 2b in 1990



(f) Site 3 and Site 4 in 1937



(g) Sites 3 and Site 4 in 1966



(h) Site 3 and Site 4 in 1990

PLATE 1

Coastal grassland sites selected for monitoring, showing gross vegetation change between 1937 & 1990



(a) View across Site 1b & crest in Dec. 1998



(b) View across 2a Sept. 1998, before burn



(c) View across 2a after burn, Sept. 1998



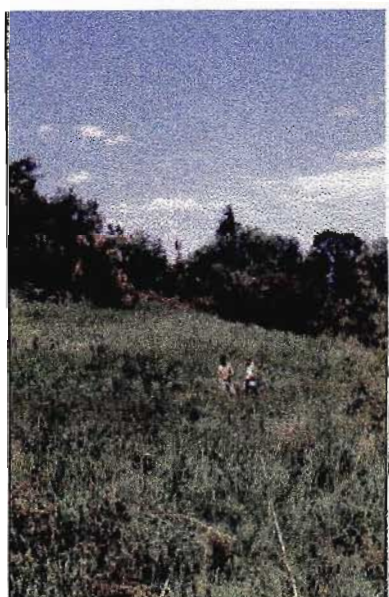
(d) View down transect 2a, Dec. 1998

PLATE 2

Coastal grassland sites 1 & 2a at the end of the study period



(a) Site 2b in Aug. 1991, baseline condition



(b) Transect 2b, Oct. 1996



(c) Burning Site 2b in Sept. 1998, note *Syzygium cordatum* shrublets in foreground



(d) View from Site 2a over Site 2b in Dec. 1998

PLATE 3

Site 2b at the beginning & end of the study period (1991-1998)



(a) View across Site 3b in Oct. 1996



(b) Transect 3b, Dec. 1998



(c) Transect 4a in Aug. 1991, after slashing dense *Chromolaena odorata* thickets



(d) Site 4a in Oct. 1996, 4b in background



(e) View down Site 4a in Dec. 1998, note burnt stems of *Solanum mauritianum*



(f) Site 4b scrub-thicket in Dec. 1998, Site 4a in foreground

PLATE 4

Views of sites 3 & 4 at different times during the study period



(a) Bush clump in Site 2b, Aug. 1991.
Phoenix reclinata and *Strelitzia nicolai*
common in bush clumps, along with
Syzygium cordatum



(b) Same *Phoenix* and
Strelitzia trees during the
first burn in Aug. 1991



(c) Bush clump in Site 2a five days after 1st
burn

PLATE 5

Fate of a bush clump in site 2b after reintroducing veld burning