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THE EFFECTS OF CATTLE ON THE DEVELOPMENT
OF PLANT COMMUNITIES IN REHABILITATING
COASTAL DUNE FORESTS AT RICHARDS BAY,
KWAZULU-NATAL, SOUTH AFRICA

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**THE EFFECTS OF CATTLE ON THE DEVELOPMENT OF PLANT COMMUNITIES IN
REHABILITATING COASTAL DUNE FORESTS AT RICHARDS BAY, KWAZULU-
NATAL, SOUTH AFRICA.**

by

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Vir Talitha, met liefde

Bos

1.

skewe geleedpotige roofdier,
op die horison draf die Winkelier -
strooi die oggend vol rooiwarm as,
hou die bewende strale van die son
in 'n kromgetrekte handjie vas

2.

lang, rankerige slingerplant
kotiljons die lug in uit die sand,
neem halfpad 'n paddastoel saam
op so 'n kosmiese wandelpad, lankal
deur lewensvoos samangos beraam

3.

'n oggend is in sy wese stil
as jy in die bos op jou hardste gil;
sweet val van my pangelaaide kop
ek kyk af en sien dat ek eintlik bewe
van afwagting en die kolonel se lot

Thabo Willeboer

The effects of cattle on the development of plant communities in rehabilitating coastal dune forests at Richards Bay, KwaZulu-Natal, South Africa.

by

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ABSTRACT

The effects of cattle on the herbaceous layer of coastal dune forest plant communities were investigated from May 1994 to March 1996 using an experimental application of three levels of grazing in a 16-year old stand of rehabilitating coastal dune forest north-east of Richards Bay. Rainfall had a dominant effect on all variables, but it was the same over all treatment levels. Treatment level did not affect species composition. Most of the univariate variables measured showed an interaction between time and level of treatment, with very few significant treatment-effects. Significant effects were generally independent of the level of treatment. However, the presence of cattle caused a consistent treatment-dependent increase in coefficient of variation in almost all measured univariate variables. This probably has longterm implications for the development of the plant community. It is concluded that cattle do have significant effects on some measures of species richness and vegetation cover of the herb layer, but it is not possible to state without any doubt that cattle will affect the process of succession significantly.

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CHAPTER 1

INTRODUCTION

BACKGROUND TO THE STUDY

The company Richards Bay Minerals has been mining a strip of coastal sand dunes northeast of Richards Bay, KwaZulu-Natal for windblown deposits of titanium, zircon, rutile and iron since July 1977 (Camp 1990, Van Aarde, Ferreira, Kritzinger, Van Dyk, Vogt & Wassenaar 1996). Ecological rehabilitation of mined dunes commenced soon after the start of mining and has continued uninterrupted since then, resulting in a series of sequentially aged rehabilitating stands, of which the oldest part is now some 19 years old.

The mining lease area, known as the Tisand lease area, is wedged between the Indian ocean to the southeast and a rural, developing part of KwaZulu-Natal to the northwest (Fig. 1). Although no figures are available for this specific area (Mr. B. Grobler, pers. comm.)*, the human population of the Lower Umfolozi district, which includes the study area, has increased from 45723 people in 1980 to 56082 people in 1991, an increase of 23% over the 10 years (Central Statistical Services 1997). To all appearances the growth in the cattle population matched and may even have surpassed that of the human population (pers. obs. 1994-1997). The increase in cattle numbers, together with a steady increase in bluegum (*Eucalyptus* sp.) plantations in and around the villages, meant that the area suitable for grazing by cattle and goats has effectively decreased. Consequently Richards Bay Minerals have experienced an increase in pressure from the local people for the use of post-mining rehabilitating areas as grazing for their cattle (Camp, pers. comm.)**. Although Richards Bay Minerals maintains a policy of keeping all cattle out of rehabilitating areas, variable amounts of grazing does take place, especially over weekends when there are no herders to keep them out.

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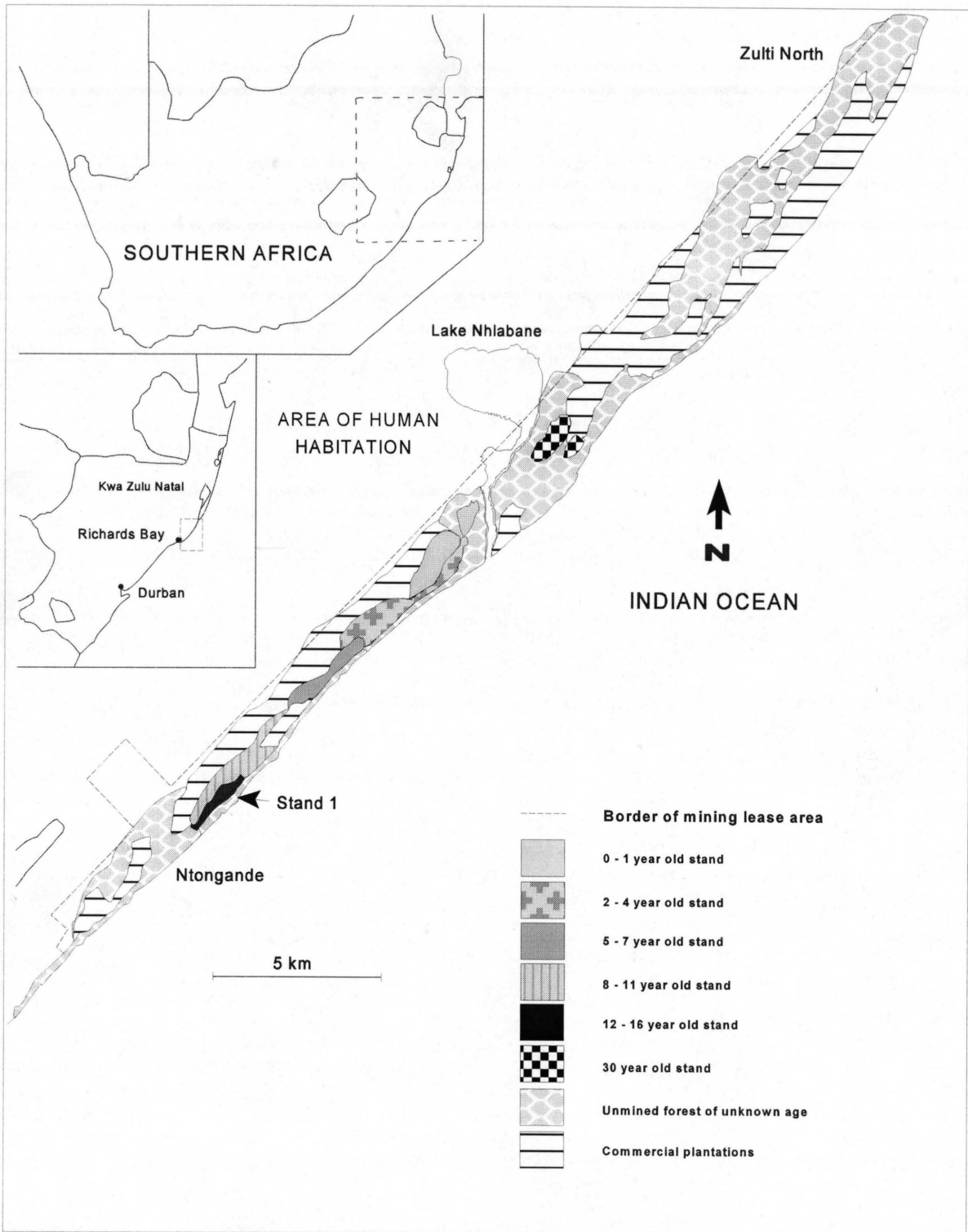


Figure 1. Map of the general study area north of Richards Bay ($28^{\circ}43'S / 32^{\circ}12'E$) showing the location of the mining lease of Richards Bay Minerals, the different aged rehabilitating stands, commercial plantations and the unmined areas. The present study was conducted in Stand 1, indicated here by an arrow.

Given all the possible effects of herbivores on a plant community (discussed in the following sections) and taking into consideration that the rehabilitating area has a relatively low plant cover over most of the area (own unpublished data) and is especially sensitive to seasonal droughts (data from the present study), it is reasonable to assume that cattle could have a significant effect on the development of the plant community. They could arguably influence the rehabilitation process in a completely unpredictable manner and put it onto a different trajectory from the expected (and required) one. It was therefore decided to investigate whether cattle have any effect on plant community development in some areas of rehabilitating coastal dune forest.

LITERATURE REVIEW

Two processes play a major role in the post-mining rehabilitation of coastal dune forests (and indeed, in most natural ecosystems). The first is disturbance. Not only the initial, major disturbance where all vegetation is removed ahead of the mining action, but also a background of smaller disturbances which continue to occur after the second process, that of plant and community succession, has commenced. Given ideal circumstances and in spite of, or perhaps because of the smaller disturbances, this process of succession should result in the eventual establishment of a vegetation complex which, if not exactly the same, would at least be similar to that of the coastal dune forest community which existed before disturbance (Mentis & Ellery 1994, Van Aarde, Ferreira & Kritzinger 1996a, Van Dyk 1997).

Disturbance is a recurrent feature of many systems (White & Pickett 1985) and can be caused by various agents. Disturbances due to human activities have occurred on the north coast of KwaZulu-Natal for at least a few thousand years (Maggs 1976, Bruton, Smith & Taylor 1980, Mentis & Ellery 1994) and is certainly a feature of the present landscape. Apart from climatic changes from the late Pleistocene to the present, with alternating glacial and interglacial periods and the consequent recession and advance of the coastline, environmental disturbances on a smaller scale still occur (Tinley 1985). For one thing, the present wind regime, largely determined by tropical cyclones which are a natural feature of climatic conditions on the north coast, sporadically cause parabolic blow-outs of the fore-dunes (Tinley 1985). For another, periodic

droughts are as much a feature of the rainfall regime as are years of exceptionally good rainfall and even floods (Tyson 1986).

Although disturbance is not the only factor that causes recruitment of new species, disturbance and succession are inextricably linked (Johnstone 1986, Glenn-Lewin & van der Maarel 1992). In the context of the present study, an understanding of these two processes are of utmost importance.

Succession

Succession is a directional, cumulative, nonrandom change in the species that occupy a given area (Barbour, Burk & Pitts 1987). The use of the word “directional” by Barbour *et al.* (1987) is somewhat unfortunate, since it implies a single, definite endpoint, while the work on community assembly by for instance Drake (1991) and Law & Morton (1996) showed clearly that there can be many endpoints to succession. Communities tend toward stable “basins of attraction” instead of entering cycles where one set of species systematically replaces another (Lockwood 1997). “Directional” then means no more than the trajectory of community development towards some undefined and possibly even unknown stable endpoint. Even the word “endpoint” must be qualified in terms of this basin of attraction, which also includes, apart from a description of the species composition of the community, aspects of community structure and function. Change doesn’t stop when the basin is reached.

Two types of succession have been recognized (Barbour *et al.* 1987): (1) Primary succession, which is the development of a community on land which has been completely denuded of all vegetation, or has not previously been occupied by any organisms (for instance new islands that form as a result of volcanic processes), and (2) secondary succession, where a biological community develops on land that was previously occupied by organisms but has since been destroyed due to any man-made or biotic or abiotic (environmental) disturbance. Primary succession is probably a rare process in nature, while secondary succession is ubiquitous (Miles 1987). Succession can be caused by environmental changes beyond biological control. For

instance a decreasing trend in rainfall in a region over a matter of years to decades can induce a succession from grassland to desert scrub (Barbour *et al.* 1987). This is known as *allogenic succession*. On the other hand, succession can be driven by the community itself, with vegetation types modifying the environment to make it more suitable for other vegetation types (or less suitable - Bastow-Wilson & Agnew 1992). This is generally known as *autogenic succession* (Barbour *et al.* 1987).

Succession is a well documented process in vegetation science (Glenn-Lewin & van der Maarel 1992) and there is also a growing body of literature on succession in other taxa (see for instance the chapters in Pickett & White 1985 on vertebrate and invertebrate succession in a variety of biomes). In the present study succession refers to plant succession and specifically to changes in the species composition and species abundance of a community in response to a particular, discrete disturbance event of any given size as in McCook (1994). The concept of plant succession was developed largely in North America in the first two decades of this century, but it was not until the 1960's that any attempt was made to give a theoretical basis to the wide ranging observations of succession (Glenn-Lewin, Peet & van der Maarel 1992). This initial attempt at synthesising plant succession theory was largely organismic in nature and leaned heavily on Clements' theory of "relay floristics" (Barbour *et al.* 1987, McCook 1994), which saw succession as a convergence of highly integrated communities towards a predictable climax community, always the same for a given area. (Although Clements' theory has generally been taken to mean that succession always ends in a predictable, stable climax, he did not regard the climax community as an unchanging concept. He explicitly stated that no such climax area lacks evidence of succession, that the most stable association is never in complete equilibrium and is never free from disturbed areas in which secondary succession is evident (Clements 1916, cited by Miles 1987).)

Since the 1970's two major conceptual trends have dominated vegetation dynamics research (Glenn-Lewin *et al.* 1992): (1) a shift away from holistic explanations of successional phenomena towards a reductionist, mechanistic approach; and (2) a shift away from equilibrium towards non-equilibrium paradigms. (See also Hastings, Hom, Ellner, Turchin & Godfray (1993) for chaotic systems theory as an alternative to the equilibrium concept in ecology). This has resulted in a

corresponding shift away from broad attempts at generalizations about successional phenomena towards a largely mechanistic, descriptive approach based on the individualistic concept of plant association first developed by Gleason (1926). However, the debate about “holism vs. reductionism” is far from over. Odum (1969) argued that an ecosystem may have an overall strategy to maintain or recover stability. In other words, the ecosystem as a whole may have properties which are unpredictable from a knowledge of the parts. Although Odum (1969) mentioned the role that complexity plays in determining these emergent properties, succession, according to him, is an orderly, self-controlled development of communities. Just a few years later Drury & Nisbet (1973), in an analysis of *inter alia* Odum’s conceptual approach, concluded that:

“...a complete theory of vegetative succession should be sought at the organismic, physiological or cellular level, and not in emergent properties of populations and communities.”(p. 360)

They emphasise, in direct contrast to Odum (1969), diversity, irregularity and complexity in succession. In other words, succession is often a disorderly process. The reductionist principle of species individuality pioneered by Gleason (1926) and expanded on by Drury & Nisbet (1973), has subsequently been adopted by most ecologists and has led to the development of a large and diverse family of models (Usher 1987). On the other hand, computer modelling has shown that there is probably a limit to the reducibility of ecosystems as a result of their inherent complexity (Jørgensen, Patten & Straškraba 1992). It is exactly this property of complexity of ecological systems which may force ecology to go back to a holistic approach (Jørgensen *et al.* 1992).

Probably the most important development in succession theory during the 1970's was the definition of three models of sequential succession (facilitation, tolerance and inhibition) by Connell & Slatyer (1977). (Lawton (1987) also includes another model, namely random colonization.) These models have been criticised as being too simplistic and empirical in nature (McCook 1994, Pickett, Collins & Armesto 1987), but have nevertheless made a major contribution towards the formulation of ideas on plant succession. They have been the basis of most plant succession research done in the last decade and provide, if not a clear theoretical basis, at least a graphic and lucid description of successional mechanisms on the population level. The models are not causal in nature, but provide empirical summaries that describe limits within

which interactions between species occur. Their biggest limitation is that they cannot, on their own, account for all the possible causes of and pathways in succession; at most they describe specific transitions within a seral development of a plant community (Pickett *et al.* 1987). Briefly then, the four models are:

- *Facilitation*: species occurring early in succession modify the habitat, making it less suitable for themselves and more suitable for later colonists.
- *Inhibition*: whichever plant species reaches a site first, holds it against all possible subsequent invaders until it dies.
- *Tolerance*: slower growing, more tolerant, competitively superior plant species invade and mature in the presence of earlier, faster growing, but less tolerant species and eventually exclude them.
- *Random colonization*: succession involves no more than the chance survival of different species at the time succession is initiated, and subsequent random colonization by new species. Species then grow and mature at different rates. There is no facilitation and interspecific interactions are not important.

There have been a number of attempts to integrate modern plant succession theory, most notably those by Huston & Smith (1987), Pickett *et al.* (1987), Glenn-Lewin *et al.* (1992) McCook (1994). However, (and probably not too surprising in view of the complexity and diversity of causes) succession still lacks a unifying theory. The view of succession as primarily a species replacement process driven only by autogenic environmental modification has been rejected (Connell & Slatyer 1977, Peet & Christensen 1980). It has been superseded by a number of non-mutually exclusive hypotheses which may all apply in varying degrees to the same successional sequence (Glenn-Lewin *et al.* 1992). Succession is seen as gradients in time or resource availability (Tilman 1985, Glenn-Lewin & van der Maarel 1992), the result of differences in life history and competitive ability (Huston & Smith 1987, Lepš and Štursa 1989, McCook 1994), the result of stochastic processes (Horn 1975, cited in Peet & Christensen 1980), the consequence of differential longevity and population processes (Peet & Christensen 1980) and as the consequence of a set of assembly rules (Diamond, cited in Lawton 1987, Law & Morton 1996 and Lockwood 1997). In the following paragraphs I will discuss some recent and important ideas

and theories regarding succession.

McCook (1994), in a lengthy review of modern succession theory, concludes that succession can best be seen as the result of differences in life history traits of species adapted to different regions of continua of various resources. To quote McCook: "In general, limits on the allocation of metabolic resources results in trade-offs between growth, and specialization for low levels of resources, particularly light. Such trade-offs result in an inverse correlation between traits that favour species early in re-vegetation of a site, such as dispersal and rapid growth, and those which favour long term dominance, such as shade tolerance, longevity, height, and resistance to damage. When these traits are inversely correlated, successional replacements will result". This is one of the strongest themes in succession theory and was probably understood before the time of Clements, although not explicitly defined before the papers on succession by Gleason (1926) Whittaker (1953) and Drury & Nisbet (1973). It is particularly the simulation model of Huston & Smith (1987) which provides compelling evidence for the importance of correlations in life history traits.

Bastow-Wilson & Agnew (1992) identified positive-feedback switches as another major mechanism which determines the outcome or pathways of succession. There is not a theoretical analysis of succession on the level of McCook (1994), but is nevertheless a testable view of mechanisms involved in the successional process. Basically the idea holds that two (or more) vegetation/environment states are stable in time or space, but not the intermediates (Bastow-Wilson & Agnew 1992). Switches operate on the level of Clements' (1916, cited by McCook 1994) facilitation model of succession, but in this case the community present on a site changes the environment to make it more suitable for itself (Bastow-Wilson & Agnew 1992). The term "switch" then refers to the fact that positive feedback by the community can switch the development of the environment and vegetation between alternative stable states, as opposed to the conventional view of facilitation succession which allows only one convergent developmental pathway (Bastow-Wilson & Agnew 1992).

Community assembly theory is a highly mechanistic view of succession and developed largely as computer models over the last two decades in response to observations in the field by *inter*

alia Diamond (1975, cited by Lockwood 1997). While succession is usually seen as being driven by outside forces or emergent properties of the community (i.e. process-oriented), assembly theory views it in terms of the chances of colonisation and persistence for a species arriving at a site. Species properties (for example life history traits) certainly play a role, but only in terms of the species' chances of successfully invading and not as an absolute determinant of where in the succession sequence it fits in. According to Diamond (1975, cited by Lawton 1987), interspecific competition for resources is the major factor governing the rules of assembly of a community, although a number of other biological interactions probably play a role (Lawton 1987). One of the most significant findings of assembly theory is that there are a number of alternative states possible, despite identical initial conditions (Post & Pimm 1983, Drake 1991, Drake, Flum, Witteman, Voskuil, Hoylman, Creson, Kenny, Huxel, Larue & Duncan 1993, Lockwood 1997). This means that the positive-feedback switch mechanism in plant communities identified by Bastow-Wilson & Agnew (1992) is probably only a special case of community assembly. The sequence of invasion by species (Robinson & Dickerson 1987, Robinson & Edgemon 1988), as well as historical factors are major determinants of the final community structure (McCune & Allen 1985). Another important finding of the computer simulations is that invasion resistance of a community builds up over time, sometimes in stages (Law & Morton 1996).

In conclusion it can be said that there are many factors involved in succession, modifying and regulating the dynamics of the process, but the controlling principles remain the same. "Succession is a unique process [with an] ubiquitous pattern" (McCook 1994).

Disturbance

Disturbance (and its related terms) has been defined in a number of ways, with the emphasis variously placed on mechanisms involved, causes (changes in the environment) and effects (responses of organisms, populations or communities) (Glenn-Lewin & van der Maarel 1992). Grime (1979, cited in Glenn-Lewin & van der Maarel 1992) defined disturbance as "the mechanisms which limit plant biomass by causing its partial or total destruction". Rykiel (1985)

sees disturbance as the cause (a physical force, agent or process) and perturbation as the response of any ecological component or ecological process (indicated by deviations in the values that describe the properties of the component or system) to the disturbance. According to White & Pickett (1985) disturbance is not defined in terms of the "normal" environment, or even "normal" disturbance events, but includes all environmental fluctuations and destructive events, relative to the spatial and temporal dimensions of the system at hand. Disturbance would then be "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett 1985).

Factors responsible for change in an ecological community are usually classified as either endogenous (arising from within the community) or exogenous (from outside the community). Natural disturbances have always been regarded as exogenous, while successional changes in disturbance - free periods were thought to have been driven by endogenous factors (White & Pickett 1985). However, these distinctions are sometimes difficult to make in natural systems. It is more convenient to regard endogenous and exogenous factors as endpoints on a continuum, one of several such continua involved in a disturbance: the relative discreteness of the disturbance event in time, the relative discreteness of the disturbance area and the relative effect on ecosystem resources (White & Pickett 1985). In fact, the processes that produce the almost ubiquitous pattern of increased species diversity at intermediate levels of disturbance (see later paragraphs in this section) will work regardless of whether the source of disturbance is exogenous or endogenous (Rosenzweig 1995) (but see Schwilk, Keeley & Bond (1997) for an exception to the rule in fire-prone plant communities).

Today disturbance is widely accepted as one of the main forces involved in the creation and maintenance of diversity both within and between communities (Whittaker 1977, Petraitis, Latham & Niesenbaum 1989 and Wu & Loucks 1995). Although the relative importance and specific mechanisms through which disturbance operates is not always known for a specific area, most ecologists agree that communities generally consist of heterogenous patches created and maintained by random abiotic and biotic disturbances (White & Pickett 1985, Wu & Loucks 1995). In fact, there are probably very few communities persisting at or near equilibrium conditions on the local scale (Sousa 1984, Rykiel 1985, Wu & Loucks 1995). Disturbance

operates on a temporally and spatially variable scale and includes environmental fluctuations as well as destructive events like predation and herbivory. This variation in scale is a major reason for heterogeneity, because disturbances may happen at more or less the same time or place (Karr & Freemark 1985) and is one of the main factors in the hierarchical patch dynamics perspective of Wu & Loucks (1995).

The effects of a disturbance is often unpredictable. The outcome depends on the "harshness" of the disturbance, as well as the characteristics of the community being disturbed (Petraitis *et al.* 1989). In some communities and under some circumstances, disturbances are critical for maintenance of coexisting species, while in others it can cause an elimination of species and long lasting changes in ecosystems (Denslow 1985 and references cited therein). In general, the effects of disturbances can be summarised into three categories (Denslow 1985): changes in environmental (or spatial) heterogeneity, changes in temporal heterogeneity, and changes in the relative abundances of species.

Disturbance as a source of spatial heterogeneity

Most disturbances have heterogenous and patchy effects. A community can be viewed as a mosaic of patches of different age, size, structure and composition (White & Pickett 1985). These mosaic patterns are themselves dynamic, since environmental characteristics change with time. Spatial variation in the abundance of species also occurs on the scale of the disturbed patch. The size and shape of a patch indirectly influences its repopulation through variation in the physical environment and biological interactions. Even at the level of the individual plant where the physical conditions may be relatively homogenous across a site, the opportunities for recruitment, growth, reproduction, and survival vary spatially (Sousa 1984).

Disturbance as a source of temporal heterogeneity

In the temporal context it is particularly the history and frequency of disturbances that are important in determining the habitat heterogeneity of an area. Fluctuating environments lead to multiple resettings of the local successional trajectory (White & Pickett 1985). Apart from the

effect of frequency differences in disturbances, and superimposed on the rate of successional changes, there is a seasonal variability in composition, especially in early successional communities (Denslow 1985). This obviously has important implications for the ultimate effect of the disturbance or disturbances, creating another source of variation in the establishment of new species at a site (see for eg. Kotanen 1996). Large disturbances that occur primarily during one season will cause less inter patch variation than small disturbances that occur year round (Abugov 1982, Sousa 1984).

Disturbance as a source of changes in species abundance

One of the principal effects of a disturbance is to alter the availability of resources for plant growth (Canham & Marks 1985, Tilman 1985). Differential responses of species to such a change in available resources (due to different life history traits (Tilman 1985, Huston & Smith 1987)), as well as differences in regeneration niche (Grubb 1977, Lavorel & Chesson 1995) will increase the potential number of coexisting species on a site. Put in another way, disturbance is one of the main mechanisms through which invasion windows are opened up for a species (Johnstone 1986). Disturbances also differ in their effect on a site and, if small scale topographical variation within even a relatively homogenous area is taken into account, could be the source of multiple levels of heterogeneity and therefore provide a complex basis for resource partitioning among coexisting species (Denslow 1985).

However, the most important factors in the effect that disturbance has on species abundance are the scale, frequency and intensity of the disturbance, as well as the region in question. The pattern of high diversity at intermediate disturbance levels (both frequency and size of disturbance - Abugov 1982, Petraitis *et al.* 1989, Vetaas 1997), which was first elucidated by Connell (1978) and Huston (1979) and before them implicitly by Whittaker (1977), only exists at relatively small spatial scales and at intermediate frequencies of disturbance (Rosenzweig 1995). The intermediate disturbance hypothesis hinges on two factors: (1) disturbances of a certain frequency and intensity prevent monopolization of resources by one or a few species, and (2) disturbances are not biologically so destructive that only a few species can exploit the resources made available (Rykiel 1985). Frequent, large disturbances will increase the homogeneity of a region if the plants

are not adapted to such a regime (Denslow 1985). The models of Petraitis *et al.* (1989) predicts that, while it is generally true that the greatest number of species could be expected at intermediate levels of disturbance, a number of possible outcomes exist, depending on the intensity of the disturbance and on the characteristics of the species. Abugov (1982) defined a phasing parameter to describe temporal patterning of disturbances - a high degree of phasing means that each time a disturbance clears one patch, it clears all of them, while conversely a low degree of phasing means that the clearing of patches by disturbance events are independent of each other. This model predicts the highest Shannon-Wiener diversity at intermediate disturbance rates regardless of the degree of phasing, but also that any given disturbance level may be associated with many possible diversities, dependent on degree of phasing.

Disturbance and succession associated with the mining of coastal sand dunes northeast of Richards Bay (Tisand lease area)

Richards Bay Minerals has been mining the coastal sand dunes north of Richards Bay since 1977. The minerals are retrieved through an opencast technique, where the dunes are stripped of all vegetation prior to the actual retrieval. A pond is constructed on which the mining and separation machinery floats. This pond moves through the dunes along a pre-planned route, removing all sand ahead of it. The heavy minerals are separated out and the remaining sand (96% of the original volume) is then deposited behind the pond to recreate the dunes as faithfully as possible (Camp 1990, Lubke, Moll & Avis 1992).

Once the dunes have been reconstructed, rehabilitation of the area commences. Two thirds of the mined area is afforested with the exotic tree *Casuarina equisetifolia* and one third is rehabilitated to indigenous vegetation. For the purposes of the present study it is only the rehabilitation to indigenous vegetation that is of importance. The re-establishment of indigenous forest is initiated by spreading the topsoil, harvested prior to mining, in a thin layer ($\approx 10\text{cm}$) on the surface of the reconstructed sand dune. Apart from a cover crop of indigenous and exotic grasses, no seed is added to the topsoil. The fast growing, mostly annual species mixture provides an effective cover within a few weeks (Camp 1990, Van Dyk 1997). This artificial community is gradually replaced

with mostly indigenous perennial herbs within the first couple of months to years, while *Acacia karroo* emerges somewhat later, but dominates the community by approximately four years of age (Van Dyk 1997). The composition then changes from an open grass- herb community to a closed, dense *Acacia* scrubland. The scrubland develops into a closed woodland within the next three years as *A. karroo* grows taller and becomes dominant in terms of structure as well as biomass (Van Dyk 1997). At 12-16 years after the start of rehabilitation *A. karroo* is still the dominant species (the canopy is by now about 12m high) and a dense herb- and shrub layer has developed on the forest floor (Van Aarde *et al.* 1996, see also Table 2).

The mining process causes an intense, local disturbance of the indigenous coastal dune forest community with a total destruction of the substrate, to the extent that the subsequent successional process could be classified as primary succession if the composition of the pioneer community (vegetation re-established post-mining) was not to such a large extent artificial. Avis (1992) found a decrease in the organic matter from 6.4% in the pre-mined topsoil to less than 2% in the mined soil, while Van Aarde, Smit & Claassens (1998) found a decrease from 2.9% in unmined topsoil to 0.8% in the topsoil of a 3-5 year old rehabilitating stand. According to Avis (1992) phosphate, calcium and sodium show reductions from 20%, 32% and 900 ppm respectively to 5%, 13% and 350 ppm in post-mined soils. Apart from phosphate which was found at higher levels in the topsoil of a 3 to 5 year old rehabilitating stand (22.4mg/kg) than in that of the unmined forest (11.4mg/kg), Van Aarde *et al.* (1998) found less calcium (1001mg/kg), potassium (39.7mg/kg), sodium (20.3mg/kg), nitrogen (440mg/kg) and carbon (0.5mg/kg) in the topsoil of the 3-5 year old rehabilitating stand than in that of the unmined forest (1934mg/kg, 53mg/kg, 34mg/kg, 1899mg/kg and 2mg/kg respectively). The mining process therefore meets all the requirements of the definition of a disturbance (according to White & Pickett 1985): it is a relatively discrete event which disrupts the community structure and function and changes the availability of resources and substrate and the physical environment.

Several studies have been or are currently being undertaken to establish and characterise various aspects of community succession in the post-mining rehabilitating areas. All of these studies point to a sequential change in the species present along a temporal gradient (see Van Aarde *et al.* 1996, Van Aarde, Ferreira & Kritzing 1996a, 1996b, Van Dyk 1997, Kritzing & Van Aarde

Appendix 9. (continued)

| Treatment level | Height class | | | |
|--------------------|--------------|------------|---------|----------|
| | Canopy | Sub-canopy | Sapling | Seedling |
| <i>(c) Density</i> | | | | |
| Control | 0.80 | 2.00 | 8.40 | 1.00 |
| | 0.80 | 2.80 | 4.00 | 1.60 |
| | 2.00 | 3.80 | 3.60 | 0.20 |
| | 1.00 | 3.40 | 2.60 | 0.80 |
| Low | 1.60 | 3.80 | 8.40 | 0.80 |
| | 2.40 | 2.80 | 11.40 | 2.20 |
| | 1.60 | 2.60 | 2.00 | 0.20 |
| | 1.00 | 2.00 | 2.80 | 0.00 |
| Medium | 1.40 | 4.20 | 10.60 | 1.40 |
| | 1.00 | 2.00 | 11.40 | 1.80 |
| | 0.40 | 0.60 | 2.40 | 1.00 |
| | 0.40 | 0.60 | 8.60 | 1.20 |
| High | 1.00 | 5.20 | 6.40 | 2.60 |
| | 2.00 | 5.40 | 13.40 | 5.20 |
| | 0.80 | 2.40 | 2.00 | 0.80 |
| | 2.20 | 3.80 | 8.00 | 2.80 |
| <i>(d) Height</i> | | | | |
| Control | 600.00 | 270.50 | 115.10 | 34.60 |
| | 860.00 | 303.33 | 126.83 | 19.33 |
| | 903.33 | 314.88 | 124.00 | 9.60 |
| Low | 640.00 | 310.87 | 126.50 | 11.60 |
| | 795.00 | 279.75 | 132.13 | 13.87 |
| | 793.33 | 200.45 | 111.97 | 36.85 |
| | 820.00 | 346.60 | 104.75 | 8.40 |
| Medium | 900.00 | 310.80 | 128.10 | 0.00 |
| | 1040.00 | 245.97 | 119.47 | 20.67 |
| | 620.00 | 303.33 | 112.13 | 43.73 |
| | 360.00 | 139.00 | 86.33 | 7.92 |
| High | 400.00 | 106.00 | 96.30 | 27.60 |
| | 1140.00 | 285.07 | 108.63 | 26.89 |
| | 990.00 | 322.20 | 114.73 | 31.63 |
| | 460.00 | 334.50 | 42.00 | 30.40 |
| | 1016.67 | 298.03 | 112.86 | 39.79 |

1998 (in press), Ferreira & Van Aarde 1996, 1997). Mentis & Ellery (1994) concluded that plant succession as a process is occurring in the rehabilitating areas and they based this conclusion on the fact that Euclidean distance of disturbed stands from an average mature stand decreased and plant species richness increased with time. They also found no significant difference between succession in the rehabilitating areas and succession in unmined, disturbed areas.

The animal-plant interaction - herbivory as a disturbance event

Because I am mainly concerned with the effect of large herbivores on plant communities, the rest of this discussion will deal mainly with large herbivores. However, where necessary I will touch on other levels of herbivory as well. Plants and animals evolved together and it may therefore be inappropriate to consider grazing a disturbance in terms of the definition given earlier (see page 10). However, herbivores have a profound effect on their environment, being able to create and maintain a specific community (Cumming 1982, McNaughton 1983, Van de Koppel, Rietkerk & Weissing 1997). This effect can vary from destruction of both the vegetation and environment, to barely discernible interactions between the plant and its herbivorous predators and between the plant and its environment (Fig. 2) (Cumming 1982). According to Crawley (1983) animals may have the following effects on plants:

- reverse the competitive abilities of plant species by feeding preferentially on the species that is the most competitive in the absence of grazing with the result that the less competitive species receives a distinct advantage,
- decrease the abundance of the least competitive species by selecting specifically for it,
- cause a switch in dominance by feeding preferentially on whichever species is the most dominant, and
- have a completely neutral effect - the herbivore takes each plant species in proportion to its abundance. The outcome would then depend on the relative grazing tolerance, regrowth potential and morphological responses to defoliation.

In spite of these obvious and often significant effects of herbivores, most models of succession attribute only minor importance to herbivory as a process bringing about change in plant

communities. For instance, grazing by large herbivores is often seen as an external factor, largely introduced by man, which may arrest or deflect succession taking place in the “natural” environment (Edwards & Gillman 1987, Gibson & Brown 1992). However, herbivory is a process which takes place on a variety of scales (Lawton 1984, McNaughton 1985) and which therefore influences the organization of almost every plant community at many different scales and on all hierarchical levels (Crawley 1983, Lawton 1984, Glenn-Lewin & van der Maarel 1992).

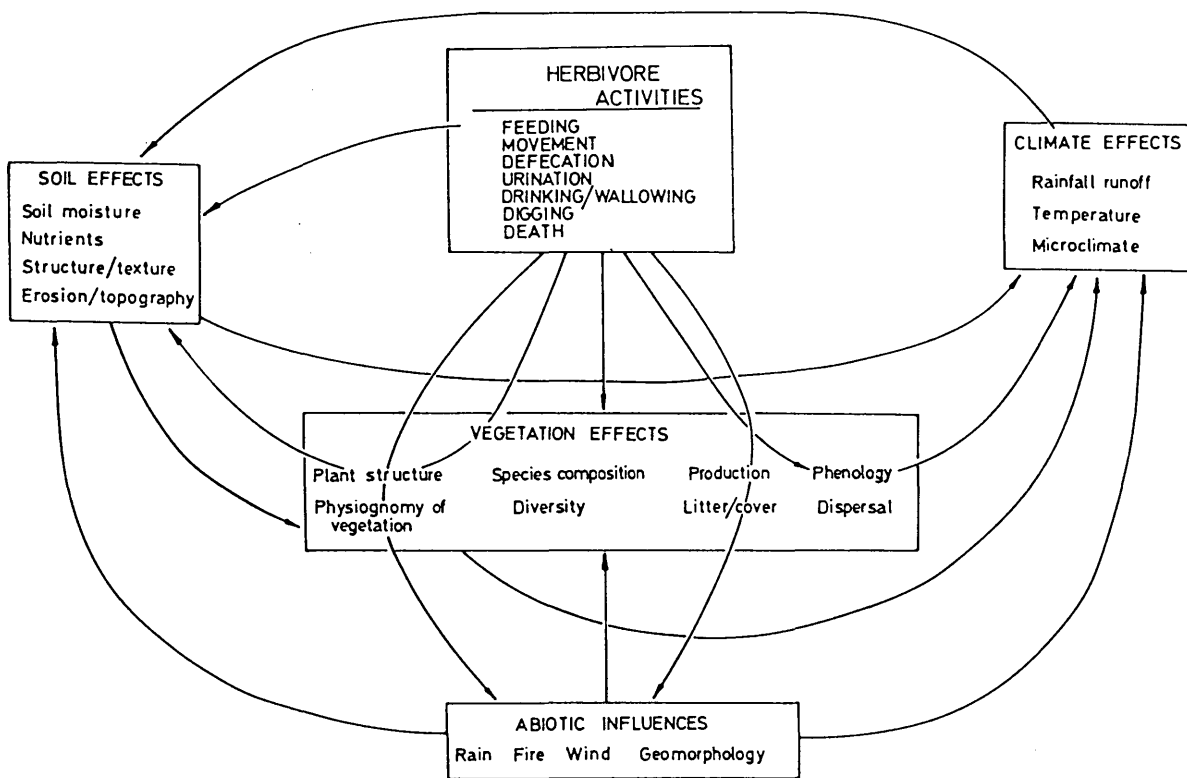


Figure 2. Schematic diagram, summarising the activities of large herbivores and the effects these activities may have on their environment. Adapted from Cumming (1982).

Large herbivores affect plant communities by damaging individual plants, altering the plants' environment and transporting plant propagules (Cumming 1982, Edwards & Gillman 1987). The effect of herbivores on individual plants finds its expression in community characteristics like vegetation cover and species composition. Plants are eaten, trampled on and urinated and defecated on as part of the herbivore's normal foraging behaviour, which certainly damage individual plants, but the consequence is a reduction in vegetation and litter cover, a change in the relative abundances of species, a change in species richness and a change in the rate of primary production (Crawley 1983, McNaughton 1984, McIntyre, Lavorel & Tremont 1995, Van de Koppel *et al.* 1997). It is also important to keep in mind that the principal impact of herbivores (on the community level) is not through their effect on single species, but through their effect on the competitive balance between species (Crawley 1983). In stable conditions the relative abundance of plant species reflects an approximate equilibrium between all the various selective pressures, including herbivory (Edwards & Gillman 1987).

The stage in the regeneration cycle of plants (which for the largest part is dependent on season) at which damage to the plant occurs will ultimately determine the magnitude of the effect of herbivory. The seedling stage is probably the most vulnerable one for many species and as a consequence herbivore pressure here could have wide-ranging community-level effects (Edwards & Gillman 1987). However, it is also true that herbivory at the time of flowering or seed set will have a markedly more detrimental effect on reproduction than herbivory which occurs during the vegetative growth phase, although many plants compensate to a large extent by redundancy in the production of flowers (Tainton 1982, McNaughton 1983). Any effect that herbivory has on the production of individual plants is likely to also affect the production of seed, through the physical removal of reproductive parts, as well as through a negative effect on nutrient balance (Edwards & Gillman 1987).

The rate of primary production is altered through the effect that herbivores have on soil structure, nutrient status and soil moisture, as well as through the direct effect of defoliation or the removal of some plants (Crawley 1983). Defoliation can reach staggering levels. Herbivores can eat anything between 20% and 90% of net primary production, depending on the community, environmental conditions and population dynamics of the herbivore (Crawley 1983).

McNaughton (1985) found that herbivores removed 66% of annual above-ground primary production (range 15-94%) in the Serengeti. Defoliation results in a redistribution of production, for example from the canopy to the herbaceous layer, changing the structure of the plant community (Cumming 1982). The effect of herbivores on primary production depends to a large extent on the plant part being utilised. For instance Morón-Rios, Dirzo & Jaramillo (1997) found that the presence of below-ground herbivores was critical in determining the effect of defoliation. Plants which were only lightly defoliated but had root-feeders suffered an overall loss in live above-ground, root and total biomass, while those that had no root-feeders had increased their biomass to more than that of the control plants. In general though, the plant's survivorship is less affected than its fecundity. Leaf eating herbivores can cause a reduction in growth rate, a delay in the onset of flowering and a decrease in the resources available for reproduction (Crawley 1983).

According to McNaughton (1983), grazing can also have a positive effect on plant fitness (indices of growth and production). Plants adapted to a regular disturbance like grazing respond to it by growing faster and forming new tillers and shoots (Tainton 1982, McNaughton 1983). It is also certainly true that in some systems, notably grasslands and savannas, grazing is almost a prerequisite for the maintenance of productivity. In these systems, grazing removes senescent material and detritus that builds up during the growing season, removing its shading effect (Tainton 1982, McNaughton 1985, 1986). This allows an increase in the quantity of photosynthetically active radiation (Tainton 1982, Pandey & Singh 1992). Increased production in response to herbivory in these systems would therefore be the rule rather than the exception. In fact, provided there is an intervening period of growth, removal of vegetative tissues to a certain proportion of their initial level is rarely translated into a commensurate proportional reduction in the final yield of those or other plant tissues (McNaughton 1983). McNaughton (1983) also mentions a number of studies which found either no effect of grazing on fruit production or an increased seedset/flower production by certain plants in response to herbivory. Herbivory does not maximize plant fitness, but plants can compensate for damage so that fitness may increase (McNaughton 1983, 1985, 1986).

There is some controversy over whether plant adaptation to herbivory exists or whether it is

simply a physiological consequence of adaptation to competition for light (Aarssen & Irwin 1991, Järemo, Nilsson & Tuomi 1996). While it is certainly true that on the community level there may be an adaptation to herbivory in the sense that there may be a rapid selection for resistant ecotypes in response to an increase in grazing pressure (Edwards & Gillmann 1987, McIntyre, Lavorel & Tremont 1995), species specific adaptations like high growth rates and the capacity to branch may be more important in competition than in tolerance to herbivory (Rosenthal & Kotanen 1994). The removal of apical buds by herbivores could release lateral meristems from inhibition of apical dominance (Aarssen 1995) or herbivory could stimulate dormant buds lower down on the plant (Tuomi, Nilsson & Åström, 1994). Adaptation to herbivory is then a by-product of the adaptation to competition for light in that plants with the ability to rapidly increase in height as a result of apical bud dominance, will also automatically be adapted to damage due to herbivory (Järemo *et al.* 1996). The explanation that competition for light is the main factor involved in plant adaptation to herbivory, is in contrast to the mechanism proposed by McNaughton (1983, 1984), which holds that herbivore-adapted plants evolved in response to a predictable damage, to the point that the plant is actually dependent on the herbivore to increase its fitness. For instance, a plant's adaptation to competition for light, although an adequate proximate explanation of plant response to herbivory, does not explain the development of defence mechanisms in plants. Plants which succeed under conditions of heavy browsing or grazing are those which are resistant in some way to these pressures, either because of physical or chemical defence mechanisms, or through a growth form that makes sensitive tissues inaccessible to herbivores (McNaughton 1984, McIntyre *et al.* 1995).

Belsky (1987) and Belsky, Carson, Jensen & Fox (1993) criticised McNaughton's (and other authors') arguments about the positive effect of herbivory on plants, because they could not find proof in the literature that herbivory did directly increase the plant's fitness. Belsky *et al.* (1993) pointed out that none of the published studies and reviews proposed an adequate mechanism through which natural selection for a herbivore-plant mutualism could have taken place. Much of the debate seems to have been a matter of semantics as well as scale. For instance, Owen & Wiegert (1984, cited by Belsky 1987) argued that photosynthesis is often limited by the availability of carbohydrate sinks in the plant. Aphids feeding on the plants then act as sinks by stimulating sugar production which eventually falls on the ground to be utilised by nitrogen-

fixing microbes. In this roundabout way the plant then benefits from being fed upon. Owen & Wiegert (1982) also proposed that saliva produced by grazers stimulates growth in grasses. These mechanisms imply that the effect of herbivores occur partly on an organismic and partly on an ecosystem level. According to Belsky (1987), McNaughton's (1983, 1985, 1986) proposed mechanisms of plant-fitness response all act on a community or ecosystem level where processes such as competition and succession can explain the persistence or disappearance of species. The level on which the effect of herbivory on plants is evaluated is therefore important. On an organismic level herbivory may have a deleterious effect on the individual plant, while the community or ecosystem attributes of plant production/fitness may be enhanced (Belsky 1987). It is immediately apparent that none of these arguments encompass any plausible evolutionary mechanisms and it is a moot point whether the proposed mechanisms are really important. Functional approaches like that of Rosenthal & Kotanen (1994) and Aarssen (1995) holds much more promise and is intuitively more interesting.

A plant's environment is altered in many ways by large herbivores. They open up gaps in the canopy through trampling and removal of plant material, and the size and dynamics of these small-scale gaps may influence the kinds of plant species which persist in the community (McIntyre *et al.* 1995). (Species tend to be differentially affected by the amount of disturbance to the micro-climatic conditions necessary for germination - see for example Molofsky & Augspurger 1992). Herbivores also have an effect on the geomorphology, soils, nutrients and production of the plant community or ecosystem in question (Cumming 1982). For instance, domestic ungulates tend to follow certain routes to and from their preferred grazing areas (in the case of an unmanaged grazing system). This results in denudation of the plant cover and eventual erosion through increased run-off, as well as donga formation and sheet erosion by wind and water, with the consequent removal of topsoil (Crawley 1983). Large herbivores may influence the soil directly by compaction or by breaking up the protective seal on the surface through hoof action (Cumming 1982, Van de Koppel *et al.* 1997). Together with a reduction in plant cover, this could lead to the eventual collapse of the soil profile, rendering the substrate unsuitable for the establishment of plants (or at the very least changing the germination conditions). In certain systems and under certain conditions, this may even cause irreversible shifts between vegetation states (Van de Koppel *et al.* 1997).

Faeces and urine deposited by large herbivores have a significant local effect on soil pH and nutrient balance (specifically the amount of available Nitrogen) (Edwards & Gillman 1987, Day & Detling 1990), and may favour the germination of certain species above others. Miller (1995) for instance found that a significantly higher number of *Acacia* species' seed germinated when herbivores were present in the system, when compared to areas that were excluded from grazing (although this was highly dependent on the species of herbivore involved). Browsing by large herbivores can also increase both the rate of litter decomposition and the pool of mineralizable carbon in the litter (Kielland, Bryant & Ruess 1997) or decrease the soil nitrate and total available soil nitrogen (Ritchie, Tilman & Knops 1998). In this way the herbivore can contribute substantially to the redistribution of nutrients within a habitat (Cumming 1982) as well as have a measurable effect on plant nitrogen - content and biomass production (Ritchie *et al.* 1998). This may influence grazing patterns, because herbivores tend to show a preference for plants with a high nitrogen content (Day & Detling 1990). Diet preferences in itself can affect the nutrient balance of the soil as well as productivity. Where herbivores selectively remove nitrogen-fixing plants (which tend to increase available nitrogen in the soil), total available soil nitrogen will decrease, with a consequent decrease in primary production (Cumming 1982).

Animals are vectors for the seeds of many plant species, transporting it both internally and externally (Edwards & Gillman 1987). Welch (1985, cited by Edwards & Gillman 1987), working in heather moorland in Scotland, found that on average 86 seedlings could be germinated from a single cow pat and more importantly, the proportions of different plant species in the dung broadly reflected known herbivore diet preferences. He also found that the contribution of seed in the dung of cattle significantly increased the cover of grasses in the vegetation.

Plant species richness may either be increased or decreased by herbivory. For instance, Pandey & Singh (1992) reported a significant increase in the diversity of a tropical savanna under the influence of grazing. Crawley (1983) on the other hand cites several studies, some of which found increases in species richness under the influence of herbivory, while others found decreases in richness. There seems to be any number of mechanisms through which this can happen, although the creation of a more heterogenous environment is apparently the most important in increasing species richness, while a reduction in richness occurs mostly through

heavy grazing by generalist herbivores (Crawley 1983). Closely related to herbivory's effect on species richness is its effect on the species composition of the community. Pandey & Singh (1992) showed that grazing had a profound and differential effect on species composition, illustrated by a lower similarity between grazed than between ungrazed sites.

There are marked patterns in plant defence allocation and palatability to herbivores. Across a wide range of ecosystems, early colonists of disturbed environments are characterised by a suite of traits that allow them to take advantage of rapid resource supply (Connell & Slatyer 1977, Grime 1977, Tilman 1985, McCook 1994). These pioneers typically exhibit rapid leaf turnover rate and invest comparatively little in secondary chemical defences (Davidson 1993). As long as resources are readily available, such plants may be capable of rapid regrowth following losses to herbivores, but as resources become a limiting factor during the course of succession, they appear to be stressed differentially (Davidson 1993 and references cited therein). Plant species associated with later stages of succession have slower growth rates and comparatively longer-lived plant parts (Connell & Slatyer 1977). With a greater likelihood of severe herbivore pressure during their lifetimes and slower rates of resource acquisition to replace lost tissue, these plants tend to direct large quantities of carbon to mechanical or chemical defence mechanisms (Cumming 1982, Bryant, Chapin, & Klein 1983, Crawley 1983, Davidson 1993). It is therefore not surprising that herbivores often appear to feed preferentially on early to mid-successional species.

Several authors have predicted that herbivory will hasten the successional process towards later seres due to this preferential feeding (Davidson 1993 and references cited therein). However, this generalization does not always hold true. Davidson (1993) found this to be the case in only ten out of 34 published studies on the effects of native herbivores on plant communities. In the others herbivory tended to retard the course of succession by falling disproportionately on later seral stages. In three of the studies herbivores, feeding on plants in the intermediate stages of succession, simultaneously retard early successional stages and hasten later ones. This dichotomous effect of herbivores on plant communities seems to reflect attributes of the plants, rather than of the herbivores, and is most likely due to changes in the absolute and relative availabilities of plant resources during the course of succession (Davidson 1993).

Herbivory in the coastal dune forests of northern KwaZulu-Natal

Herbivory is an integral part of most ecosystems - about 33% (range 14% to 56%) of all species in any ecosystem are herbivorous (Crawley 1983). This is obviously a generalization and will depend on the characteristics of the ecosystem in question, and especially on the herbivores present in the community. Comparatively little is known about the ecology of invertebrate herbivores in the coastal dune forest system of northern KwaZulu-Natal, but it is reasonable to assume that they make up the majority of the herbivore species in the area, given the relative paucity of mammal and other vertebrate herbivores (see below). The dominance of a herbivore system by insect herbivores in terms of species numbers and very often also in terms of biomass, is a pattern found in other areas of the world (Lawton 1984, Coley & Barone 1996).

However, in the present study, where the physical damage of the vegetation and their environment through trampling and soiling as well as the consumption of plant parts will be considered as a single disturbance effect, it is more sensible to assume that herbivory by invertebrate herbivores is of similar intensity over the whole study area. Having said this, it must be noted that variability in population numbers and distribution of herbivorous insect populations (pers. obs.), and the consequent variable utilisation of plants, is a potential complicating factor in the interpretation of the results of the present study.

Non-mammalian, vertebrate herbivores probably contribute very little to herbivory in the study area. Of all the reptiles listed by Berruti & Taylor (1992) as occurring on the eastern shores of Lake St. Lucia (30 km north of the study area), only Bell's hinged tortoise (*Kinixys belliana*) is a vegetarian. All of the vegetarian birds listed by Berruti & Taylor (1992) and Kritzing (1996) for the same area are either frugivorous or granivorous. The coastal dune forests of Natal are home to relatively few mammalian herbivores, probably because most plant production, as in wet tropical and subtropical forests in general, occurs in the canopy and arboreality has its problems (Coley & Barone 1996). Rautenbach, Skinner & Nel (1980) lists 70 mammal species which are occurring or did occur in the Maputaland area, while Ferreira (1993), lists 26 in the rehabilitating area. Of these only 17 species which are either herbivorous or omnivorous or granivorous, utilise the coastal dune forest itself as habitat, and only 2 utilise only leaves and/or fruit (Table 1).

Table 1. Plant-eating mammals of the coastal dune forest of KwaZulu-Natal (Adapted from Rautenbach *et al.* 1980, Skinner & Smithers 1990, Berruti & Taylor 1992 and Ferreira 1993).

| Species | Food items |
|---|--|
| <i>Otolemur crassicaudatus</i> (Thicktailed bushbaby) | Omnivore; fruit and plant material; insects. |
| <i>Cercopithecus aethiops</i> (Vervet monkey) | Omnivore; mostly fruit, some leaves and insects. |
| <i>Thryonomys swinderianus</i> (Greater canerat) | Herbivore; roots, shoots of grasses and reeds. |
| <i>Otomys angoniensis</i> (Angoni vlei rat) | Herbivore; stems, rhizomes of grasses and reeds. |
| <i>Lemniscomys rosalia</i> (Single-striped mouse) | Herbivore; seeds and plant material. |
| <i>Mus minutoides</i> (Pygmy mouse) | Omnivore; seed, insects, termites. |
| <i>Mus musculus</i> (House mouse) | Omnivore; seeds, shoots, insects. |
| <i>Mastomys natalensis</i> (Multimammate mouse) | Omnivore; seed, fruit, insects. |
| <i>Aethomys chrysophilus</i> (Red veld rat) | Omnivore; seed, ? |
| <i>Saccostomus campestris</i> (Pouched mouse) | Omnivore; seed, partially insectivorous. |
| <i>Dendromus melanotis</i> (Grey climbing mouse) | Omnivore; mostly insects; also seeds. |
| <i>Cephalophus natalensis</i> (Red duiker) | Herbivore; fallen leaves, fruit, flowers, fine |
| <i>Tragelaphus scriptus</i> (Bushbuck) | Herbivore; leaves. |

It is highly unlikely that any of these species would under normal circumstances occur in numbers sufficient to affect the dynamics of the coastal dune forest's plant community. If such high numbers do occur, it would most likely be in the form of a population explosion in reaction to some uncommon phenomenon. Some of them (e.g. kudu (*Tragelaphus strepsiceros*) and porcupine (*Hystrix africae australis*)) only occur in the dune forest opportunistically (Skinner & Smithers 1990) and have not been recorded in the rehabilitating areas. Another point worth noting is that none of them is specialised to feed on the herbaceous layer of the forest, most depending rather on fruit and fallen leaves.

In natural grazing (and browsing) systems, as in the savanna areas of Africa, plants have developed defence mechanisms against damage by mammalian herbivores (Cumming 1982, Davidson 1993). In the dune forest system, with a relatively small mammalian herbivore contingent, it is reasonable to assume that these defence mechanisms are not so well developed. The introduction of a large herbivore, like domestic cattle, may therefore have a profound effect on the dynamics and structure of the plant community of the coastal dune forest.

AIMS OF THE STUDY

- 1) To quantify the effect of the disturbance created by cattle on the developing plant community of the rehabilitating area and to determine whether this effect, if present, is statistically significant.
- 2) To relate the disturbance created by cattle and its possible effect(s) to general disturbance and succession theory.

GENERAL HYPOTHESES

Following from the above discussion on succession and disturbance, and influenced by observations on cattle in the rehabilitating coastal dune forest north of Richards Bay, the following general (working) hypotheses were formulated:

Cattle activity causes a disturbance in the herbaceous layer of rehabilitating coastal dune forest and this disturbance will have an effect on the successional development of the plant community. The effect of cattle on the process of succession will be evident from their effect on species composition, species richness and vegetation cover of the herbaceous layer.

KEY QUESTIONS

- 1) What is the species composition of the herbaceous layer of the rehabilitating coastal dune forest?
- 2) Does a disturbance created by cattle change the species composition of the herbaceous layer to a composition different from what could be expected in the absence of grazing?
- 3) What is the species richness of the herbaceous layer?
- 4) Does a disturbance created by cattle change the species richness of the herbaceous layer more

(or less) than what could be expected in the absence of grazing?

- 5) What is the plant cover and height of the herbaceous layer?
- 6) Does a disturbance created by cattle change the cover and height of the herbaceous layer more (or less) than what could be expected in the absence of grazing?
- 7) What is the density, physiognomy and species composition of the broadleaved tree species emerging in the understorey of the rehabilitating areas?
- 8) Does a disturbance created by cattle change the density and/or physiognomy and/or species composition of the emerging broadleaved tree species more (or less) than what could be expected in the absence of grazing?
- 9) If a disturbance by cattle has a significant effect on any of the variables mentioned above, is this effect dependent on the level of disturbance?

STATISTICAL HYPOTHESIS

Main hypothesis

H_0 1: *Disturbance caused by cattle will not have a significant effect on the selected plant community variables which reflect aspects of the process of succession in rehabilitating coastal dune forest.*

H_1 1: *Disturbance caused by cattle will have a significant effect on the selected plant community variables which reflect aspects of the process of succession in rehabilitating coastal dune forest.*

(H_0 1 is the only hypothesis which will be tested)

Conditions for rejection of hypothesis

The null hypothesis (H_0 1) will be rejected if any of the two following conditions are true:

- if there is a significant difference between the controls and any or all of the grazing treatments after grazing but not before in the following variables; or
- if there is a significant change, independent of seasonal and successional changes, for any or

all of the grazing treatments but not for the controls in the following variables:

- 1) species composition of the herbaceous layer,
- 2) number of species per pin,
- 3) number of species per 1m² quadrat,
- 4) number of species per paddock,
- 5) number of species per treatment level,
- 6) herbaceous cover of the herbaceous layer,
- 7) ground cover of the herbaceous layer, and
- 8) height of the herbaceous layer.

Secondary hypothesis.

H₀2: *The effects of a disturbance to the herbaceous layer of rehabilitating coastal dune forest is independent of the level of disturbance.*

H₁2: *The effects of a disturbance to the herbaceous layer of rehabilitating coastal dune forest is dependent on the level of disturbance.*

(H₀2 is the only hypothesis which will be tested)

Conditions for rejection of secondary hypothesis.

The null hypothesis (H₀2) will be rejected if the following condition is true:

- if there is a significant difference between any or all of the grazing treatments (excluding the control) after grazing but not before in the variables listed under ‘Conditions for rejection of primary hypothesis’.

CHAPTER 2

STUDY AREA

The climate and geography of the area as well as the mining process is described in detail in Van Aarde *et al.* (1996) and Van Dyk (1997), but the main points are summarised here. The study was conducted in rehabilitating coastal dune forest vegetation established after mining in the Tisand lease area of Richards Bay Minerals. The study area is situated 8.6 km north and 9.3 km east of Richards Bay, KwaZulu-Natal, South Africa ($28^{\circ}43' S$ and $32^{\circ}12' E$ - Fig. 2) and falls in the Mocambique coastal plain sector of the east coast as classified by Tinley (1985).

Information on climate is taken from Avis (1992) and Ferreira (1996). Most rain falls from January to March, with February being the wettest month. The area seldom experiences extended droughts, with rainfall being recorded for about seven months of the year (approximately 30% of annual precipitation occurs in the winter). Annual rainfall is 1292 mm. Daily maximum temperatures range from $22.6^{\circ}C$ in June to $30.0^{\circ}C$ in January. In spite of extremes being moderated by the sea, it reaches a maximum of $40.8^{\circ}C$ in January. Frost does not occur. Daily minimum temperatures range from $10^{\circ}C$ in June to $20.6^{\circ}C$ in January. Most of the winds blow either north-easterly or south-westerly, parallel to the coast. Wind occurs throughout the year, with the autumn months being the calmest. Relative humidity, as measured at Richards Bay, ranges from 59% in August to 72% in April and November.

The coast line in the study area is characterised by a linear, alternating pattern cut in unconsolidated Quaternary to Recent Sands, facing alternatively south-south-east and east (Tinley 1985). The topography of the area is characterised by longitudinal sand dunes, lying parallel to the coastline, and rising to an elevation of between 40m and 90m above sea level. The slope angles of the sea-facing dunes are moderately steep to steep, while the landward facing slopes are more gentle. There are no major drainage lines, except for the Nhlabane estuary which transects the northernmost section of the area.

The sand dunes on the north coast of KwaZulu-Natal typically consist of a covering layer of fine to medium grained aeolian sands, extending to depths of 70m, overlying older aeolian sands, or

accumulating against partially lithified carbonated cemented sands (Davies Lynn and Partners 1992). The minerals mined by Richards Bay Minerals occur only in the covering layer of windblown sands.

A general description of the vegetation of the area is given in Table 2, adapted from Van Aarde *et al.* (1996). More detailed descriptions are provided by Venter (1972), Lubke, Moll & Avis (1992), Mentis & Ellery (1994) and Van Dyk (1997).

Table 2. Characteristics of rehabilitating and unmined coastal dune forests of different ecological age, adapted from Van Aarde *et. al.* 1996.

| Age of habitat in years | Description |
|-------------------------|---|
| 0 to <1 | Rehabilitating area with a pioneer community consisting mostly of grasses and annual herbs. Vegetation is low (≈ 50 cm) and is characterized by <i>Sorghum</i> spp. <i>Pennisetum americanum</i> , <i>Dactyloctenium geminatum</i> , <i>Zornia capensis</i> and <i>Bulbostylis contexa</i> . |
| 1 to <2 | Rehabilitating area consisting of a simple grassland community with scattered <i>Acacia karroo</i> colonizing. Vegetation (≈ 70 cm) is characterized by <i>Dactyloctenium geminatum</i> , the creeper <i>Canavalia maritima</i> , <i>Pennisetum americanum</i> , and juvenile <i>Acacia karroo</i> . |
| 2 to >5 | Rehabilitating area consisting of an <i>Acacia karroo</i> shrubland with thick undergrowth dominated by grass species. The vegetation is characteristically 1 to 1.5 m high, with <i>Acacia karroo</i> and <i>Dodonea angustifolia</i> the most prominent woody species, and <i>Chrysanthemoides monilifera</i> and <i>Passerina rigida</i> occurring frequently. The ground cover consists of <i>Dactyloctenium geminatum</i> , <i>Canavalia maritima</i> , and the two herbs <i>Bulbostylis contexa</i> and <i>Mariscus dubius</i> . |
| 5 to <8 | Rehabilitating area comprising an <i>Acacia karroo</i> scrubland 1.5 to 3 m high, with sparse undergrowth. <i>Acacia karroo</i> dominates the canopy, while some <i>Dodonea angustifolia</i> is still present. The middle stratum, although sparse, is characterized by <i>Vepris lanceolata</i> and <i>Brachylaena discolor</i> . The ground cover consists mainly of <i>Panicum maximum</i> , <i>Digitaria diversinervis</i> , <i>Acacia karroo</i> , and <i>Dactyloctenium australe</i> . |
| 8 to <11 | Rehabilitating area comprising an <i>Acacia karroo</i> woodland 3 to 8m high, with few secondary dune forest species present. The canopy is dominated by <i>Acacia karroo</i> , while a number of other woody species, including <i>Brachylaena discolor</i> and <i>Rhus nebulosa</i> are also present. Ground cover consists of a number of species, with <i>Digitaria diversinervis</i> the most important. |
| 11 to <16 | Rehabilitating area comprising an <i>Acacia karroo</i> woodland 9 to 12 m high and characterized by secondary dune forest tree species colonizing. These include <i>Trichilia emetica</i> , <i>Trema orientalis</i> , <i>Mimusops caffra</i> , <i>Celtis africana</i> , <i>Vepris lanceolata</i> , <i>Albizia adianthifolia</i> , <i>Kraussia floribunda</i> , and <i>Apodytes dimidiata</i> . Climbers include <i>Sarcostemma viminale</i> and <i>Adenia gummifera</i> with <i>Digitaria diversinervis</i> making up the most important part of the ground cover. |
| 30 to <35 | Unmined area consisting of secondary coastal dune forest with a canopy - 12 to 15m or higher - dominated by <i>Acacia karroo</i> . Other important canopy trees include <i>Celtis africana</i> , <i>Mimusops caffra</i> , <i>Allophylus natalensis</i> , <i>Teclea gerrardii</i> and <i>Ochna natalitia</i> . The middle stratum consists of species such as <i>Teclea gerrardii</i> and <i>Celtis africana</i> . The herb and shrub layer is dominated by <i>Isoglossa woodii</i> and <i>Dracaena aletroformis</i> occurs commonly. |
| Mature stand | Unmined area consisting of secondary coastal dune forest, with a canopy 12 to 15 or higher. A number of species are abundant, <i>Celtis africana</i> , <i>Mimusops caffra</i> , <i>Allophylus natalensis</i> , <i>Teclea gerrardii</i> and <i>Ochna natalitia</i> . The middle stratum consists of species such as <i>Ochna natalitia</i> , <i>Clausena anisata</i> , <i>Diospyros natalensis</i> , <i>Tricalysia sonderiana</i> , <i>Carissa bispinosa</i> and <i>Maytenus undata</i> . The herb and shrub layer is dominated by <i>Isoglossa woodii</i> and the fern <i>Microsorium scolopendrium</i> . |

CHAPTER 3

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Four replicates of four treatment levels were applied in the oldest part of the rehabilitating dune forest (≈ 16 years old at the time of the study; Stand 1 - see Fig. 1). The replicates were grouped together in four blocks, each consisting of low, medium and high disturbance paddocks, as well as a control paddock (grazing excluded) (Fig. 3). These blocks were randomly placed within Stand 1. The paddocks were constructed of single stranded lightly galvanised barbed wire, strung between treated timber poles. The fences were 1.2m high. To save on construction time and fencing material, each group of four treatments was constructed as a single paddock, 0.5ha in extent, divided into four smaller paddocks. Each treatment paddock was therefore 0.125ha in size. Treatment levels were randomly assigned to the paddocks within each block.

Five grazing cycles* were applied to the treatment paddocks over the study period. A grazing cycle consisted of three treatment levels which were applied by allowing cattle to graze for different periods of time in each of the treatment paddocks, while at the same time not allowing any grazing in the fenced control paddocks. The lengths of time for each treatment level varied somewhat, depending on the collective weight of the cattle that were used for each treatment. In general however, a low treatment level meant two days of grazing, a medium level translated into four days and a high level eight days. (See below for a full description of the cattle used and how they were weighed.)

The period between subsequent surveys and grazing cycles was intended to be about 3 months. In practice this time schedule was influenced by external circumstances like the unstable political situation in KwaZulu-Natal during the study period (especially in the middle of 1994) so that the

* To prevent confusion in the rest of the thesis, distinction is made between the terms “grazing cycle”, which indicates the application of grazing to the treatment paddocks over a period of some 16 days, and “survey cycle”, which indicates the instance immediately before each grazing cycle when data were collected on a number of plant variables.

Summary of experimental design:

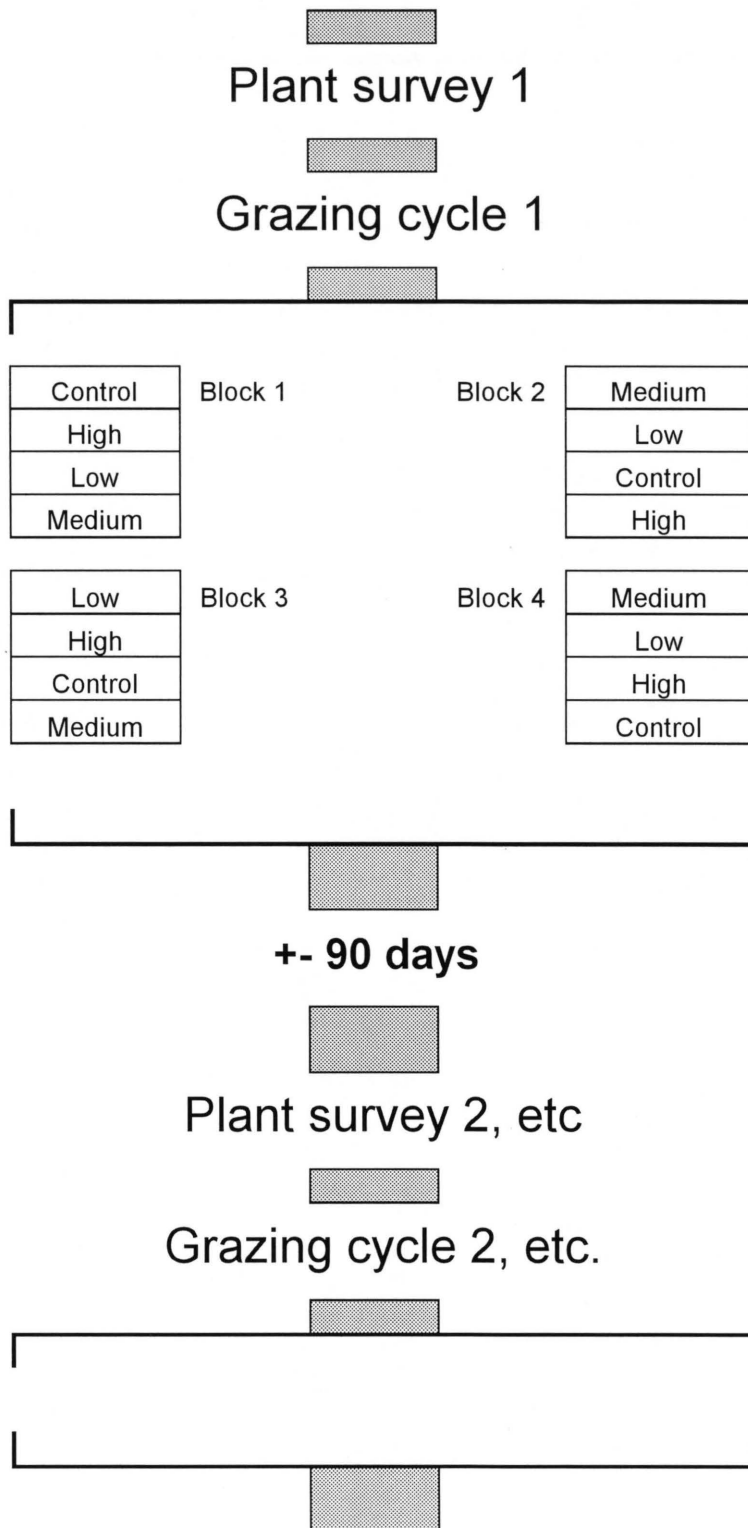


Figure 3. Diagram of experimental design, showing the schedule of application of grazing and the sequence of plant surveys and grazing cycles. Two cattle stayed inside a paddock for two days in the low treatment level, for four days in the medium and for 8 days in the high treatment levels. Paddocks were grouped together in blocks of four and assigned randomly within a block to a treatment level. The period between successive cycles varied between 90 and 150 days. See text for description of paddocks.

period between the first two cycles were somewhat longer (Fig. 4). Grazing cycle 3 also had to be moved forward a couple of weeks to wait for rain to fall in order to ensure that the cattle at least had some food in the paddocks. This resulted in a total of five grazing cycles over a period of about 16 months. Figure 4 shows the time schedule for the grazing and survey (see next section) cycles superimposed on the monthly rainfall for the study period.

SURVEY PLOT DESIGN AND TIME OF DATA RECORDING

Data were collected at the beginning of the study period, before any grazing was applied, as well as immediately before the start of each grazing cycle. This resulted in six plant surveys (Fig. 4) during which data on a number of plant community variables were recorded at permanent quadrats established in all the treatment and control paddocks. Data capturing was done with a Psion XP data logger (Psionet Distributors, 67 Rosmead Avenue, Kenilworth, Cape Town) and then downloaded onto a personal computer.

Six permanent quadrats, of one square metre each, were placed within each treatment or control paddock. The quadrats were randomly located on the intersections of a grid with lines 5m apart. This effectively meant that there was a 5m wide band around the edges of each paddock where no data recording took place. All quadrats were permanently marked by driving creosoted wooden stakes into the ground at the four corners of a marked square, so that the tips of the stakes were about 20cm above the ground. Because these wooden markers were often difficult to see, a creosoted and painted marker pole, 1.5m in height, was placed about 1.5m from the top left-hand corner of the quadrat.

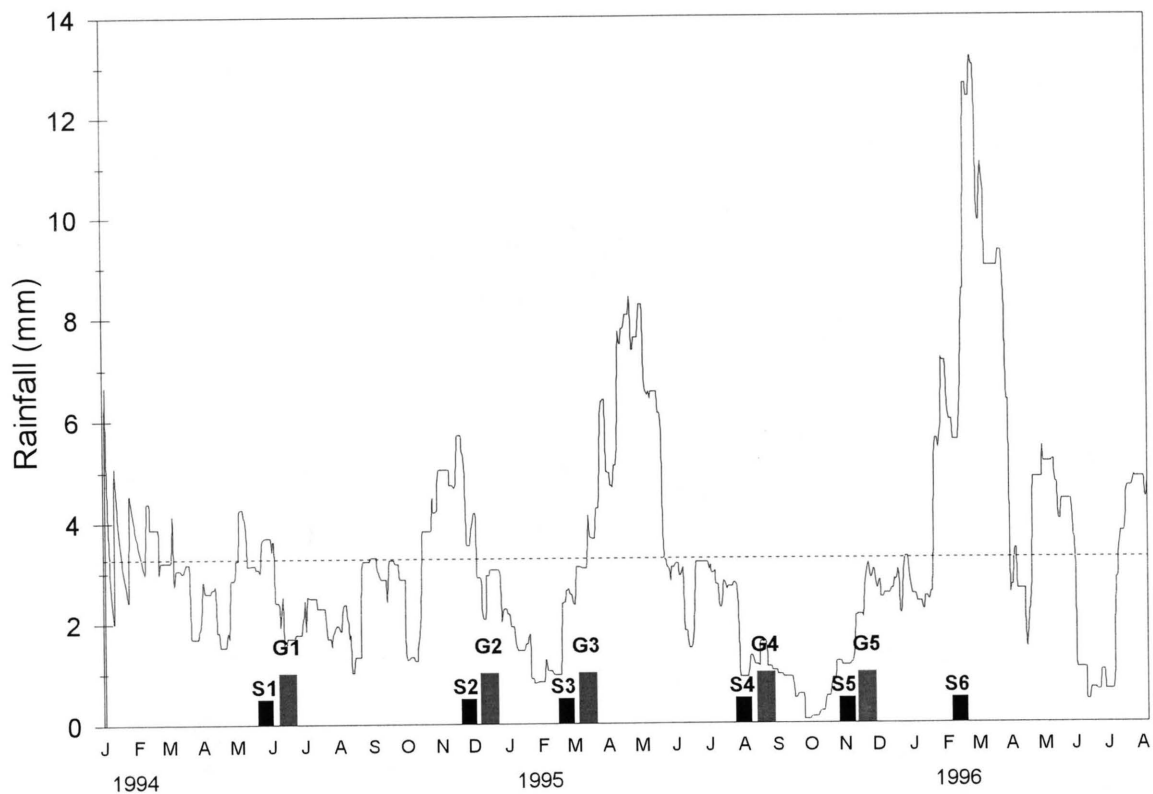


Figure 4. Mean (of three measurements per day) daily rainfall in the rehabilitating area from January 1994 to August 1996 and schedule of plant surveys and grazing cycles. The dotted line represents the mean daily rainfall over a ten year period, including the period of the present study. Rainfall was measured at the Ecology Centre and in Stand 1. S1-S6 represents plant surveys and G1-G5 represents the grazing applications.

SURVEY METHOD AND VARIABLES MEASURED OR RECORDED DURING EACH SURVEY

Species presence

The permanent quadrats were used to record species present in 1m². Due to the preponderance of climbers and clonal plants in the herbaceous layer of the rehabilitating forest, a species was taken as being present if any part of the plant fell inside the quadrat and not only if it was rooted inside. In other words, all species that contributed cover in any way to the 1m² of the quadrat, even if it was only through a small branch or leaf, was present (Fig. 5a). A species could therefore have a score of either 0 or 1 at a specific quadrat and a score (“frequency value”) of 0 to 6 for a paddock.

The following variables were determined from the data obtained with this method:

- 1) number of species per 1m² quadrat,
- 2) total number of species in all of the 1m² quadrats in a paddock (number of species per paddock), and
- 3) total number of species in all of the 1m² quadrats in all paddock in a treatment level (number of species per treatment level).

Data on species presence, combined with the number of species per pin (see next section) produced various scales of species richness, ranging from a single point through to the size of all the quadrats in a treatment level. Sampling at each scale (from single point upwards) resulted in a decreasing chance of sampling the same individual plant and an increasing chance of sampling different plant species and species groups. The number of species found in each 1m² quadrat is analogous to the point diversity referred to by Whittaker (1977) and is an indication of the “internal alpha diversity” of a homogenous community.

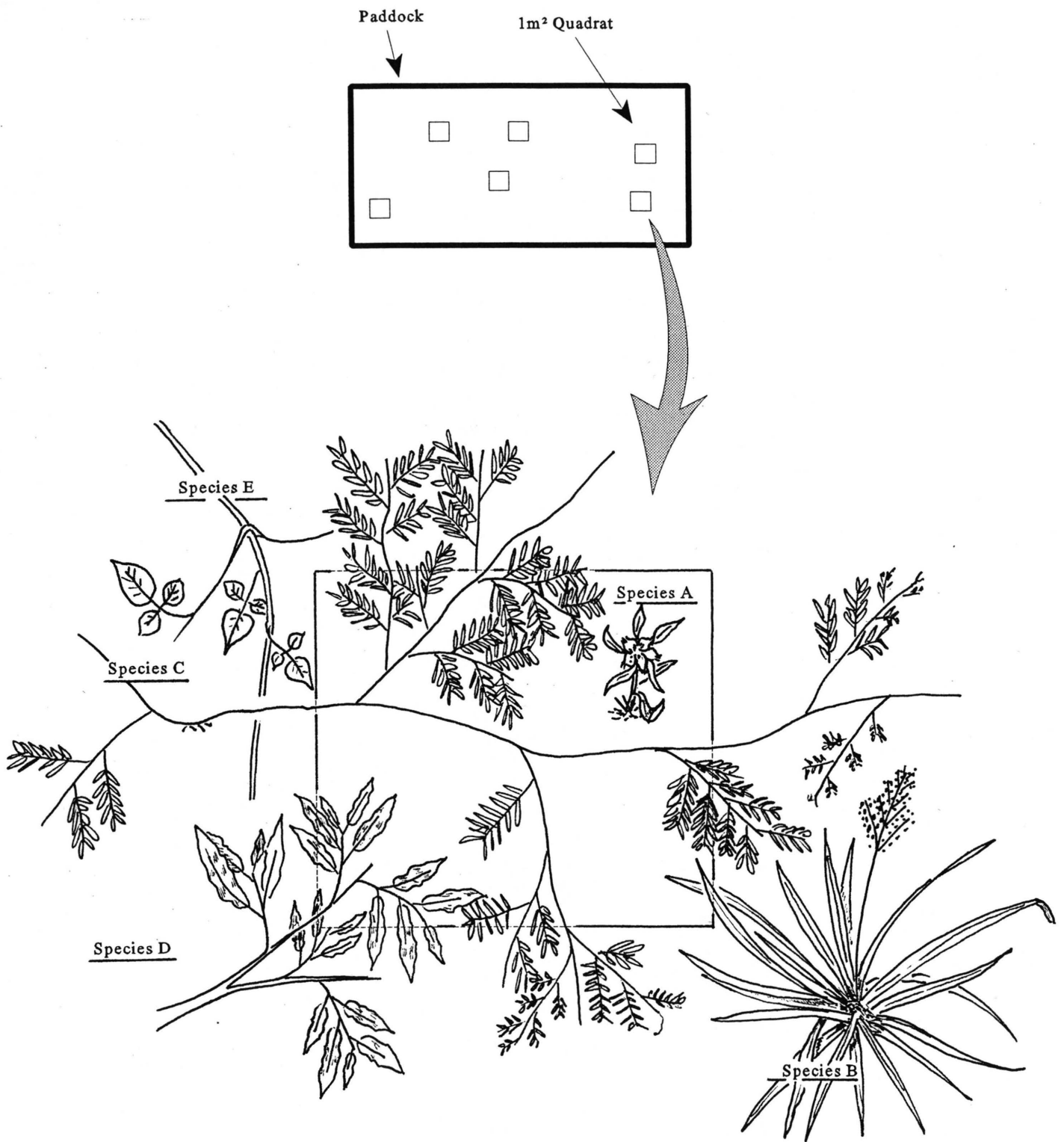


Figure 5a. Schematic diagram of a quadrat used in the plant survey. Six 1m² quadrats were placed randomly inside each paddock. When viewed from above, a species was recorded as present if any part of it contributed to the cover of the quadrat, regardless of whether it was rooted inside the quadrat or not. In this case species A, B, C and D would be present while species E would not be.

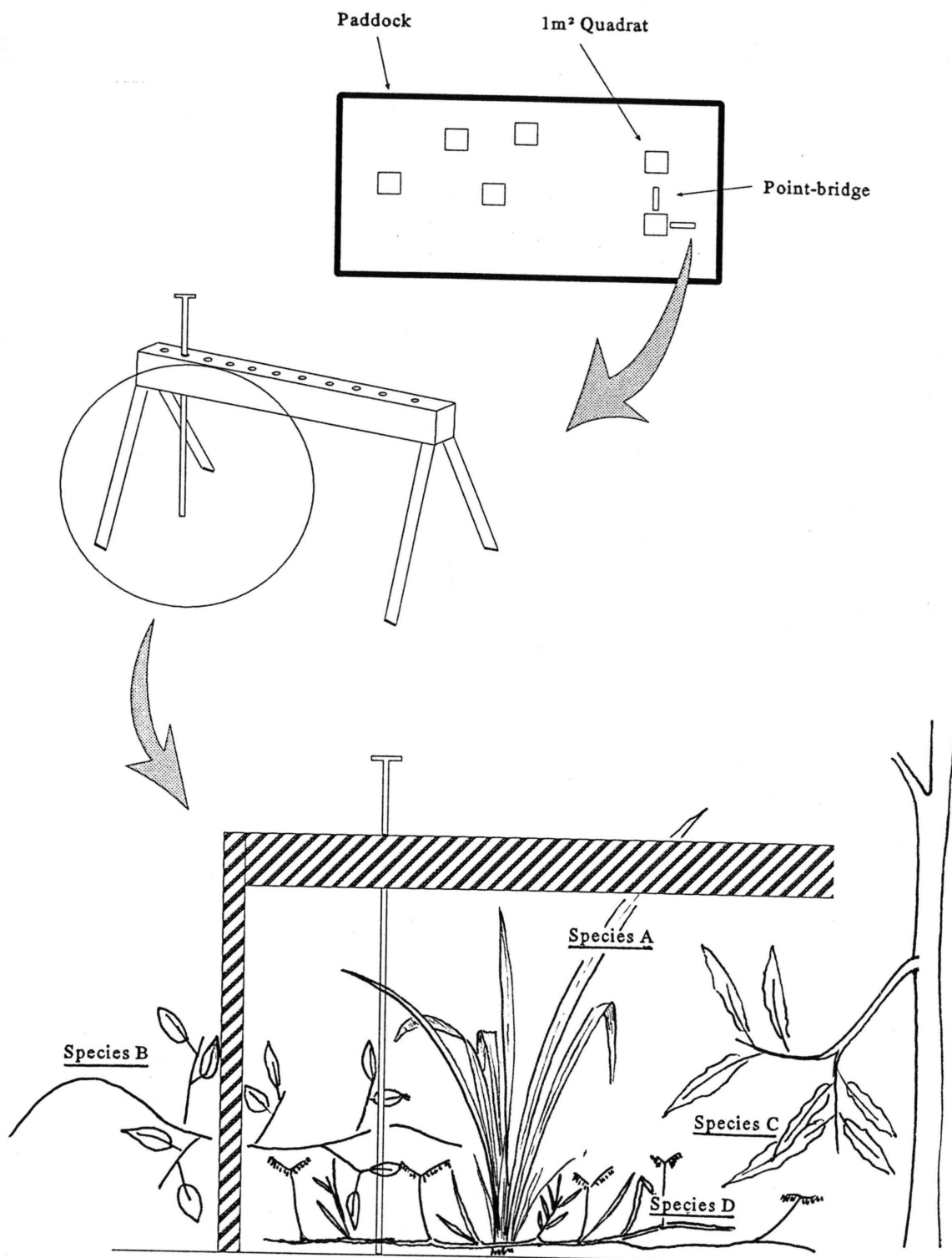


Figure 5b. Schematic diagram of the point-bridge used in the plant surveys. The bridge was placed at right angles to the left and front of the 1m² quadrat. An 8mm pin was placed through the holes in an aluminium beam and the species touching it recorded. The height at which the first species was touched was also recorded. All horizontally growing stems touching the pin below 10cm was recorded separately.

Species presence was also determined using the point-bridge described in the next section. With this method, a species is present when it is touched by a descending pin of the point-bridge. For each species a frequency value was obtained similar to the one described above for a 1m² quadrat - the number of pins in a paddock at which the specific species was recorded. A species could therefore have a score of anything between 0 and 122 (the total number of pins per paddock) for a paddock.

Vegetation cover and height

The plant cover of the herbaceous layer was measured at six of the permanent quadrats using a point bridge. The design is based on the point bridge described by Barbour *et al.* (1987). The bridge consisted of an aluminium u-shaped beam (1m x 100mm x 40mm) turned on its side, with 11 x 8mm diameter vertical holes drilled along the length of the beam and 1m long supporting legs on both ends (Fig. 5b). A 1.2m long stainless steel pin with a diameter of 8mm, marked at 50mm intervals and bluntly sharpened at one end, fitted through the holes in the beam when the bridge was assembled.

The bridge was placed at right angles to the left and front sides of the permanently marked quadrats, with care being taken to place its legs in the same position relative to the quadrat every time the survey was done (Fig. 5b). By successively putting the pin through each hole in the bridge's beam and then recording whether the pin touched any plant parts, the herbaceous cover on the rehabilitating forest floor could be computed for a number of cover classes. Dividing the number of pins touching a plant part in a cover class by the total number of pins (22) and multiplying by 100, gave a percentage plant cover per class.

Two cover classes were defined on the basis of the mean heights of different plant structures:

- 1) ground cover was defined as the percentage of pins touching any horizontally growing stem of any plant up to a height of 10cm above the ground.
- 2) herbaceous cover was defined as the percentage of pins touching any other plant part at any height above 10cm and up to 1m above ground.

By recording the height of the first touch as well as the different species that was touched by each pin, this method also allowed the recording of the following variables:

- 1) mean height of the herb layer,
- 2) number of species that was touched by the pin, and
- 3) number of times that a particular species was touched by a pin at a specific quadrat or paddock.

Understorey woody plants

To distinguish this part of the project from the plot survey of woody plants which was done once only at the end of the application of grazing (see next section), I will refer to this section as the sapling-survey and collectively to all woody plants recorded in this section as saplings. Woody plants in the understorey of the rehabilitating forest mainly consist of the saplings and seedlings of broadleaved coastal forest species and few *Acacia karroo* (Van Dyk 1997). To monitor the effect of cattle on these plants, four individual woody plants were identified at each of the permanent quadrats and marked with plastic tags. The individual plants were chosen in a similar fashion to a point-centred-quarter method, the closest individual in each of four quarters around the centre of the permanent quadrat being identified, marked and a number of variables measured. Only plants $\geq 20\text{cm}$ and $\leq 1.5\text{m}$ in height were taken, because it was difficult to find individual plants smaller than 20cm in the dense herb layer and it was unlikely that cattle would have much direct effect on a woody plant once it grows taller than 1.5m. The distance from the centre of the quadrat to each marked individual was measured, as well as the height of the canopy (measured from the lowest point where leaves were visible to the topmost visible leaf) and two diameters, measured at right angles with each other through the centre of the canopy.

Individual plants in each quarter were replaced if a new sapling closer to the centre of the quadrat had grown above 20cm, or if an older, closer one had decreased in height to below 1.5m. It was replaced by the next closest individual if it was destroyed, had decreased in height to below 20cm or had grown taller than 1.5m. A note was made if more than one condition occurred at the same time. The same measurements described above were then made on the new plant. In some cases, where a plant happened to fall into the range of two different quadrats, it was assigned to the first

of the two quadrats. At the second of the two quadrats, the next closest plant for the quarter was then taken. If the closest plant in a quarter happened to fall outside the boundaries of the paddock or monitoring site, a code (NTQ) was assigned to the quarter and the distance between quadrat and plant was taken as 49.24m, which was slightly further than what any plant inside the paddock could be from any quadrat's centre point.

The following variables were recorded for woody plants in the understorey:

- 1) number of species per paddock,
- 2) density per hectare, calculated as $10000/(\text{average distance in m})^2$,
- 3) crown volume (crown was defined as the part of the tree covered by leaves), calculated as: $\text{volume} = h\pi(a/2)(b/2)$, where h =height of crown, a =diameter 1 and b =diameter 2),
- 4) reason for replacement: there were four possible reasons for replacement of any tree from the original cohort identified before any grazing had taken place-
 - a tree could either grow taller than 1.5m (and therefore leave the cohort through the upper boundary where it was out of reach of cattle),
 - it could grow taller than 20cm (entering the cohort from the bottom),
 - it could be absent (presumably destroyed, but could also be totally hidden from view),
 - it could decrease to below 1.5m and therefore enter the cohort from the top, or
 - it could decrease to below 20cm and therefore leave the cohort at the lower boundary.
- 5) rate of loss from group (attrition rate), derived from the replacements,
- 6) tree height, measured from ground level to the topmost plant part,
- 7) height class frequency distribution, and
- 8) species composition per paddock.

Plot survey of woody plants

The woody plant survey described above proved to be adequate in order to track changes in the fortunes of marked juvenile woody species forming the emerging sub-canopy layer in the rehabilitating areas, but inadequate to describe all the changes in species composition/importance amongst all woody plants in the experimental paddocks. A survey of all woody plants was

therefore done in each of the treatment and control paddocks in the oldest part of the rehabilitating area. Because no such survey was done before treatment had been applied, a repeated measures type analysis was not possible. However, because each treatment replicate had its corresponding control, a normal control-treatment type of analysis was possible for certain variables.

For this survey, each paddock was physically divided with ropes into 24 blocks of 25 m² each. Five of these blocks were selected randomly. All woody species rooted in each block were categorised into four different height classes: seedling (0.01m - 0.5m), sapling (0.51m - 2m), sub-canopy (2.01m to below forest canopy height) and canopy (trees with their crowns at the same height as the forest canopy). At each block the following variables of all these plants were recorded for each height class:

- 1) number and identity of all woody plants rooted inside the block,
- 2) tree height, for trees less than 5m in height measured from ground level to the topmost plant part and for all trees taller than 5m estimated by eye,
- 3) crown volume, calculated in the same manner as in the sapling survey (see previous section),
- 4) for all canopy and sub-canopy trees the diameter of all major structural stems at breast height; for all saplings the diameter of all major structural stems at 10cm above the ground; and for all seedlings the stem diameter at ground height,
- 5) the number of stems per paddock, counted at the height where stem diameter was measured,
- 6) density, calculated as individuals per 25m² (the size of each block), and
- 7) species composition per paddock.

Biomass production of treatment and control paddocks

To get an estimate of the production in the herb layer in response to a disturbance caused by cattle, a complete harvest of all the herbaceous vegetation below 1m in height in a 25 m² block was done after the last grazing cycle. The block was chosen randomly as part of the survey of woody species described in the preceding section.

If a block happened to have a preponderance of woody plants in the herbaceous layer, the harvest site was moved to a block to the left of the chosen one and then in a clockwise direction around it every time it happened to fall on a "non-representative" block. This was done to ensure that the sample was representative of the herbaceous layer and not influenced by the patchy distribution of woody plants and fallen branches of canopy trees. It meant sampling was effectively done in a stratified random manner. The harvested material was oven dried at 90°C for 7 days, and then weighed.

SOURCING, MANAGEMENT AND WEIGHING OF CATTLE

Due to the logistical problems of keeping cattle during the periods when they were not used in the experiment, cattle had to be obtained from the local community for every grazing cycle. A new group of eight cattle were used for each grazing cycle. This obviously resulted in a large variation in size and sex of the cattle, even though all attempts were made to use only heifers in the 200kg -300kg size class.

Cattle were kept confined to a holding pen for two days before the start of each grazing cycle. During this time they were weighed and prophylactically treated against cowdriosis, babesiosis and helminthiasis. They were also examined for any obvious signs of wounds or disease and treated accordingly. Throughout the period of each grazing cycle, they were weighed in the morning before they were put out to graze. A standard analog agricultural scale (Salter Suspended Weigher Model 235) was used and weights recorded to the closest kilogram.

The eight cattle used in the study were grouped into four pairs on the basis of their weight at the start of the grazing cycle. The pairs were chosen so that each pair's mean weight would be as close as possible to the mean weight of the group as a whole. Cattle pairs were then randomly assigned to the four replicates of each treatment level for each day of treatment, starting with the low treatment level and continuing through to the high. The total applied mass per treatment paddock for the total amount of time that they spent in the paddocks was kept relatively constant for each treatment level. Each paddock assigned to the low treatment level therefore had a

cumulative mass of about 1000kg applied, the medium treatment level about 2000kg, and the high treatment level about 4000kg. Data on applied mass were analysed to determine whether the desired treatment ratio of 1:2:4 for low : medium : high was actually achieved. (Because no facilities for weighing existed at the time of the first grazing cycle, the cattle's weights were estimated by eye and an average of that taken as the weight of one steer per day. These weights were not used in the analysis.)

Grazing within the paddocks took place for about eight hours per day after which the cattle were returned to the holding pen for the night, where water was provided and where they were fed on *Eragrostis* sp. hay. At the end of each treatment level, the cattle would stay confined to the holding pen for a day, where they were watered and again fed only with hay before moving on to the next treatment level. On the basis of their mean weight each morning, the amount of hay was increased from about 1kg/animal /day at the start of the experiment, to about 4kg/animal/day at the end, when they were hard put to find sufficient nourishment from the vegetation inside the treatment paddocks. Most of the cattle developed diarrhoea after about two days if they fed exclusively on the low roughage soft green vegetation of the herbaceous layer inside the rehabilitating forest. The hay was therefore supplied to counter this effect, as well as to provide some extra nourishment.

CATTLE DIET PREFERENCES AND FEEDING HABITS

The cattle pairs were observed and their habits and feeding preferences recorded during the first grazing cycle. For this an observer spent one hour in each paddock per day of the grazing cycle. During this time he recorded at 5 minute intervals what activity each animal was engaged in and if it happened to be feeding, the plant species it was feeding upon. The activity classes were: resting (standing), resting (lying down), walking, ruminating, social activity, foraging (investigating its surroundings for the purposes of feeding), or feeding (actually eating some plant material).

Each species' relative presence in the cattle's diet (R_{diet}) was determined and compared with their

occurrence* in the total plant community (R_{env}) at the time of the observations. A selection value (Pellew 1984) for each species was calculated:

$$\text{Selection value (SV)} = R_{\text{diet}} / R_{\text{env}}$$

$SV > 1$ indicated a preference above the occurrence of the species in the environment (i.e. a positive selection), while $SV < 1$ indicated negative selection.

ABIOTIC AND BIOTIC DETERMINANTS OF COMMUNITY STRUCTURE

Rainfall was measured using standard rain gauges at only two of the four blocks of paddocks due to logistic constraints. Because the blocks were relatively close together, it was assumed that all paddocks (all treatments) experienced the same amount of precipitation. In order to determine other environmental differences between the paddocks, the following variables were estimated or measured (10 quadrats per paddock):

- 1) the closest species of canopy tree in each of four quarters around a quadrat (a canopy tree is defined as any tree with the largest part of its canopy exposed to unfiltered sunlight at more or less the same height as the average height of the forest),
- 2) height (measured with a rangefinder) of the closest canopy tree in each of four quarters around a quadrat,
- 3) stem diameter at breast height of the four closest canopy trees in each of four quarters around a quadrat,
- 4) number of stems at breast height per tree for the four closest canopy trees in each of four quarters around a quadrat, and
- 5) the percentage leaf and/or branch cover on a colour negative photograph of the canopy, measured with a Quantimet 520 image analyser (Cambridge Instruments, London). The photograph was taken from a point 1m above the quadrat with the camera pointing directly upwards, using a Nikon FE 35 mm camera with a 17mm lens.
- 6) light intensity at five points at each permanent quadrat - one at each corner of the quadrat and

* Species occurrence in the plant community was based on a plant survey conducted immediately before the start of the first grazing cycle.

one in the middle, measured 50cm above ground level with a Goldilux light meter (Measuring Instruments Technologies (Pty) Ltd., Pretoria).

STATISTICAL ANALYSIS

Univariate variables

In order to enable the use of Analysis of Variance (ANOVA) and linear regression, all univariate data were tested for assumptions of normality both before and after transformation with both the G-test and Kolmogorov-Smirnov test (Sokal & Rohlf 1995). Square root, 4th root or log₁₀ transformation and, in the case of the percentage vegetation cover, also arcsine transformation was used to try and correct for non-normality. The data were considered to be normally distributed if either or both of the tests were not significant. The Cochran-C test and Bartlett's test for homogeneity of variances (Sokal & Rohlf 1995) were used to test for assumptions of homoscedasticity.

Because the same individual measuring units were measured repeatedly, Repeated-Measures Multivariate Analysis of Variance with profile analysis (MANOVAR following Potvin, Lechowicz & Tardif 1990, also described in O'Brien & Kaiser 1985, Morrison 1990, Von Ende 1993) was used to test for both treatment and grazing cycle (which in the present study could also be seen as survey and/or time) effect. When time is the within-subject factor in a repeated measures experiment, the circularity condition of univariate repeated-measures ANOVA is usually not met because values on adjacent dates are more highly correlated than values from separated dates (O'Brien & Kaiser 1985, Von Ende 1993). MANOVAR, with the repeated measures taken as independent variables, is the method of choice in this case because it makes no assumptions of circularity (Von Ende 1993). However, Repeated Measures ANOVA (ANOVAR following Potvin *et al.* 1990) based on a split plot design (Von Ende 1993), was performed to test for the main treatment effect because it is generally regarded as the more powerful method and some relaxation of the restrictive assumptions are possible using corrected significance levels (Potvin *et al.* 1990). Where ANOVAR showed significant treatment effects,

the T-method (Sokal & Rohlf 1995), also known as Tukey's honestly significant difference (Tukey's HSD), was used to test for differences between treatment levels over all surveys as well as within each survey. Significant time (survey) effects were not investigated further as the differences between individual surveys were irrelevant within context. However, the general quadratic and linear trend over time in the values of each specific variable was analysed with orthogonal polynomial contrasts (Gurevitch & Chester 1986, Von Ende 1993) as part of MANOVAR.

MANOVA for multiple response variables was used to test for differences between treatment levels within each survey in case there was a correlated response by the response variables which would not have been picked up by multiple univariate ANOVAs (Scheiner 1993). Strictly speaking this is a multivariate test, but it is dealt with here because it tests the same concept as the univariate tests. MANOVA tests the overall effect of treatment level on all response variables used and should precede any univariate ANOVAs. Because MANOVA is generally robust as far as the assumption of normality is concerned, all the variables (herbaceous and ground cover, as well as species per pin, per quadrat and per paddock) were used. For the test of surveys 1,2,3,5 and 6, all five variables were used, while survey 4's data were analysed using only species per quadrat and per paddock because vegetation cover was not measured during survey 4 for logistic reasons. The T-method (Sokal & Rohlf 1995) was used to compare all pairs of means within a survey whenever ANOVA showed up a significant difference.

In MANOVAR the test statistic Roy's Greatest Root was given preference in cases where the results differed among the four statistics supplied by the computer program used for the analysis, because it has the greatest power of the four (Scheiner 1993). Only Roy's greatest root is quoted in the results. MANOVA for multiple response variables assumes multivariate normality of the data, which is difficult to test for because it needs very large sample sizes. In this case the test statistic Pillai's Trace was therefore used because it is generally the most robust (of the four tests statistics supplied) for deviations from multivariate normality (Olson 1976, cited in Potvin *et al.* 1990, Scheiner 1993). All MANOVA, MANOVAR and ANOVAR analyses were done on the mainframe computer at the University of Pretoria, using the SAS statistical software package (SAS Institute Inc. 1989a,b). Significance was taken at the 95% level ($p=0.05$) in all cases but a

Bonferroni adjustment (= probability divided by number of comparisons made) was used in the case of multiple comparisons (polynomial comparisons in MANOVAR) to maintain an overall α of 0.05.

Least squares linear regression (Sokal & Rohlf 1995) was used to determine whether there were any significant relationships between time (survey number) and a specific variable for each treatment level, as well as between treatment level and a specific variable for each survey. The slopes of the regression lines of the different treatment levels were tested for equality using the method described by Sokal & Rohlf (1995, p495). Multiple unplanned comparisons between the regression lines of the treatment levels were done using the T'-method (Sokal & Rohlf 1995). Significance was taken at the 95% level ($p=0.05$) in all analyses.

Where neither the requirements for normality nor homoscedasticity could be met, or where the sample sizes were too small to test for normality, non-parametric statistical tests were used. These were the Kruskal-Wallis test (Kruskal & Wallis 1952) for one-way analysis of the effect of treatment level within surveys and Friedman's randomized block test (Sokal & Rohlf 1995) for two-way analysis over surveys and treatment level. The Kruskal-Wallis test is analogous to a one-way ANOVA, while Friedman's test, which treats the different survey cycles as blocks and therefore tests the total effect over time, is analogous to an ANOVA for randomized block - designs. No multiple comparisons between samples could be done after either Kruskal-Wallis or Friedman's tests. The reason for this is that all non-parametric *post-hoc* tests are based on a single Mann-Whitney *U* test, which requires a sample size >8 before it becomes possible to get significant differences (Sokal & Rohlf 1995). The sample size in all cases in the present study was less than or equal to six.

Categorical data on the direction of changes in height of saplings (see later) were tested using the G-test for goodness of fit (Sokal & Rohlf 1995) and height class distributions were tested with a Kolmogorov-Smirnov two-sample test. Both these tests are non-parametric. The Kolmogorov-Smirnov two-sample test, using a Bonferroni-adjusted probability of 0.008, was also used to test for differences between treatment levels in number of species per treatment level (sample size was too small to allow either a test for homoscedasticity or Friedman's test). In the case of height

class distribution of sapling species before and after grazing, no adjustments were made in the accepted probability level, since the large number of comparisons would have made this meaningless. The tests in this case were done only to illustrate a point and no statistical conclusions were drawn from them. Even though multiple two sample tests like these increase the chances of making a type 1 error (in effect it causes a decrease in pairwise α), the results are not without value in context. If attention is focussed on the results of each separate test, it becomes less important whether the type 1 error probability increases for the whole group of tests (H. Groeneveld, pers. comm.)*. There is in any case no test available to test between multiple frequency distributions, sensu Analysis of Variance.

Multivariate variables (=plant community species composition)

Data on species presence were analysed using non-metric multi-dimensional scaling (referred to in here as MDS and described in Clarke & Warwick 1994) to elucidate differences in species composition. There are a number of ordination methods available to describe differences in plant community composition, but MDS is generally regarded as the most robust and least affected by the conversion of dissimilarity (or similarity) into distance (Gauch, Whittaker & Singer 1981, James & McCulloch 1990, Clarke & Warwick 1994). MDS supplies a “stress” value, which is a measure of how well the dimensional plot represents the actual rank order of similarities between the units (Clarke 1993, Clarke & Warwick 1994). To test whether the treatment levels differed significantly within and between surveys, one-way and two-way analysis of similarity (-ANOSIM) (Clarke 1993) was used. The software program PRIMER (Carr 1996) was used to do both the MDS and ANOSIM analyses.

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CHAPTER 4

RESULTS

DETERMINISTIC AND STOCHASTIC FACTORS WHICH COULD INFLUENCE THE EXPERIMENT

Treatment mass of cattle

Total metabolic weight per treatment level per grazing cycle differed significantly between grazing cycles (Kruskal-Wallis; low: $H=13.34$, $p<0.004$; medium: $H=12.74$, $p<0.005$; high: $H=14.14$, $p<0.003$). Arguably more important, however, is that the ratio of low : high; low : medium and medium : high treatment levels (Table 3) had to be similar for all grazing cycles. This ratio was chosen initially as 0.3:1, 0.5:1 and 0.3:1 respectively after consultation with Mr. Kelson Camp at the Agricultural College, Cedara (Camp, pers. comm.)*. After the first grazing cycle this was adjusted to 0.25:1; 0.5:1 and 0.5:1 respectively, because the amount of disturbance in the high treatment level appeared to be less than what cattle would be able to cause in normal

Table 3. Ratios of total applied cattle mass between treatment levels for all grazing cycles. Values for the 1st grazing cycle are based on estimates of mass, all others were measured. Based on data in Appendix 2.

| Grazing cycle | Ratios | | |
|--------------------|----------|------------|-------------|
| | Low:High | Low:Medium | Medium:High |
| 1 st | 0.33 | 0.50 | 0.67 |
| 2 nd | 0.25 | 0.50 | 0.50 |
| 3 rd | 0.24 | 0.56 | 0.42 |
| 4 th | 0.25 | 0.50 | 0.50 |
| 5 th | 0.20 | 0.39 | 0.50 |
| Mean | 0.25 | 0.49 | 0.52 |
| Standard deviation | 0.05 | 0.06 | 0.09 |

* Mr. Kelson Camp, Cedara Agricultural College, Cedara, KwaZulu-Natal, South Africa.

circumstances. Although these ratios were only achieved during the fourth grazing cycle, differences in ratios between grazing cycles were not significant (two-way ANOVA; $F=2.23$, $p=0.16$) and mean ratios come very close to the target. However, the ratios differed significantly between treatment levels (two-way ANOVA; $F=31.46$, $p<0.001$).

Cattle diet preferences and habits

Cattle spent most of their time feeding while in the treatment paddocks (Fig. 6a). Although in general it seemed as if cattle had more time for other activities while in the low treatment level paddocks, there were no significant differences between treatment levels for each category of activity (all H -values ≤ 7.54 , all p -values > 0.05 ; data in Appendix 3).

The cattle utilised 19 species (47% graminoid, 32% woody and 21% herbaceous) from a total of 67 available species during the 14 days which they spent in the treatment paddocks. Compared to this, the plants that made up the herbaceous layer consisted of 8% graminoid species, 34% woody species and 58% herbaceous (including climbers and erect forbs). There was a sharp increase with increased treatment level in the number of species which were negatively selected, although the numbers of positively selected species remained about the same (Table 4). *Dactyloctenium australe* had the highest selection value (SV) in all treatment levels and the lowest SV was shared by *Sarcostemma viminale* (low), *Panicum maximum* (medium) and *Coccinia variifolia* (high). Overall the most preferred species was *D. australe* and the least

Table 4. The numbers of species in three different treatment levels for which cattle selected positively (higher occurrence in diet than in plant community), neutral (equal occurrence in diet and plant community) and negatively (lower occurrence in diet than in plant community).

| | Treatment level | | | |
|--------------------|-----------------|--------|------|----------------|
| | Low | Medium | High | All treatments |
| Negative selection | 1 | 7 | 8 | 7 |
| Neutral selection | 1 | 1 | 2 | 1 |
| Positive selection | 8 | 9 | 8 | 11 |

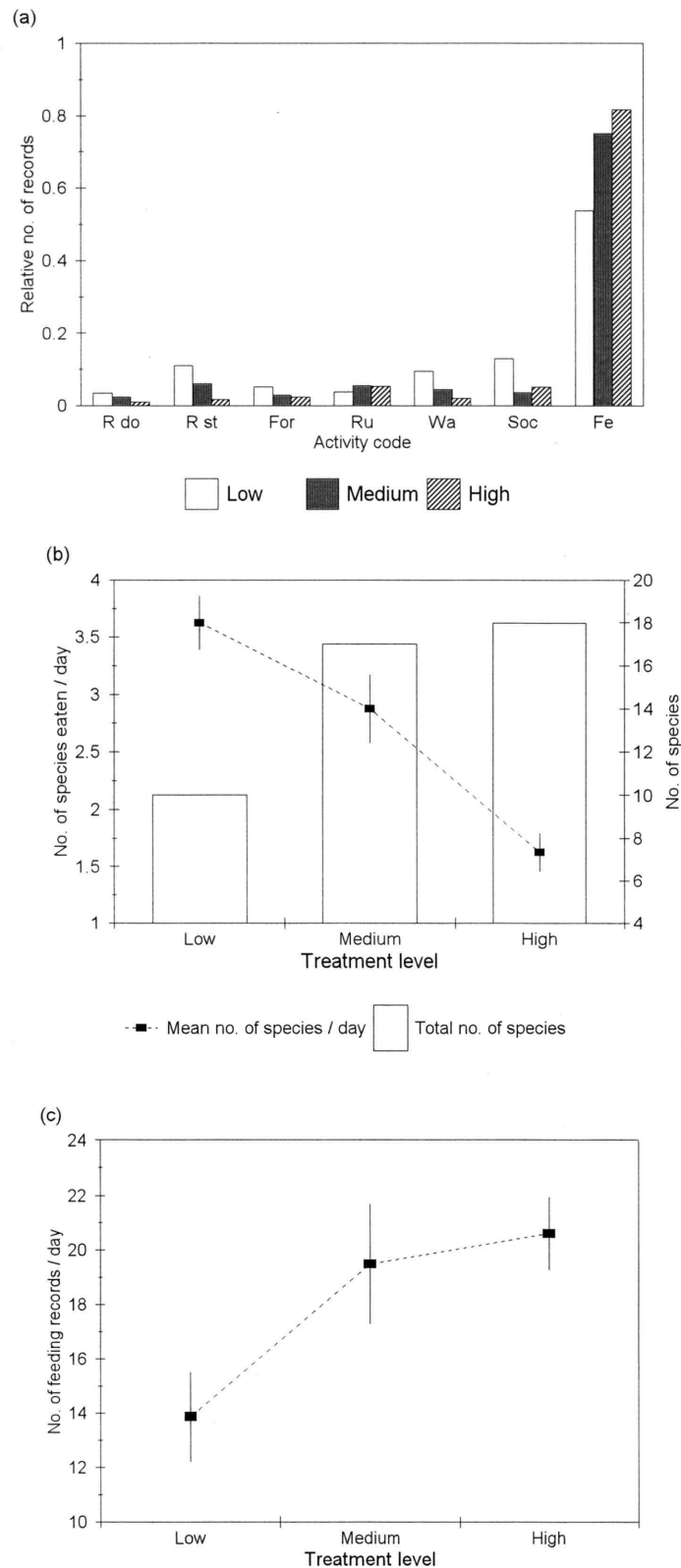


Figure 6. (a) Daily activity pattern of cattle while grazing in low, medium and high treatment paddocks. Rdo = Resting down; Rst = Resting standing; For = Foraging; Ru = Ruminating; Soc = Social activity; Fe = Active feeding. (b) Mean number of species eaten per day and the total number of species eaten in the low, medium and high treatment paddocks. (c) Mean number of feeding records per day in the low, medium and high treatment paddocks.

preferred *Secamone filiformis* (Table 5). More than 50% of their diet consisted of three species, *D. australe* (grass), *Commicarpus chinensis* (herb) and *Asystasia gangetica* (herb), although they selected relatively widely up to 95% of the diet (Table 5). The total number of species eaten per treatment level increased from 10 in the low treatment level to 17 in the medium, and 18 in the high, while the mean number of species utilised per day decreased significantly (Kruskal-Wallis, $H=8.64$, $p=0.04$) the higher the treatment level (Fig. 6b). The mean number of feeding records per day also increased with increase in treatment level (Fig. 6c), although this difference was not significant (Kruskal-Wallis, $H=5.13$, $p>0.05$).

Table 5. The percentage contribution to the total diet and selection values of all plant species utilised by cattle during the first grazing cycle, given separately for three treatment levels as well as over all treatment levels. Selection value was calculated as the species' relative occurrence in the diet, divided by the species' relative occurrence in the environment. Plant species are ranked according to their selection value in the total diet.

| Species | Selection value | | | Total diet | % contribution to diet |
|--------------------------------|-----------------|--------|-------|------------|------------------------|
| | Low | Medium | High | | |
| <i>Dactyloctenium australe</i> | 11.03 | 17.19 | 15.84 | 12.21 | 25.85 |
| <i>Brachylaena discolor</i> | 1.00 | 1.58 | 6.95 | 10.33 | 2.19 |
| <i>Apodytes dimidiata</i> | 0.00 | 1.00 | 0.39 | 9.69 | 1.03 |
| <i>Brachiaria chusqueoides</i> | 4.27 | 2.84 | 6.76 | 5.03 | 5.79 |
| <i>Commicarpus chinensis</i> | 4.91 | 4.03 | 2.88 | 3.83 | 15.81 |
| <i>Asystasia gangetica</i> | 2.96 | 3.42 | 2.05 | 2.50 | 15.11 |
| <i>Aneilema aequinoctiale</i> | 1.71 | 2.03 | 1.43 | 1.46 | 4.48 |
| <i>Digitaria diversinervis</i> | 0.00 | 1.20 | 3.11 | 1.40 | 11.71 |
| <i>Senecio deltoideus</i> | 0.00 | 0.17 | 5.57 | 1.38 | 5.85 |
| <i>Kraussia floribunda</i> | 2.14 | 0.39 | 0.39 | 1.31 | 0.56 |
| <i>Laportea peduncularis</i> | 2.94 | 0.45 | 0.56 | 1.12 | 7.83 |
| <i>Antidesma venosum</i> | 0.00 | 0.00 | 1.00 | 1.00 | 0.22 |
| <i>Scutia myrtina</i> | 2.14 | 3.15 | 0.06 | 0.96 | 0.91 |
| <i>Adenia gummifera</i> | 0.00 | 4.73 | 0.00 | 0.91 | 0.68 |
| <i>Sideroxylon inerme</i> | 0.00 | 0.00 | 1.00 | 0.54 | 0.11 |
| <i>Sarcostemma viminale</i> | 0.85 | 0.39 | 0.14 | 0.37 | 0.95 |
| <i>Coccinia variifolia</i> | 0.00 | 0.11 | 0.06 | 0.08 | 0.18 |
| <i>Panicum maximum</i> | 0.00 | 0.07 | 0.14 | 0.07 | 0.24 |
| <i>Secamone filiformis</i> | 0.00 | 0.12 | 0.06 | 0.06 | 0.51 |

An MDS of the species utilised by cattle in the three treatment levels, distinctly separates the three treatment levels when all days of treatment is taken together (Fig. 7c). There is some overlap between treatment levels if only the first two days is considered, but a distinct separation of the low treatment level paddocks from the medium and high if only the last two days are considered. Although the medium and high levels cluster relatively closely together here, it is still possible to draw a line around the paddocks from each group without including any of the other one (Fig. 7a&b).

Abiotic and biotic determinants of community structure

Rainfall

Rainfall followed a broadly seasonal pattern during the study period, although the daily rainfall was below the 10 year average for a considerable period before the third survey (Fig 4). It improved somewhat after the second survey (and grazing application) but it was only at the time of the fourth survey that summer rainfall went appreciably above the 10 year average.

Canopy tree structure and density and incandescent light

Only one species of canopy tree was found *viz. Acacia karroo*. None of the variables (density, mean stem diameter at breast height, mean number of stems per tree and mean height) showed significant differences between the different treatments (all H-values ≤ 3.22 , all p-values > 0.05). The percentage (leaf and branch) canopy cover (=canopy density) at each survey quadrat within all the treatment paddocks differed significantly between paddocks (one-way ANOVA; $F=15.38$, $p<0.001$), but not between the means for the treatment levels (ANOVA; $F=1.18$, $p=0.36$). The mean light intensity on the forest floor ranged from 102 lux down to 0.85 lux (Table 6). Differences between the paddocks were not significant (ANOVA: $F=1.31$, $p=0.20$). Data in Appendix 4.

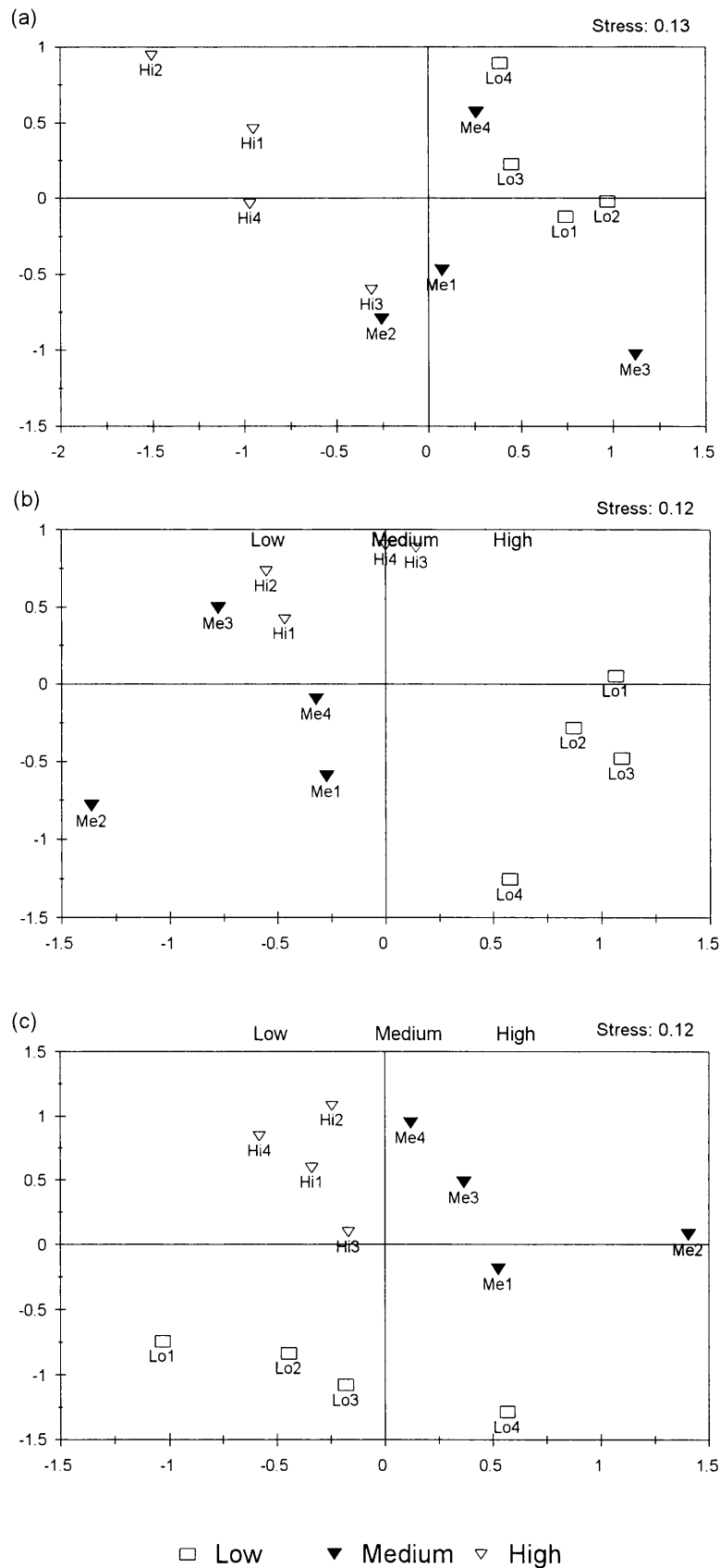


Figure 7. Multiple dimensional scaling of the feeding preferences of cattle (preferred plant species) in the low, medium and high treatment paddocks. First two days in treatment level (a), last two days in treatment level (b) and all days of treatment level (c). See text for details.

Table 6. Mean and standard error of the light intensity (measured in lux) on the forest floor in four treatment levels. Light intensity was measured at 5 points at 6 quadrats per paddock.

| | Control | Low | Medium | High |
|----------------|---------|-------|--------|-------|
| Mean | 21.46 | 16.90 | 24.45 | 22.80 |
| Standard Error | 4.56 | 2.03 | 2.82 | 2.94 |

PLANT SPECIES RICHNESS, VEGETATION COVER AND HEIGHT

Number of species per pin

Although the trend in species number per pin was not clear, in general there was a decrease over time in all treatment levels and the decrease tended to be larger the higher the treatment level (Fig. 8, Table 7). Coefficient of variation (CV) remained about the same over time in the control and low treatment level (Table 7). In the medium treatment level the CV increased after survey 1, remained about the same for a while and then decreased again by the time of survey 6, while in the high treatment level the CV increased almost linearly after survey 1 until survey 5 and then decreased again by survey 6 (Table 7). After survey 1 the number of species increased in all treatment levels, dropped after survey 3, and increased again by survey 5 (Fig. 8).

Table 7. The mean (\pm standard error) number of plant species per pin in four treatment levels over five surveys. Coefficient of variation (%) is given in parentheses. Data on number of species per pin were not collected during survey 4. n=4 in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | |
|-----------------|----------------------------|----------------------------|----------------------------|----------------------------|----------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 5 | Survey 6 |
| Control | 1.80 \pm 0.12 (13.54) | 2.17 \pm 0.14 (12.66) | 1.60 \pm 0.10 (12.98) | 1.76 \pm 0.12 (13.25) | 1.57 \pm 0.03 (3.21) |
| Low | 1.76 \pm 0.14 (16.28) | 2.18 \pm 0.18 (16.46) | 1.38 \pm 0.09 (13.71) | 1.92 \pm 0.11 (11.80) | 1.72 \pm 0.12 (14.19) |
| Medium | 1.84 \pm 0.09 (9.66) | 2.05 \pm 0.20 (19.75) | 1.29 \pm 0.11 (16.30) | 1.75 \pm 0.15 (17.37) | 1.58 \pm 0.09 (11.42) |
| High | 1.65 \pm 0.07 (8.22) | 2.14 \pm 0.14 (13.37) | 1.12 \pm 0.11 (19.48) | 1.37 \pm 0.23 (33.31) | 1.32 \pm 0.10 (15.55) |

Data were transformed to fourth root to correct for non-normality and heteroscedasticity. MANOVAR showed that there was a statistically significant effect of time (survey days), but no significant interaction between time and treatment level (Table 8). ANOVAR also showed no significant treatment or time-treatment level interaction, but a significant time effect (Table 8). There was a significant overall linear relationship over time, but no significant linear or quadratic interactions (Table 8). Least squares linear regression showed no significant relationships between the number of species/pin and time (r^2 values were also comparatively low for all treatment levels) and also no overall difference in the response of treatment levels over time ($F=0.27$, $p=0.85$).

Table 8. Results from a MANOVAR and ANOVAR test for differences between four levels of treatment over five surveys, in the number of plant species per pin. ($n=4$). *Roy's GR* is Roy's Greatest Root; *G-G adj. p* is the probability for ANOVAR, adjusted with the Greenhouse-Geisser ϵ (Von Ende 1993). Based on data in Appendix 5.

| Test | Effect | Roy's GR | F | p | G-G adj. p |
|-----------|--------------------|----------|----------|--------|------------|
| MANOVAR | Survey | 15.94 | 35.85*** | <0.001 | - |
| | Survey x Treatment | 1.41 | 3.86 | 0.04 | - |
| ANOVAR | Treatment | - | 1.80 | 0.20 | - |
| | Survey | - | 32.92*** | <0.001 | <0.001 |
| | Survey x Treatment | - | 1.28 | 0.26 | 0.29 |
| Linear | Survey | - | 9.10‡ | 0.01 | - |
| | Survey x Treatment | - | 1.00 | 0.43 | - |
| Quadratic | Survey | - | 0.03 | 0.86 | - |
| | Survey x Treatment | - | 1.50 | 0.26 | - |

‡ = significance at $p=0.025$ (Bonferoni adjustment); *** = significance at $p=0.001$

Number of species per quadrat

There was a gradual decreasing trend with each successive survey in number of species/1m² in the control, but not in the other treatments (Fig. 9). The main effect of the disturbance created by the cattle was to increase the amount of variation in the values (Fig. 9), although this was not completely dependent on treatment level. Again, as in most of the other variables, there was a decrease after the second and a sharp increase in values after the third survey. Coefficient of variation for the control paddocks decreased somewhat over time, but tended to increase in all treatment paddocks (Table 9).

Table 9. The mean (\pm standard error) number of plant species per quadrat in four treatment levels over six surveys. Coefficient of variation (%) is given in parentheses. n=4 in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | | |
|-----------------|----------------------------|-----------------------------|----------------------------|-----------------------------|-----------------------------|----------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 4 | Survey 5 | Survey 6 |
| Control | 8.54 \pm 0.92 (21.46) | 8.63 \pm 0.51 (11.74) | 7.63 \pm 0.45 (11.89) | 8.46 \pm 0.58 (13.78) | 7.25 \pm 0.39 (10.70) | 6.46 \pm 0.21 (6.45) |
| Low | 9.71 \pm 0.88 (18.13) | 9.88 \pm 0.52 (10.44) | 7.63 \pm 0.45 (11.89) | 11.25 \pm 1.24 (21.99) | 11.17 \pm 1.51 (27.06) | 8.63 \pm 1.42 (32.85) |
| Medium | 8.92 \pm 0.77 (17.17) | 10.25 \pm 0.72 (13.96) | 8.71 \pm 0.62 (14.18) | 10.25 \pm 0.90 (17.49) | 10.33 \pm 1.14 (22.15) | 8.58 \pm 0.67 (15.65) |
| High | 9.71 \pm 0.89 (18.30) | 10.63 \pm 0.95 (17.95) | 7.67 \pm 0.66 (17.12) | 11.29 \pm 1.63 (28.86) | 10.63 \pm 1.45 (27.30) | 8.67 \pm 1.23 (28.44) |

The untransformed data were normally distributed and homoscedastic. There was a significant treatment-time interaction in the number of species per quadrat (MANOVAR; Table 10). There was a significant quadratic time effect, while the linear time-treatment interaction was significant (Table 10). ANOVAR showed that both the treatment and time effect, as well as the time-treatment interaction were significant (Table 10). Tukey's HSD over all surveys showed that control differed from low and high treatment levels (minimum significant difference (msd) $(p=0.05, df=20) = 1.87$). In survey 2 control and high treatment levels differed significantly (Tukey's HSD; minimum significant difference (msd) $(p=0.05, df=12) = 1.803$), in survey 4 control differed from both low and high (msd $(p=0.05, df=12) = 2.35$), in survey 5 control differed from all other treatment levels (msd $(p=0.05, df=12) = 2.37$) and in survey 6 control differed from all other treatment levels (msd $(p=0.05, df=12) = 1.97$). The regression of time against number of species per quadrat was significant only in the control ($y=9.20-0.39x$, $p=0.04$; $r^2=0.71$, $p=0.04$). None of the regression coefficients differed significantly from each other ($F_s=0.48$, $p=0.70$).

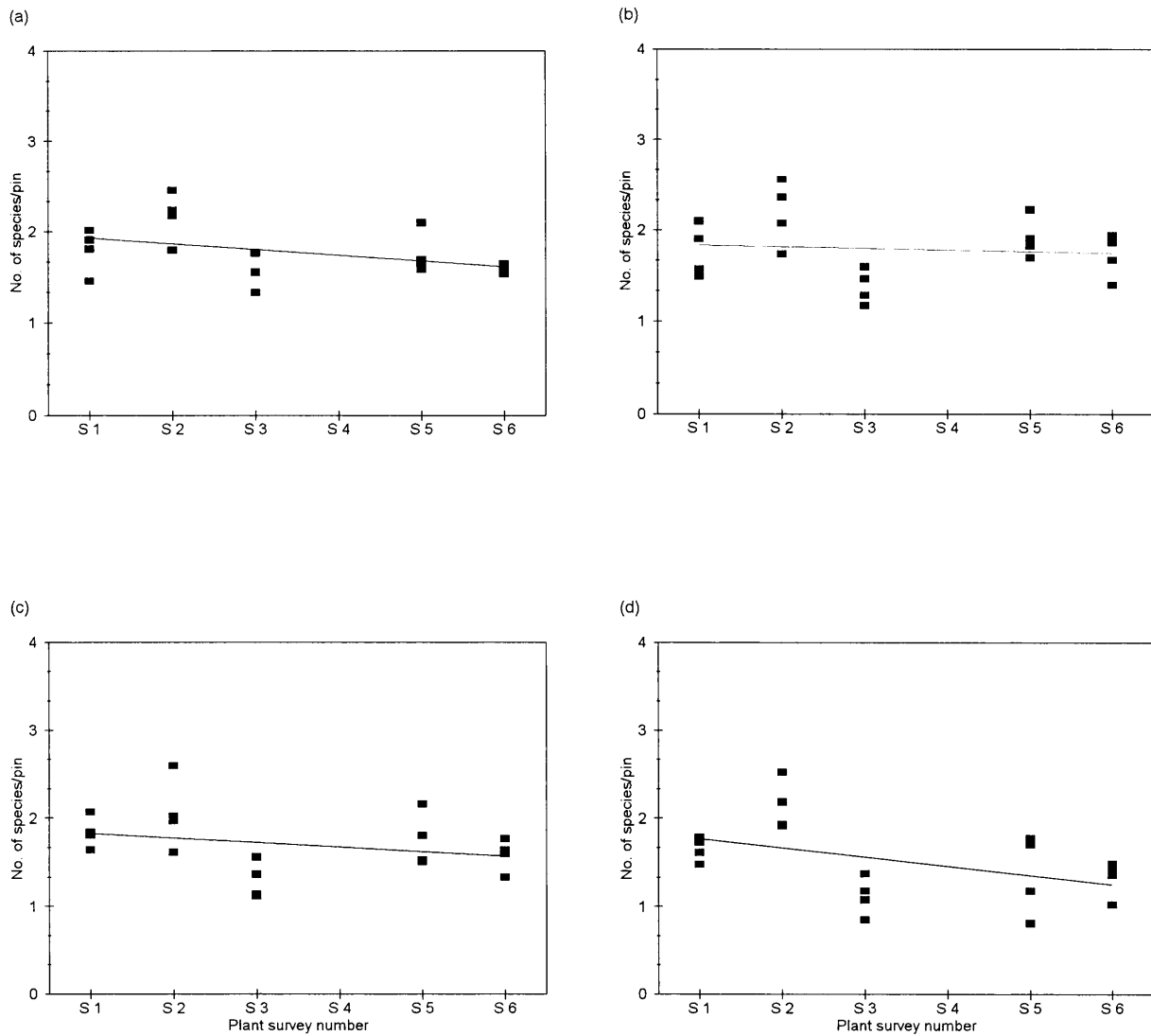


Figure 8. The number of species per pin over 5 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted through least squares linear regression on the mean values per survey and can be described by (a): $y = 1.19 - 0.01x$ ($p=0.30$), $r^2 = 0.33$ ($p=0.30$); (b): $y = 1.17 - 0.005x$ ($p=0.78$), $r^2 = 0.03$ ($p=0.78$); (c): $y = 1.17 - 0.01x$ ($p=0.47$), $r^2 = 0.18$ ($p=0.47$) and (d): $y = 1.18 - 0.03x$ ($p=0.30$), $r^2 = 0.34$ ($p=0.30$).

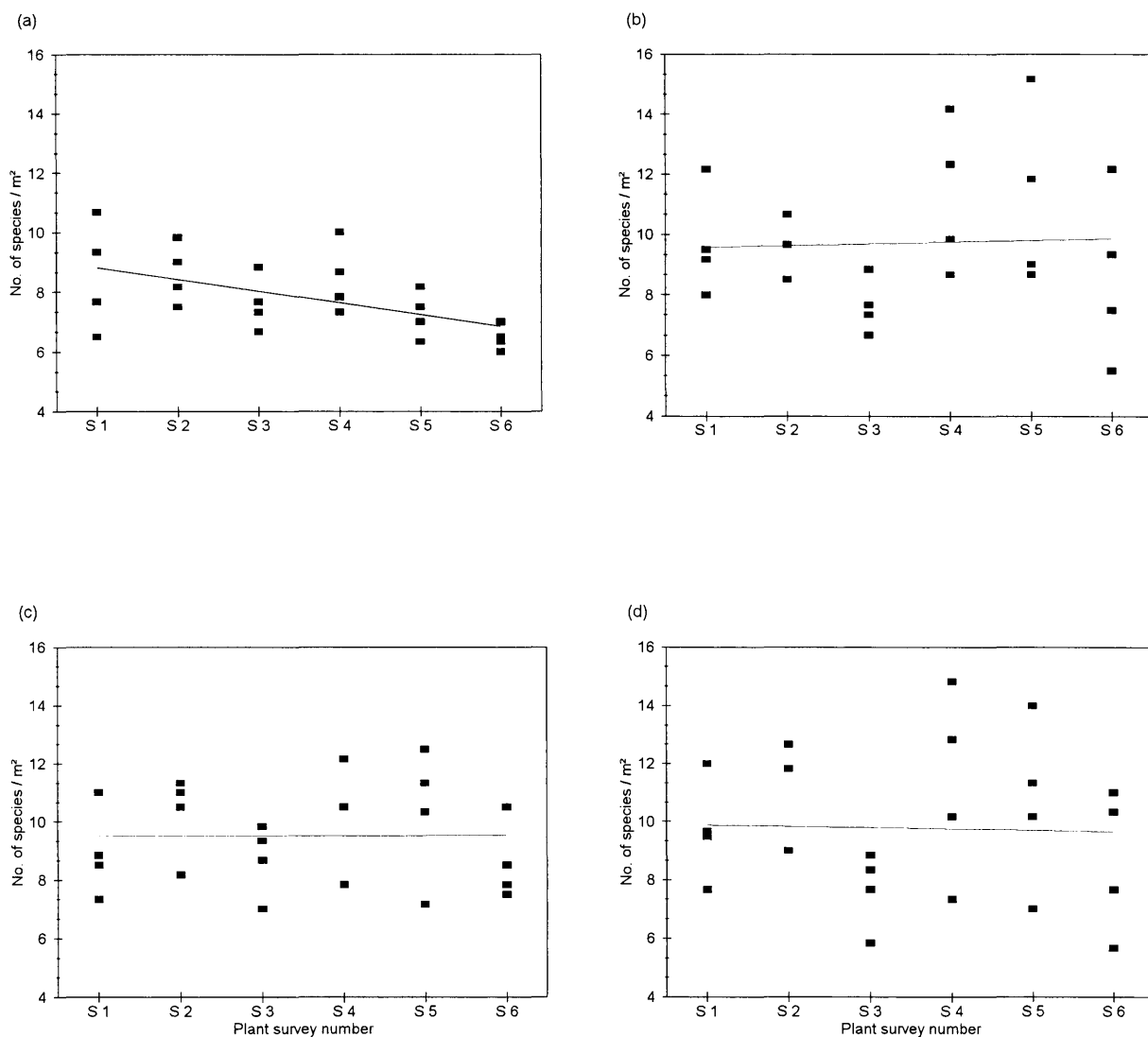


Figure 9. The number of species per 1m² quadrat over 6 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted through least squares linear regression on the mean values per survey and can be described by (a): $y = 9.20 - 0.39x$ ($p=0.04$), $r^2 = 0.71$ ($p=0.04$); (b): $y = 9.50 + 0.06x$ ($p=0.88$), $r^2 = 0.008$ ($p=0.88$); (c): $y = 9.49 + 0.004x$ ($p=0.99$), $r^2 = 0.001$ ($p=0.99$) and (d): $y = 9.92 - 0.05x$ ($p=0.90$), $r^2 = 0.004$ ($p=0.90$).

Table 10. Results from a MANOVAR and ANOVAR test for differences in the number of plant species per 1m² quadrat between four levels of treatment over six surveys. (n=4). *Roy's GR* is Roy's Greatest Root; *G-G adj. p* is the probability for ANOVAR, adjusted with the Greenhouse-Geisser ϵ (Von Ende 1993). Based on data in Appendix 5.

| Test | Effect | Roy's GR | F | p | G-G adj. p |
|-----------|--------------------|----------|----------|--------|------------|
| MANOVAR | Survey | 1.94 | 34.20*** | <0.001 | - |
| | Survey x Treatment | 0.344 | 6.20*** | <0.001 | - |
| ANOVAR | Treatment | - | 4.50** | 0.01 | - |
| | Survey | - | 31.19*** | <0.001 | <0.001 |
| | Survey x Treatment | - | 3.61*** | <0.001 | <0.001 |
| Linear | Survey | - | 1.10 | 0.30 | - |
| | Survey x Treatment | - | 4.26‡ | 0.01 | - |
| Quadratic | Survey | - | 10.48‡ | 0.002 | - |
| | Survey x Treatment | - | 0.78 | 0.51 | - |

‡ = significance at p=0.025 (Bonferoni adjustment); ** = significance at p=0.01; *** = significance at p=0.001

Number of species per paddock

Although the number of species per paddock decreased with time in the control and showed a slight increase in all the other treatment levels the most striking effect was a consistently larger amount of variation the higher the treatment level (Fig. 10, Table 11). The drop in values after survey 3 is echoed in most of the other variables measured. In general CV's increased in the low, medium and high treatment levels (except for a decrease in the low treatment level at the time of survey 2), but showed a decreasing trend in the control until survey 3, after which it started increasing again (Table 11).

Table 11. The mean (\pm standard error) number of plant species per paddock in four treatment levels over six surveys. Coefficient of variation (%) is given in parentheses. $n=4$ in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | | |
|-----------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 4 | Survey 5 | Survey 6 |
| Control | 19.50 \pm 1.04 (10.68) | 19.50 \pm 0.96 (9.82) | 19.25 \pm 0.25 (2.60) | 19.50 \pm 0.29 (2.96) | 18.25 \pm 0.48 (5.25) | 15.25 \pm 0.95 (12.41) |
| Low | 22.25 \pm 2.06 (18.49) | 24.00 \pm 0.82 (6.80) | 23.25 \pm 1.75 (15.05) | 26.75 \pm 2.06 (15.38) | 26.75 \pm 3.12 (23.32) | 23.00 \pm 3.67 (31.95) |
| Medium | 22.50 \pm 1.55 (13.82) | 24.25 \pm 1.44 (11.84) | 22.75 \pm 1.89 (16.59) | 25.25 \pm 2.75 (21.78) | 25.00 \pm 2.45 (19.60) | 22.75 \pm 2.84 (24.96) |
| High | 21.00 \pm 2.12 (20.20) | 25.00 \pm 3.34 (26.73) | 19.75 \pm 2.63 (26.59) | 25.75 \pm 4.19 (32.55) | 26.25 \pm 4.23 (32.23) | 23.75 \pm 4.15 (34.95) |

Because the data were not normally distributed even after transformation, non-parametric statistical tests were used. None of the treatment levels differed significantly from each other within any of the surveys (Kruskal-Wallis test; all H -values ≤ 5.99 , all p -values > 0.05). However, Friedman's randomized block design, treating the surveys as blocks, showed that there was a highly significant difference overall between the treatment levels ($X^2=73.76$, $p < 0.001$).

Number of species per treatment level and per survey

The total number of species per survey dropped at the time of survey 3 (Fig. 11). The drop was mainly due to a decrease in the total number of species in the high treatment level. However, there was apparently also a gradual decline in total number of species in the control paddocks, while in all other treatments the number of species gradually increased. Multiple Kolmogorov-Smirnov two-sample tests showed that control differed significantly from all the other treatments at a Bonferroni-adjusted probability of 0.008 (probability of 0.05 divided by number of comparisons), while the other three treatment levels did not differ significantly from each other (maximum difference control:low=0.30, control:medium=0.23, control:high=0.24; $p < 0.008$).

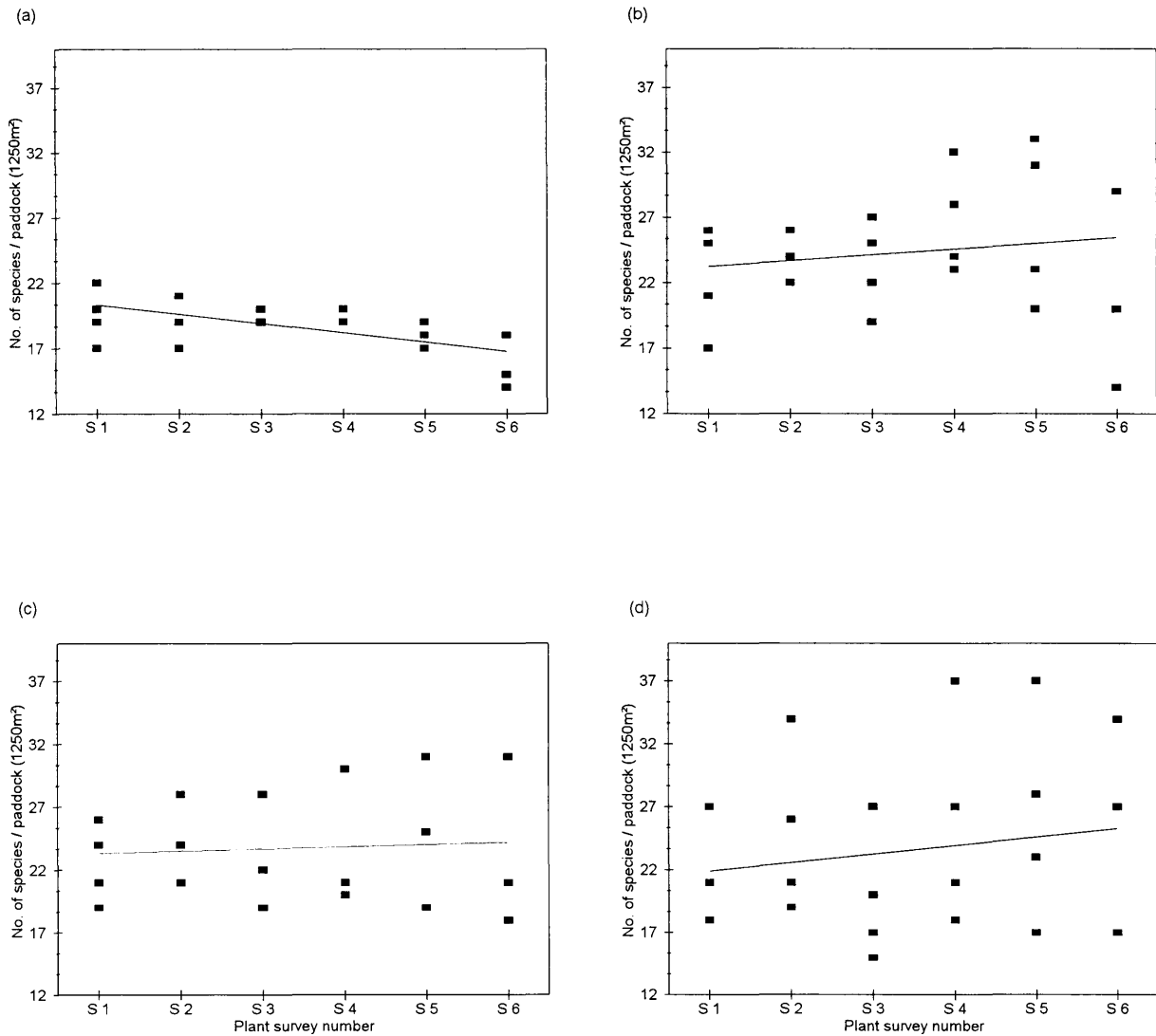


Figure 10. The number of species per paddock over 6 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted on the mean values per survey through least squares linear regression for descriptive purposes only and can be described by (a): $y = 21.02 - 0.71x$, $r^2 = 0.62$; (b): $y = 22.78 + 0.44x$, $r^2 = 0.18$; (c): $y = 23.15 + 0.17x$, $r^2 = 0.07$ and (d): $y = 21.23 + 0.67x$, $r^2 = 0.22$.

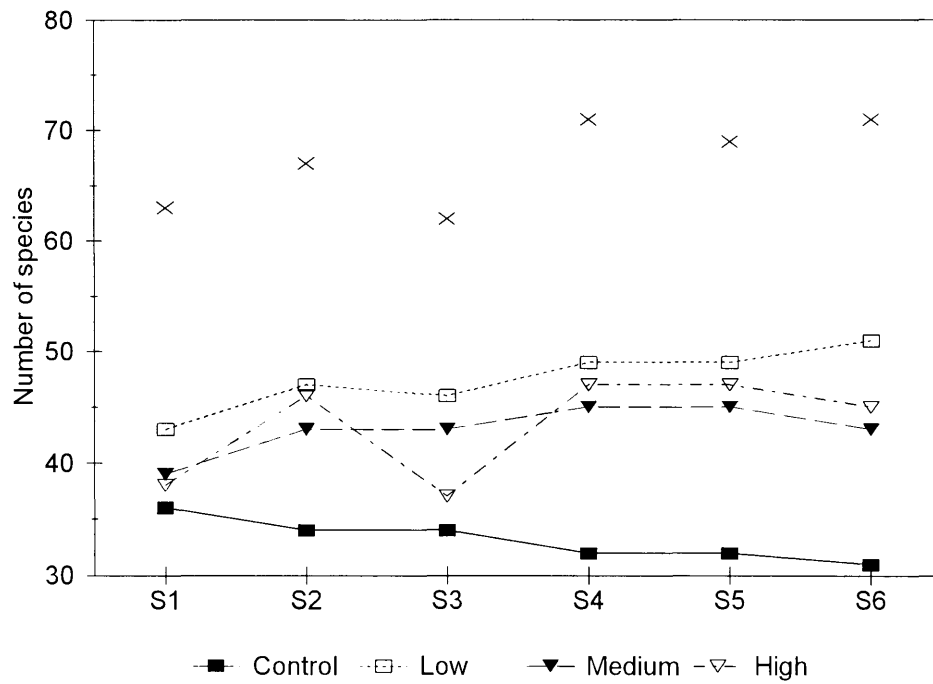


Figure 11. The total number of species per treatment level over 6 plant surveys in the control, low, medium and high treatment level paddocks. Crosses represent the total number of species found in that survey, over all treatment levels.

Herbaceous cover

The effect of the cattle on the percentage herbaceous cover was strongly dependent on the level of treatment. (Fig. 12, Table 12). There was an increase in all treatment levels after the first survey cycle followed by a sharp decrease after the second survey cycle, the magnitude of which depended on the treatment level. By the time of the fifth survey, the cover values had started to recover somewhat (Table 12), although the highest treatment levels were still lower than the control and low treatment level. Except for the high treatment level, which increased markedly after survey 2 and then decreased again by the time of survey 6, CV's stayed about the same over time for all treatment levels (Table 12). In general CV tended to be dependent on the level of treatment while control tended to have a lower CV than the other treatment levels over time (Table 12).

Table 12. The mean (\pm standard error) percentage herbaceous cover in four treatment levels over five surveys. Coefficient of variation (%) is given in parentheses. n herbaceous cover was not collected during survey 4. n=4 in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | |
|-----------------|----------------------------|----------------------------|-----------------------------|------------------------------|-----------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 5 | Survey 6 |
| Control | 94.89 \pm 1.62 (3.41) | 98.67 \pm 0.65 (1.31) | 96.40 \pm 1.17 (2.43) | 99.05 \pm 0.48 (0.96) | 97.92 \pm 1.21 (2.48) |
| Low | 93.56 \pm 2.88 (6.15) | 97.35 \pm 1.97 (4.04) | 85.04 \pm 2.72 (6.40) | 97.35 \pm 0.95 (1.96) | 96.02 \pm 0.84 (1.75) |
| Medium | 92.99 \pm 1.56 (3.35) | 96.78 \pm 1.65 (3.40) | 84.47 \pm 2.06 (4.88) | 94.13 \pm 2.17 (4.62) | 92.42 \pm 2.49 (5.40) |
| High | 90.15 \pm 2.03 (4.50) | 97.35 \pm 1.71 (3.51) | 75.19 \pm 7.44 (19.78) | 80.87 \pm 10.99 (27.18) | 87.31 \pm 5.04 (11.54) |

Because data on herbaceous cover were not normally distributed and were heteroscedastic, non-parametric tests were used to test for differences between treatment levels and survey cycles. Friedman's randomized block test showed a significant difference only between treatment levels ($X^2=47.44$, $p < 0.001$). However, in a one-way Kruskal-Wallis test of the individual survey cycles, only survey 3 showed a significant difference between treatment levels ($H=8.45$, $p=0.04$; all other H -values ≤ 6.19 , p -values > 0.05).

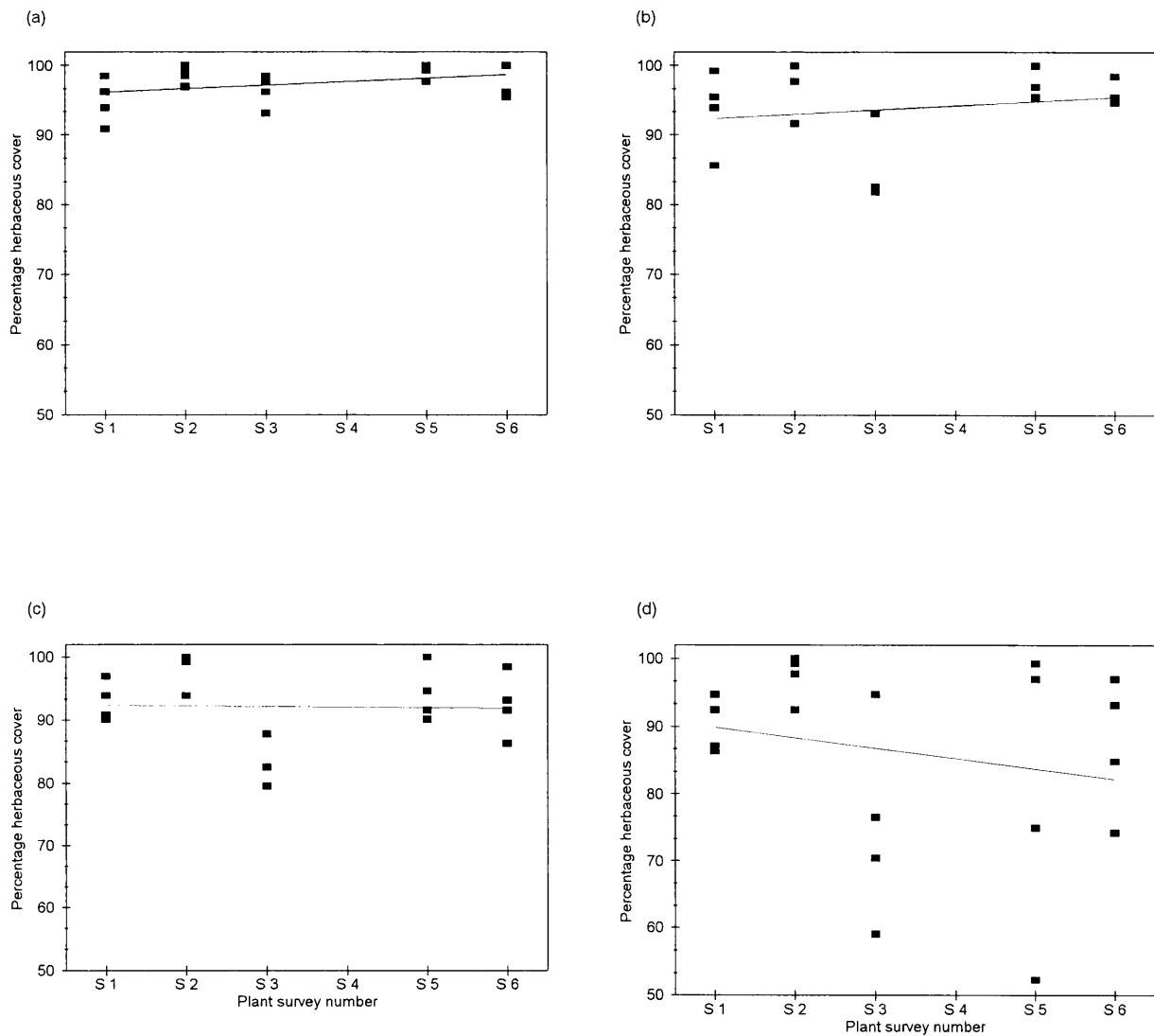


Figure 12. The percentage herbaceous cover over 5 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted (for descriptive purposes only) through least squares linear regression on the mean values per survey and can be described by (a): $y = 95.46 + 0.64x$, $r^2 = 0.35$; (b): $y = 92.39 + 0.49x$, $r^2 = 0.02$; (c): $y = 93.3 - 0.38x$, $r^2 = 0.02$ and (d): $y = 92.82 - 2.22x$, $r^2 = 0.17$.

Ground cover

The overall picture of the changes in percentage ground cover was very similar to the changes in herbaceous cover (Fig. 13, Table 13). There was a drop in cover values after the second survey (except in the control, which actually showed an increase), followed by a gradual recovery. The effect was strongly dependent on the treatment level - the values dropped more and took longer to recover the higher the treatment level. Coefficient of variation in the high treatment level increased to a maximum at the time of survey 5 and decreased again by the time of survey 6 (Table 13). Again, as with the percentage herbaceous cover, CV's in control tended to be the lowest of all treatment levels, while CV's in the medium and high treatment levels stayed about the same over time (Table 13).

Table 13. The mean (\pm standard error) percentage ground cover in four treatment levels over five surveys. Coefficient of variation (%) is given in parentheses. Data on ground cover were not collected during survey 4. $n=4$ in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | |
|-----------------|-----------------------------|-----------------------------|------------------------------|------------------------------|------------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 5 | Survey 6 |
| Control | 66.48 \pm 3.02 (9.09) | 63.64 \pm 5.14 (16.15) | 66.67 \pm 6.59 (19.77) | 73.67 \pm 2.67 (7.24) | 81.63 \pm 2.11 (5.16) |
| Low | 60.99 \pm 8.39 (27.53) | 59.28 \pm 4.66 (15.73) | 47.54 \pm 6.20 (26.10) | 59.09 \pm 5.64 (19.10) | 66.29 \pm 7.98 (24.07) |
| Medium | 66.86 \pm 3.62 (10.84) | 54.17 \pm 6.08 (22.45) | 42.99 \pm 5.01 (23.31) | 55.30 \pm 6.35 (22.98) | 57.58 \pm 6.21 (21.57) |
| High | 63.07 \pm 4.70 (14.92) | 54.36 \pm 5.34 (19.66) | 38.26 \pm 10.06 (52.60) | 40.53 \pm 15.58 (76.89) | 50.59 \pm 13.84 (54.72) |

An arcsine transformation was done to correct for non-normality and heteroscedasticity. There were significant differences between the surveys, but no time-treatment interactions, for both ANOVAR and MANOVAR (Table 14). There was also a significant quadratic time effect (Table 14). Least squares linear regression showed a significant positive relationship between time and ground cover for the control ($y=0.006+0,0006x$, $p=0.02$; $r^2=0.78$, $p=0.02$), but not for any of the other treatment levels. There were no significant differences between the regression coefficients (slopes) of the four treatment levels ($F_s=1.97$, $p=0.17$).

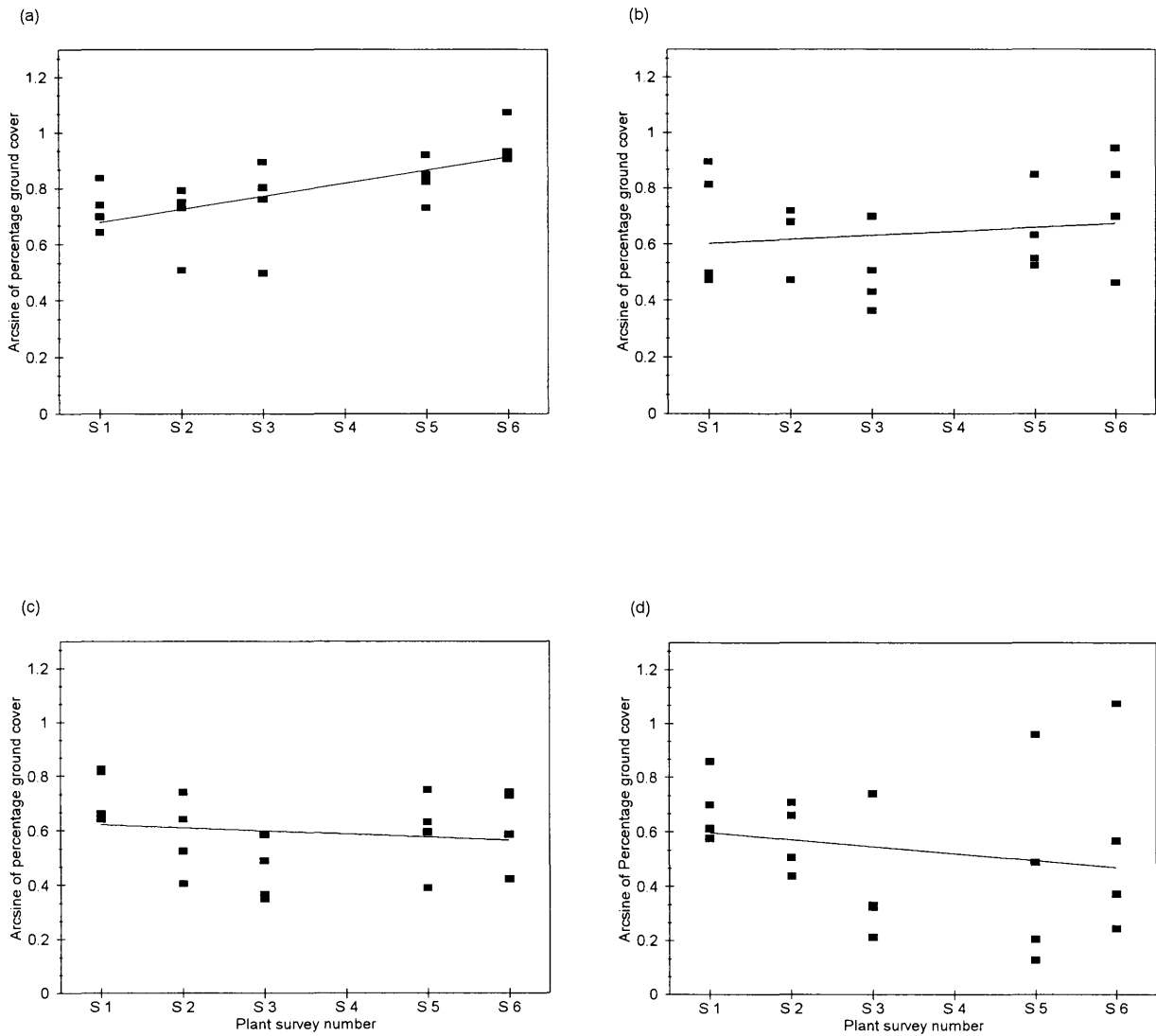


Figure 13. The percentage ground cover (arcsine transformed) over 5 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted through least squares linear regression on the mean values per survey and can be described by (a): $y = 0.006 + 0.0006x$ ($p=0.05$), $r^2 = 0.78$ ($p=0.05$); (b): $y = 0.006 + 0.0001x$ ($p=0.68$), $r^2 = 0.06$ ($p=0.68$); (c): $y = 0.007 - 0.0002x$ ($p=0.58$), $r^2 = 0.11$ ($p=0.58$) and (d): $y = 0.006 - 0.0004x$ ($p=0.36$), $r^2 = 0.28$ ($p=0.36$).

Table 14. Results from a MANOVAR and ANOVAR test for differences in the percentage ground cover between four levels of treatment over five surveys. (n=4). *Roy's GR* is Roy's Greatest Root; *G-G adj. p* is the probability for ANOVAR, adjusted with the Greenhouse-Geisser ϵ (Von Ende 1993). Based on data in Appendix 5.

| Test | Effect | Roy's GR | F | p | G-G adj. p |
|-----------|--------------------|----------|---------|--------|------------|
| MANOVAR | Survey | 3.96 | 8.91** | 0.003 | - |
| | Survey x Treatment | 1.10 | 3.02 | 0.06 | - |
| ANOVAR | Treatment | - | 2.13 | 0.15 | - |
| | Survey | - | 8.02*** | <0.001 | <0.001 |
| | Survey x Treatment | - | 1.96 | 0.05 | 0.08 |
| Linear | Survey | - | <0.001 | 0.95 | - |
| | Survey x Treatment | - | 3.36 | 0.06 | - |
| Quadratic | Survey | - | 26.81‡ | <0.001 | - |
| | Survey x Treatment | - | 0.68 | 0.58 | - |

‡ = significance at $p=0.025$ (Bonferoni adjustment); ** = significance at $p=0.01$; *** = significance at $p=0.001$

Vegetation height

The increase in the height of the herbaceous layer after the first survey combined with a relatively sharp decrease at the time of the third survey, is similar to those of almost all the other variables (Fig. 14, Table 15). The effect of the cattle on herb height was in general also dependent on treatment level - there was an increase in height with each successive plant survey in the ungrazed control, less so in low and medium treatment levels, but almost no increase over time in the high treatment level (Table 15). Coefficient of variation showed no consistent response over time to treatment level (Table 15).

The data were not normally distributed, even after transformation. Nonetheless, MANOVAR and linear regression tests were done because the data were at least homoscedastic and Sokal & Rohlf (1995, p407) states that "the consequences of non-normality of errors are not too serious because means will tend to follow a normal distribution more closely than the distribution of the variates themselves". The tests were done on the logarithmic (\log_{10}) transformed data because that came the closest to being normally distributed (G-test: $G=98.66$; $\chi^2_{critical(0.001, 61df)} = 97.04$). There was a significant overall time effect as well as a time-treatment interaction in the effect of cattle on vegetation height and both a significant linear relationship over time and a significant linear

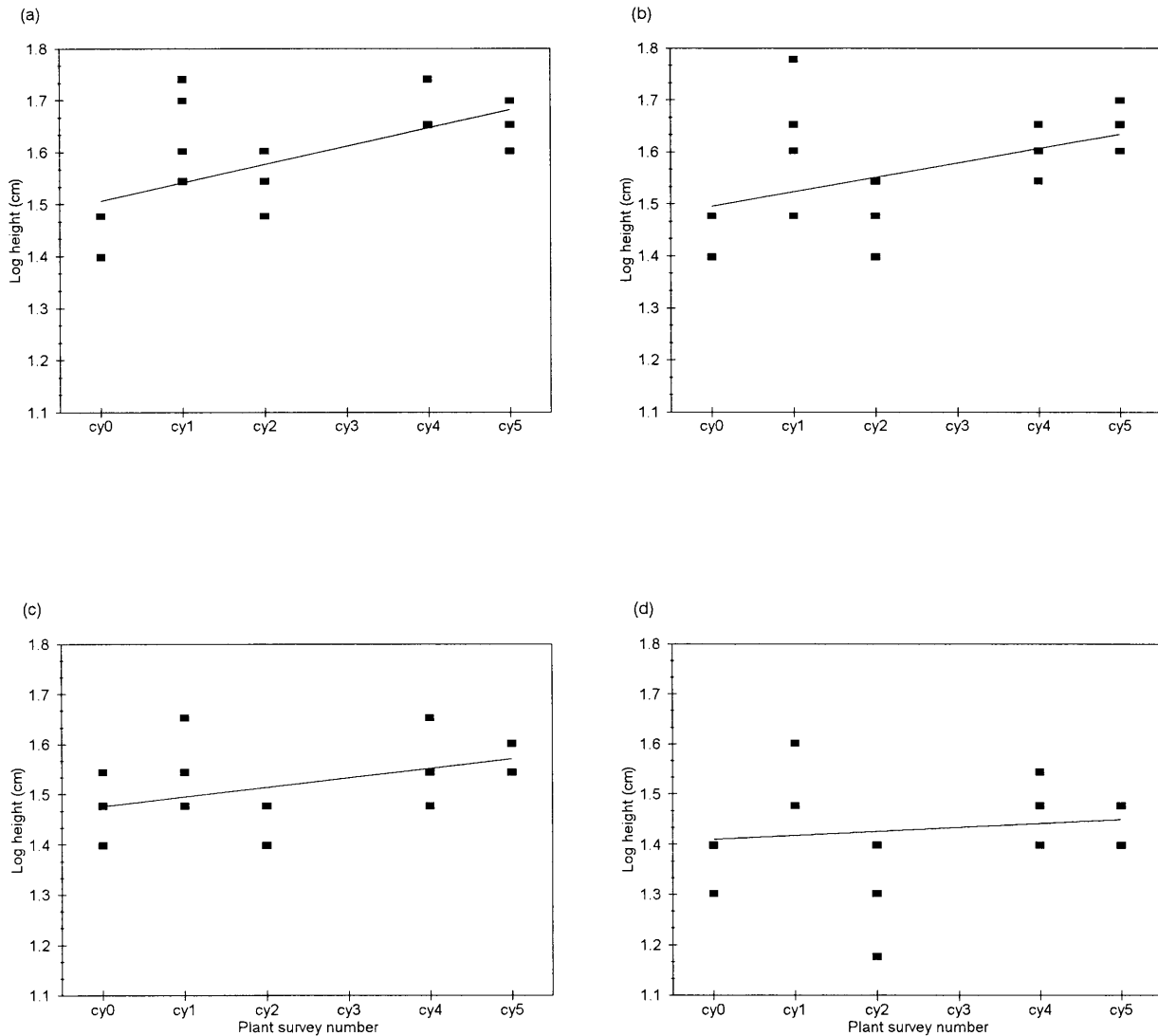


Figure 14. Log₁₀ height of the herbaceous layer over 5 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. The lines were fitted through least squares linear regression on the mean values per survey and can be described by (a): $y = 1.45 + 0.05x$ ($p=0.17$), $r^2 = 0.53$ ($p=0.17$); (b): $y = 1.46 + 0.03x$ ($p=0.26$), $r^2 = 0.39$ ($p=0.26$); (c): $y = 1.45 + 1.06x$ ($p=0.32$), $r^2 = 0.32$ ($p=0.32$) and (d): $y = 1.40 + 2.54x$ ($p=0.81$), $r^2 = 0.02$ ($p=0.81$).

Table 15. The mean (\pm standard error) height of the herbaceous layer in four treatment levels over 5 surveys. Data on vegetation height were not collected during survey 4. n=4 in all cases. Based on data in Appendix 5.

| Treatment level | Survey number | | | | |
|-----------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| | Survey 1 | Survey 2 | Survey 3 | Survey 5 | Survey 6 |
| Control | 27.50 \pm 1.44 (10.50) | 45.00 \pm 4.56 (20.29) | 35.00 \pm 2.04 (11.66) | 47.50 \pm 2.50 (10.53) | 45.00 \pm 2.04 (9.07) |
| Low | 28.75 \pm 1.25 (8.70) | 43.75 \pm 6.25 (28.57) | 30.00 \pm 2.04 (13.61) | 41.25 \pm 2.39 (11.61) | 43.75 \pm 2.39 (10.94) |
| Medium | 30.00 \pm 2.04 (13.61) | 36.25 \pm 3.15 (17.36) | 27.50 \pm 1.44 (10.50) | 36.25 \pm 3.15 (17.36) | 38.75 \pm 1.25 (6.45) |
| High | 23.75 \pm 1.25 (10.53) | 35.00 \pm 2.89 (16.50) | 21.25 \pm 2.39 (22.53) | 28.75 \pm 2.39 (16.65) | 28.75 \pm 1.25 (8.70) |

interaction between time and treatment level (MANOVAR, Table 16). ANOVAR showed a significant difference between treatment levels and over time, but no time-treatment level interaction (Table 16). Tukey's HSD over all surveys showed that control differed significantly from the high treatment level ($\text{msd}_{(p=0.05, df=20)} = 12.101$). In survey 3 control and high treatment levels differed significantly ($\text{msd}_{(p=0.05, df=12)} = 8.44$), in survey 5 control differed from both medium and high and low from high ($\text{msd}_{(p=0.05, df=12)} = 11.03$) and in survey 6 high differed from all other treatment levels ($\text{msd}_{(p=0.05, df=12)} = 11.03$).

Table 16. Results from a MANOVAR and ANOVAR test for differences in the vegetation height between four levels of treatment over five surveys. (n=4). Roy's GR is Roy's Greatest Root; G-G adj. p is the probability for ANOVAR, adjusted with the Greenhouse-Geisser $\epsilon = 0.56$ (Von Ende 1993). Based on data in Appendix 5.

| Test | Effect | Roy's GR | F | p | G-G adj. p |
|-----------|--------------------|----------|----------|--------|------------|
| MANOVAR | Survey | 18.64 | 41.94*** | <0.001 | - |
| | Survey x Treatment | 2.68 | 7.38** | 0.004 | - |
| ANOVAR | Treatment | - | 16.74*** | <0.001 | - |
| | Survey | - | 22.34*** | <0.001 | <0.001 |
| | Survey x Treatment | - | 1.31 | 0.24 | 0.26 |
| Linear | Survey | - | 53.15‡ | <0.001 | - |
| | Survey x Treatment | - | 4.70‡ | 0.02 | - |
| Quadratic | Survey | - | 1.37 | 0.25 | - |
| | Survey x Treatment | - | 2.16 | 0.15 | - |

‡ = significance at $p=0.025$ (Bonferoni adjustment); ** = significance at $p=0.01$; *** = significance at $p=0.001$

The regression of time (survey number) against height was not significant for any of the treatment levels, neither did the regression coefficients differ significantly from each other over all treatment levels ($F_s=0.41$, $p=0.75$).

Multiple response variables: species richness and vegetation cover

The results of the MANOVA for multiple response variables is given in Table 17. There was a statistically significant difference between treatment levels only in survey 3. This difference was mainly due to the two variables number of species per pin and herbaceous cover, in both of which cases it was the control which differed from the high treatment level (Tukey's HSD; $msd_{\text{species per pin}} = 0.43$, $msd_{\text{herbaceous cover}} = 17.36$).

SPECIES COMPOSITION OF THE HERBACEOUS COMMUNITY

Total species numbers

A total of 92 species were recorded in quadrats (Appendix 1) in all experimental paddocks over all surveys, 77 of which were also recorded with the point-bridge (species presence at a pin). When the analysis is based on species presence at a pin, the total number of species is 83 (Appendix 1). The total number of species in both quadrats and pins over all surveys and including all treatment levels is 98. Woody species made up 33% of the total number of species, although a large part of these were sprawling woody shrubs rather than trees (for e.g. *Scutia myrtina*, *Rhus natalensis*, *R. nebulosa*, *Grewia caffra* and *Carissa bispinosa*).

Similarity in species composition between surveys (time), treatment paddocks, and blocks of treatment paddocks.

A multi-dimensional scaling of all the paddocks over all surveys (Fig. 15) shows the relationship between change in community composition over time and change due to treatment level. Although the stress value is relatively high (0.22), it is still possible to see that the pattern was

Table 17. Results from MANOVA tests for differences between four levels of treatment in six surveys, using the variables species per pin (sp/pin), species per quadrat (sp/q), species per paddock (sp/padd), herbaceous cover (herb cov) and ground cover (grnd cov) as multiple response variables. Species per pin, herbaceous cover and ground cover was not measured during survey 4. (n=4). Based on data in Appendix 5.

| Survey no. | Overall treatment effect | | | Single variable | | | | | | | | | |
|------------|--------------------------|-------|------|-----------------|------|------|------|---------|------|----------|------|----------|------|
| | Pillai's trace | F | p | sp/pin | | sp/q | | sp/padd | | herb cov | | grnd cov | |
| | | | | F | p | F | p | F | p | F | p | F | p |
| 1 | 0.74 | 0.66 | 0.80 | 0.53 | 0.67 | 0.46 | 0.72 | 0.62 | 0.62 | 0.91 | 0.46 | 0.28 | 0.84 |
| 2 | 0.68 | 0.59 | 0.86 | 0.13 | 0.94 | 1.55 | 0.25 | 1.68 | 0.22 | 0.18 | 0.91 | 0.72 | 0.56 |
| 3 | 1.58 | 2.23* | 0.03 | 3.74* | 0.04 | 0.94 | 0.45 | 1.23 | 0.34 | 4.41* | 0.03 | 2.98 | 0.07 |
| 4 | 0.34 | 0.83 | 0.56 | - | - | 1.32 | 0.31 | 1.45 | 0.28 | - | - | - | - |
| 5 | 0.83 | 0.77 | 0.70 | 2.14 | 0.15 | 2.13 | 0.15 | 1.84 | 0.19 | 2.15 | 0.15 | 2.30 | 0.13 |
| 6 | 1.06 | 1.09 | 0.41 | 3.16 | 0.06 | 1.17 | 0.36 | 1.60 | 0.24 | 2.58 | 0.10 | 2.41 | 0.12 |

* = significance at p=0.05

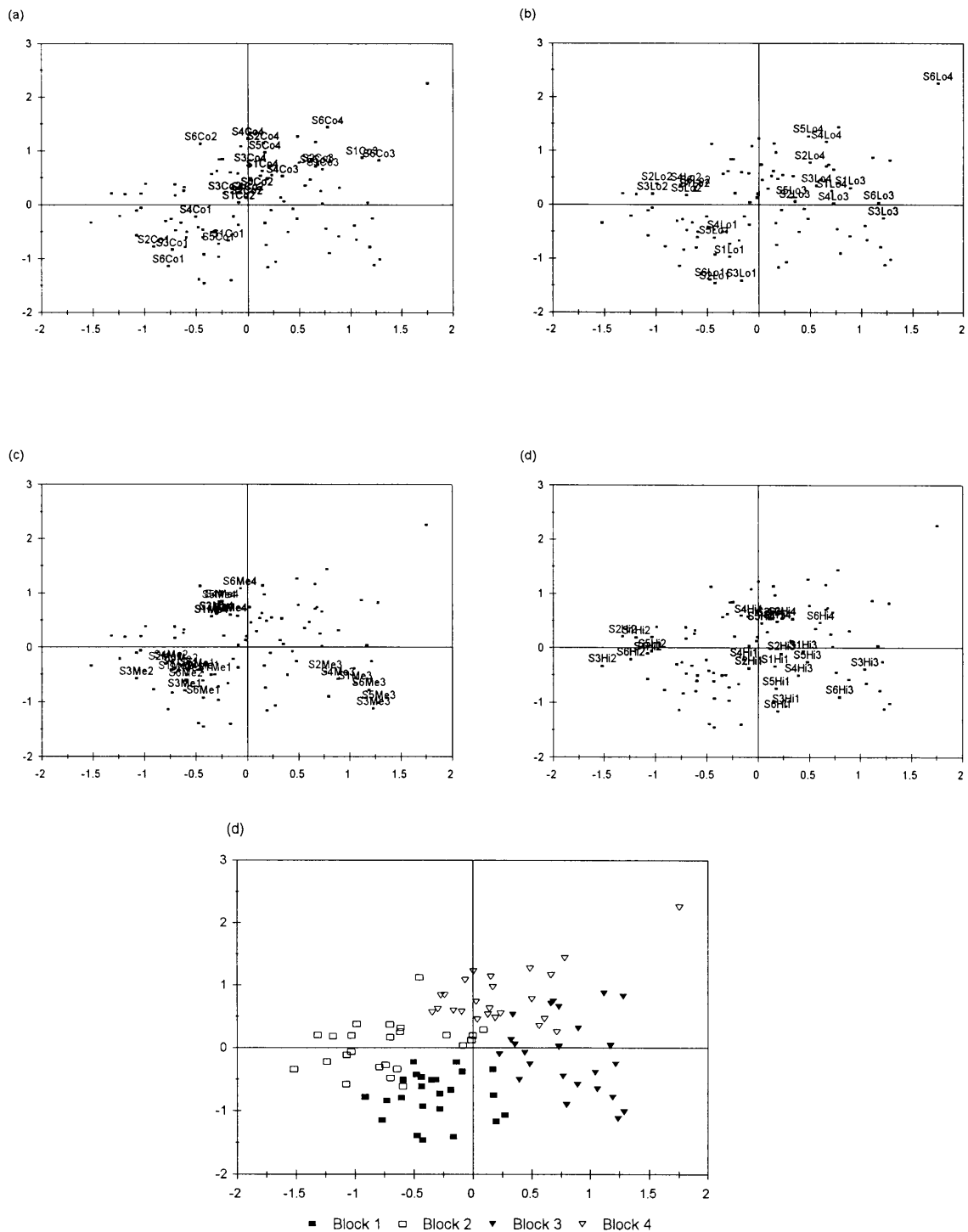


Figure 15. Multiple dimensional scaling (MDS) of all paddocks over all surveys with the control, low, medium and high paddocks labelled in figures (a), (b), (c) and (d) respectively. Figure (e) represents the same MDS with the paddocks labelled according to the block in which it was situated. Stress = 0.22. Based on plant species' relative occurrence in a 1m² quadrat. The letter "S" followed by a number is the survey number; Co = control, Lo = low, Me = medium and Hi = high (treatment level codes). The number following the treatment-level code is the block number.

dominated by site differences. Paddocks from each block of treatment paddocks (four different treatment levels, see also Fig. 3) grouped closer together than paddocks from the same treatment level but from different blocks. Aside from one outlier in survey 6 (paddock no. 4 in the low treatment level) there were no large shifts in the paddocks' similarity to either their original species composition or to the composition of adjacent paddocks. The dominance of the effect of site on the species composition of a paddock is illustrated by Figure 17. When the mean similarity of all the paddocks within all blocks is plotted against time together with the mean similarity of all paddocks within all treatment levels, it is evident that the changes in similarity between blocks were mirrored by changes in similarity between treatment paddocks (Fig. 17). The mean similarity between blocks in a specific survey was also higher than between treatment paddocks.

However, some change in the species composition under the influence of grazing is visible if the different surveys are analysed separately. At the time of survey 1 the paddocks within each treatment block clustered together closer (except for the outlier Lo4) than those from the same treatment level, but from different blocks (Fig. 16). This pattern changes so that by the time of survey 6, it is easier to confidently draw a line around the paddocks that belong to a specific treatment, rather than those from a specific block. Stress values were relatively high in some of the surveys (Fig. 16).

The mean similarity between the control paddocks seems to have stayed the same over all the surveys, while mean similarity for the other treatment levels apparently declined at different rates (Fig. 18). However, the regression coefficients were not significantly different from zero, nor were the differences between the coefficients significant (slopes ranged between -1.56 to -0.11, all p -values > 0.05 ; all r^2 -values ≤ 0.37 , all $p > 0.05$; $F_s = 0.35$, $p = 0.79$). Bray-Curtis similarity values are given in Appendix 6.

The mean similarity of the control paddocks (at each survey) to their average initial species composition declined at a faster rate than was the case for the other treatment levels (Fig. 19). The relationship between time and similarity to initial composition was significant for control ($y = 94.06 - 3.57x$, $p = 0.05$; $r^2 = 0.79$, $p = 0.05$) and low ($y = 86.66 - 1.51x$, $p = 0.01$; $r^2 = 0.93$, $p = 0.01$)

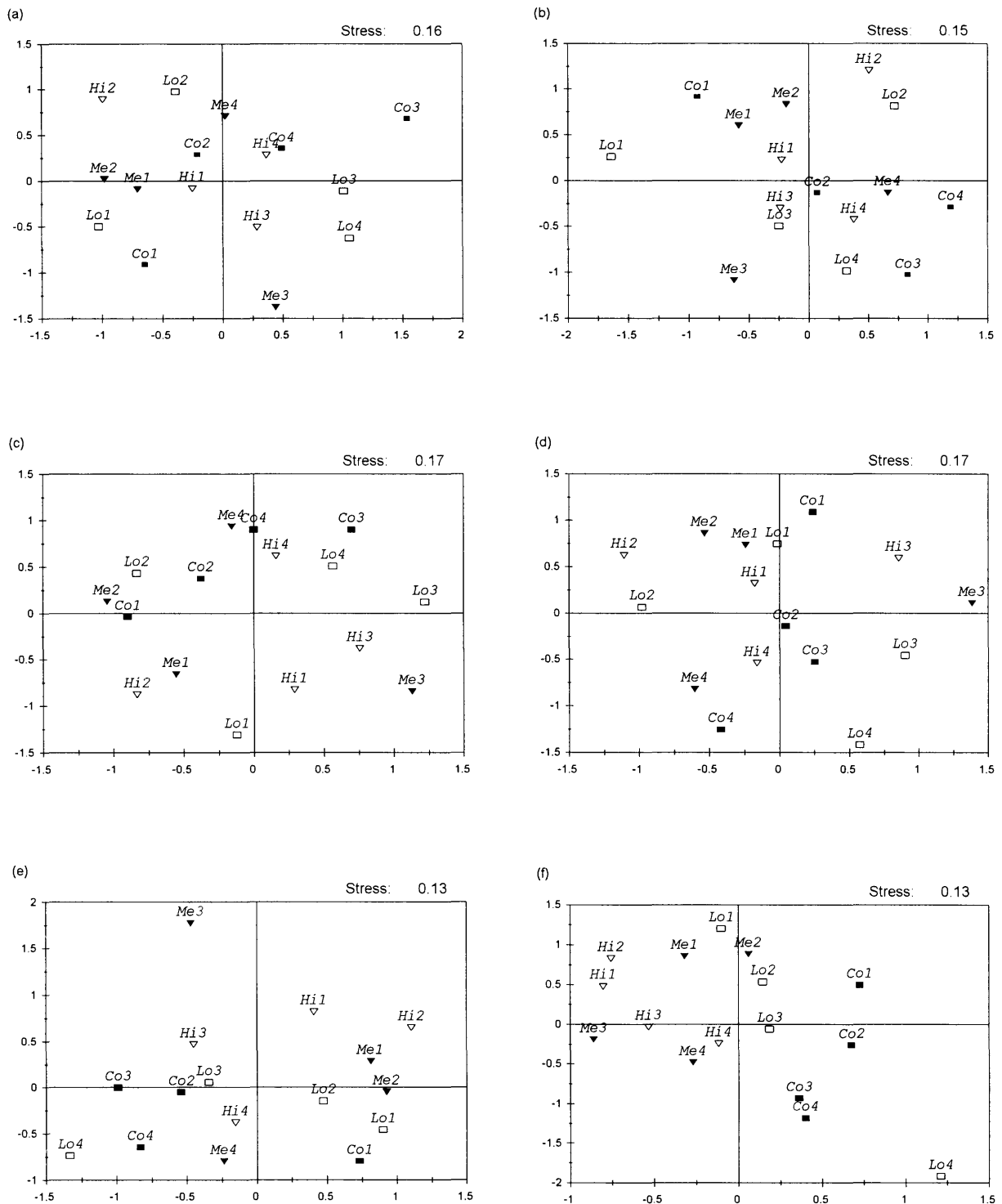


Figure 16. Multiple dimensional scaling (MDS) of all paddocks for each survey: survey 1 (a), survey 2 (b), survey 3 (c), survey 4 (d), survey 5 (e) and survey 6 (f). Based on plant species' relative occurrence in a 1m² quadrat. Treatment level codes: Co = control, Lo = low, Me = medium and Hi = high treatment level. The number following the treatment-level code is the block number.

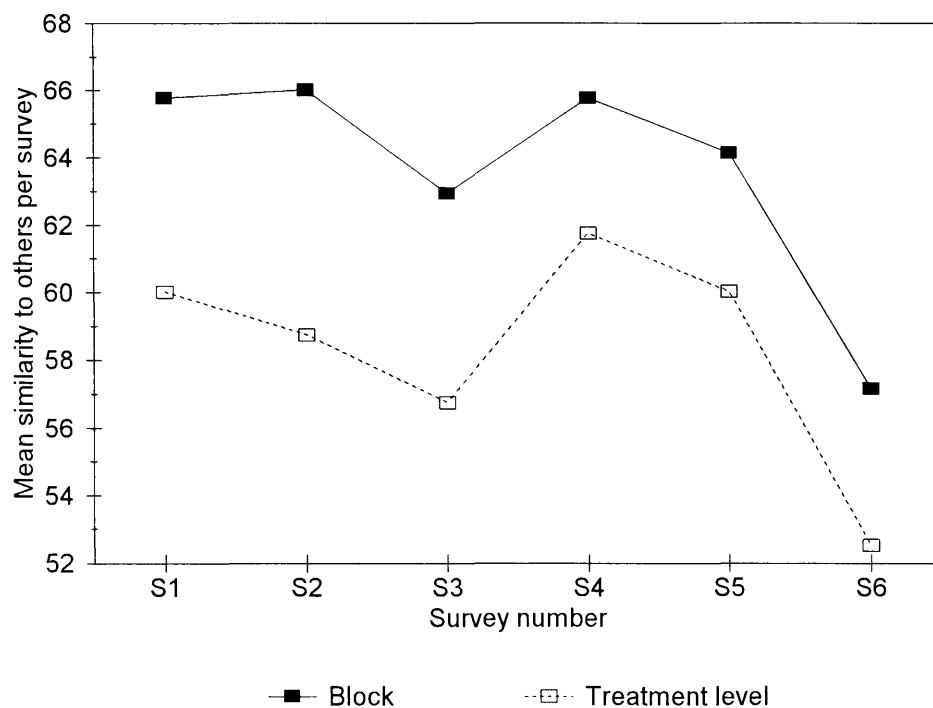


Figure 17. Bray-Curtis similarity of paddocks (in six surveys) to other paddocks of the same treatment level (with the mean calculated over all blocks) or the same block (with the mean calculated over all treatment levels).

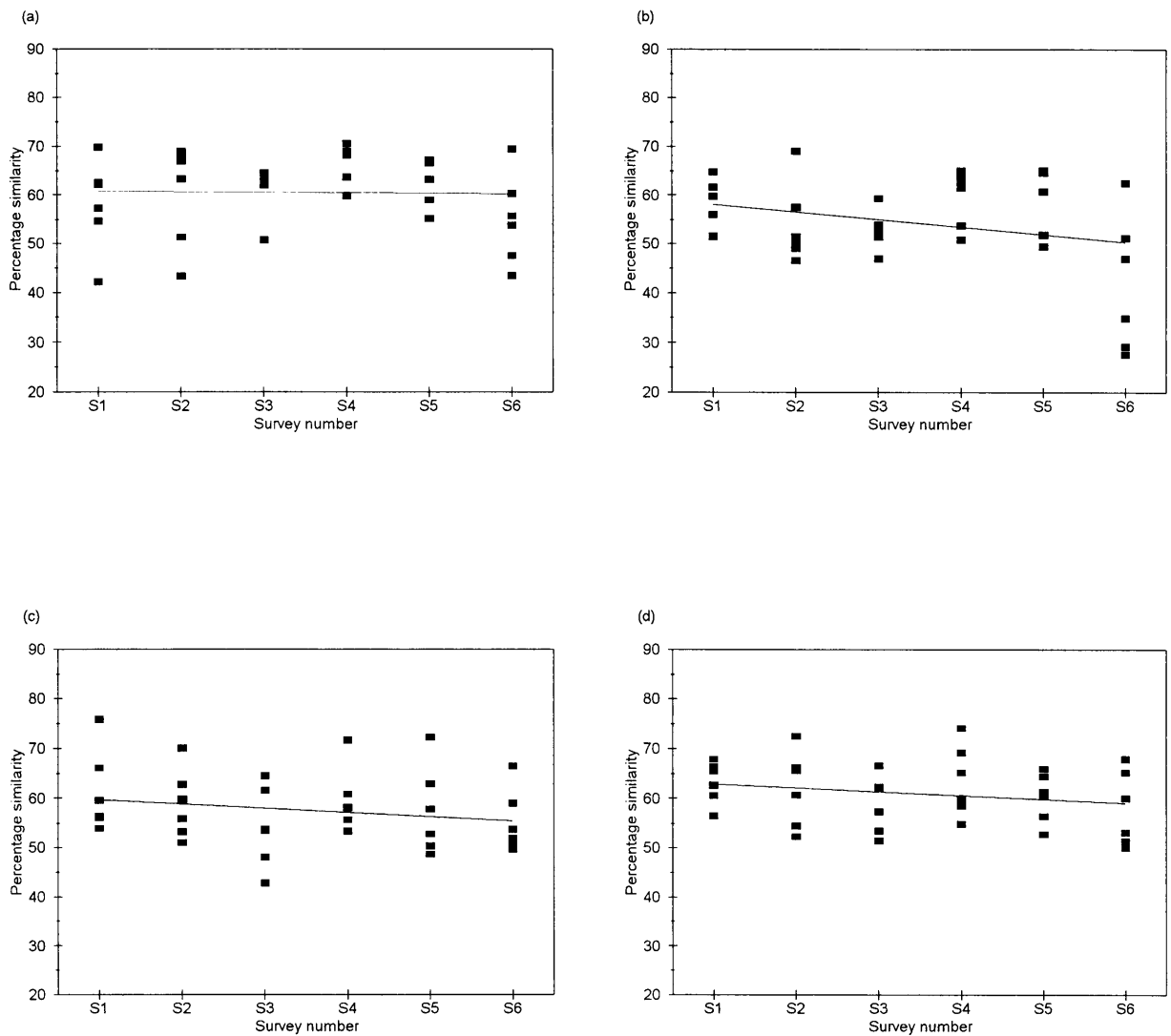


Figure 18. Bray-Curtis similarity of treatment paddocks to other paddocks of the same treatment level in each survey for the control (a), low (b), medium (c) and high (d) treatment paddocks. Based on plant species' presence in a 1m² quadrat. The lines were fitted through least squares linear regression to the mean values per survey and can be described by (a): $y = 60.85 - 0.11x$ ($p=0.92$), $r^2 = 0.003$ ($p=0.92$); (b): $y = 59.65 - 1.56x$ ($p=0.38$), $r^2 = 0.20$ ($p=0.38$); (c): $y = 60.52 - 0.85x$ ($p=0.21$), $r^2 = 0.35$ ($p=0.21$) and (d): $y = 63.64 - 0.76x$ ($p=0.20$), $r^2 = 0.37$ ($p=0.20$).

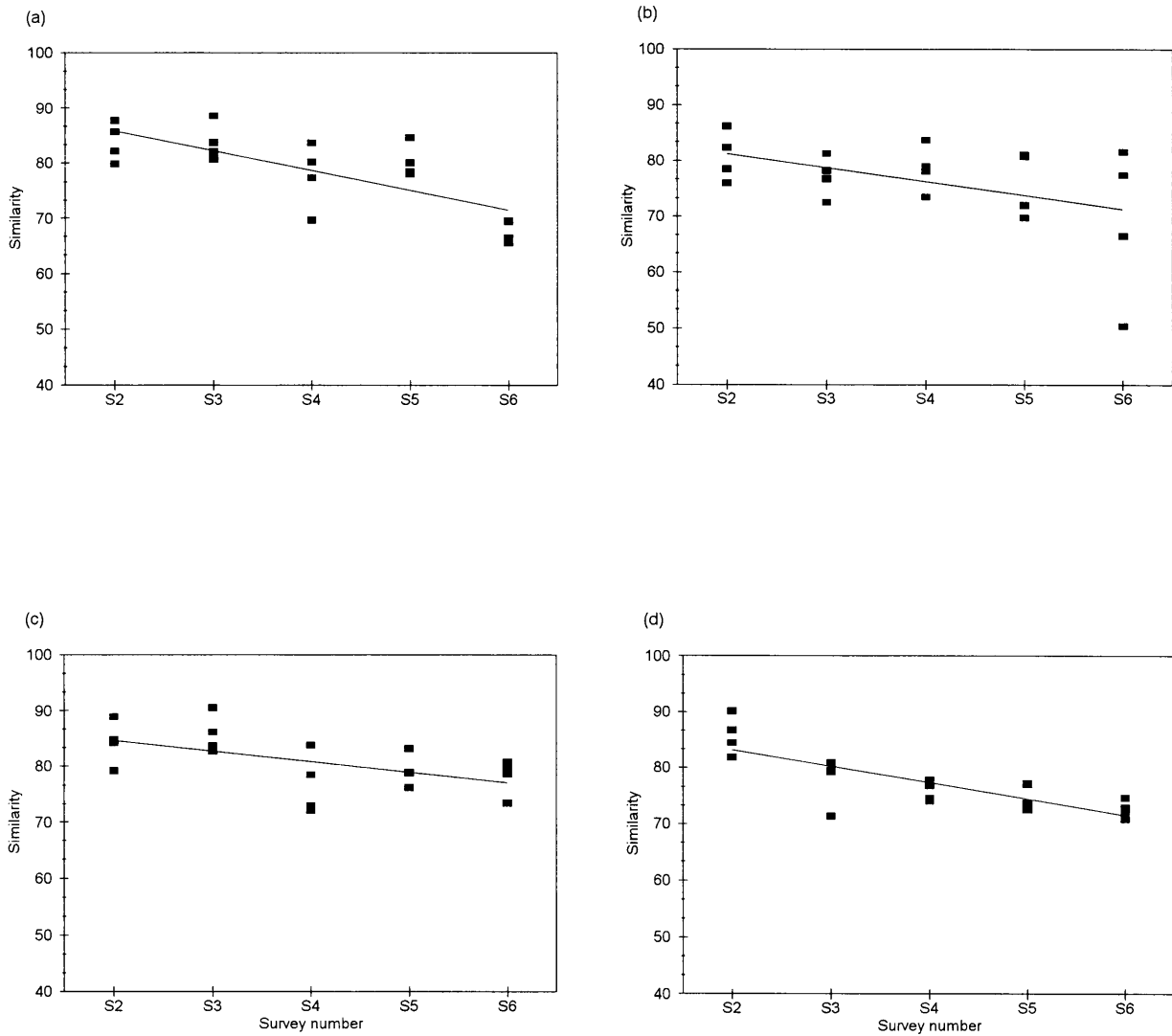


Figure 19. Bray-Curtis similarity of treatment paddocks to their average initial species composition for the control (a), low (b), medium (c) and high (d) treatment paddocks. Based on plant species' presence in a 1m² quadrat. The lines were fitted through least squares linear regression to the mean values per survey and can be described by (a): $y = 94.06 - 3.57x$ ($p=0.05$), $r^2 = 0.79$ ($p=0.05$); (b): $y = 86.66 - 1.51x$ ($p=0.01$), $r^2 = 0.93$ ($p=0.01$); (c): $y = 89.45 - 1.56x$ ($p=0.25$), $r^2 = 0.41$ ($p=0.25$) and (d): $y = 86.40 - 2.15x$ ($p=0.08$), $r^2 = 0.71$ ($p=0.08$).

treatment levels, although there were no overall significant differences between the regression coefficients ($F_s=1.22$, $p=0.35$). Bray-Curtis similarity values are given in Appendix 7.

Analysis of similarity supported the pattern seen in the MDS. There were no significant differences between either the treatment levels (two way crossed ANOSIM; $R= -0.004$, $p=0.52$) or the different surveys ($R= -0.09$, $p=0.98$). There were also no significant differences between the treatment levels within any of the surveys when tested with one-way ANOSIM (Global R -values ranged from -0.11 to 0.11 , all p -values >0.05). However, the blocks of treatment paddocks differed significantly in all of the surveys. The pairs of blocks situated closest to each other (blocks 1 and 2) were never significantly different, while blocks situated further away from each other were different most of the time (one-way ANOSIM; Table 18).

Table 18. Results of an analysis of similarity between blocks of treatment paddocks (see Fig. 3 for description of blocks and paddocks) in 6 surveys. (n=4).

| Statistic | Survey 1 | Survey 2 | Survey 3 | Survey 4 | Survey 5 | Survey 6 |
|--|----------------|----------------|----------------|----------------|----------------|----------------|
| Global R | 0.53*** | 0.51*** | 0.61*** | 0.50*** | 0.46*** | 0.45*** |
| p | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | 0.001 |
| Pairwise tests: test statistic R with probability in parentheses | | | | | | |
| Block1 : Block2 | 0.25 (p=0.06) | 0.19 (p=0.11) | 0.24 (p=0.143) | -0.03 (p=0.57) | -0.02 (p=0.51) | 0.13 (p=0.23) |
| Block1 : Block3 | 0.57 (p=0.03)* | 0.55 (p=0.03)* | 0.62 (p=0.03)* | 0.57 (p=0.03)* | 0.56 (p=0.03)* | 0.55 (p=0.03)* |
| Block1 : Block4 | 0.78 (p=0.03)* | 0.85 (p=0.03)* | 0.89 (p=0.03)* | 0.81 (p=0.03)* | 0.91 (p=0.03)* | 0.63 (p=0.03)* |
| Block2 : Block3 | 0.79 (p=0.03)* | 0.55 (p=0.03)* | 0.79 (p=0.03)* | 0.67 (p=0.03)* | 0.31 (p=0.11) | 0.54 (p=0.03)* |
| Block2 : Block4 | 0.43 (p=0.03)* | 0.49 (p=0.06) | 0.64 (p=0.03)* | 0.52 (p=0.03)* | 0.46 (p=0.09) | 0.59 (p=0.03)* |
| Block3 : Block4 | 0.40 (p=0.06) | 0.48 (p=0.03)* | 0.53 (p=0.03)* | 0.55 (p=0.03)* | 0.50 (p=0.03)* | 0.35 (p=0.089) |

* = significance at p=0.05; *** = significance at p=0.001

UNDERSTOREY WOODY PLANTS

Of all the univariate variables measured (number of species per paddock, density, crown volume, reason for replacement, direction of change in height and attrition rate) it was only number of species per paddock, density and attrition rate which were normally distributed and homoscedastic. These were therefore tested for differences using ANOVA and linear regression, while the rest was either not tested or tested with non-parametric tests.

Number of sapling species per paddock and per survey

Grazing had very little influence on the number of sapling species per paddock, but values declined slightly over time in most of the paddocks (Fig. 20, Table 19a). Coefficients of variation in control and low treatment levels seemed to stay about the same over time, while CV's in medium and high showed an increasing trend (Table 19a). The regression of time on species number was significant for the control ($y=11.93-0.18x$, $p=0.01$; $r^2=0.94$, $p=0.01$), low ($y=12.33-0.43x$, $p=0.01$; $r^2=0.94$, $p=0.01$) and high ($y=14.18-0.38x$, $p=0.03$; $r^2=0.84$, $p=0.03$) treatment levels, but not for medium. The regression coefficients did not differ significantly from each other ($F_s=1.81$, $p=0.20$). In total (over all treatment levels) there were 39 species in survey 1, 38 in survey 2, 40 in survey 3, 39 in survey 5 and 37 in survey 6.

Treatment level did not have a significant effect within any of the individual survey cycles (one-way ANOVA; all F -values ≤ 1.10 , all p -values > 0.05). However, the treatment levels were significantly different when tested with two-way ANOVA without replication ($F=45.70$, $p < 0.001$). Tukey's HSD showed that the high treatment levels differed significantly from all the others, but none of the other treatments differed from each other (Tukey's HSD; $msd_{\text{species per paddock}} = 0.61$).

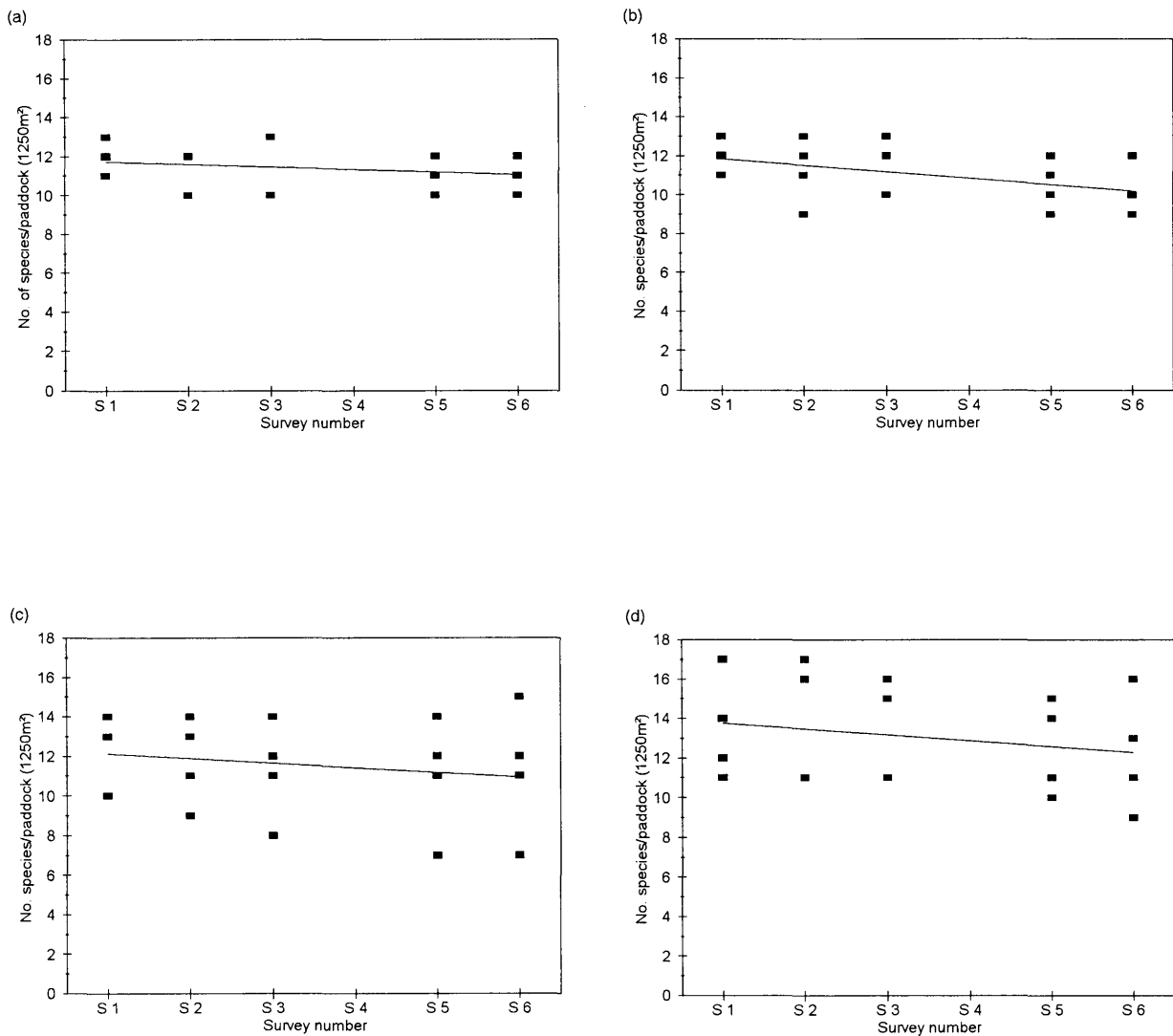


Figure 20. Number of sapling species paddock over 6 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. For logistic reasons the number of sapling species per paddock were not recorded during survey 4. The lines were fitted through least squares linear regression on the mean values per survey and can be described by (a): $y = 11.93 - 0.18x$ ($p=0.01$), $r^2 = 0.94$ ($p=0.01$); (b): $y = 12.33 - 0.43x$ ($p=0.01$), $r^2 = 0.94$ ($p=0.01$); (c): $y = 12.53 - 0.33x$ ($p=0.06$), $r^2 = 0.74$ ($p=0.06$) and (d): $y = 14.18 - 0.38x$ ($p=0.03$), $r^2 = 0.84$ ($p=0.03$).

Table 19. Mean (\pm standard error) number of sapling species per paddock (a), mean (\pm standard error) density (trees/ha \times 1000) of sapling trees per paddock (b), and the mean (\pm standard error) crown volume ($\text{cm}^3 \times 1000$) of sapling trees per paddock (c) in four treatment levels over five surveys. Coefficient of variation (%) is given in parentheses. Crown volume was not measured during survey 1 and none of the three variables were measured during survey 4. Based on data in Appendix 8.

| | Survey 1 | Survey 2 | Survey 3 | Survey 5 | Survey 6 |
|-----------------------------------|-----------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| (a) Number of species per paddock | | | | | |
| Control | 11.75 \pm 0.48 (8.15) | 11.50 \pm 0.50 (8.70) | 11.50 \pm 0.87 (15.06) | 11.25 \pm 0.48 (8.51) | 11.00 \pm 0.41 (7.42) |
| Low | 12.00 \pm 0.41 (6.80) | 11.25 \pm 0.85 (15.18) | 11.25 \pm 0.75 (13.33) | 10.50 \pm 0.65 (12.30) | 10.25 \pm 0.63 (12.28) |
| Medium | 12.50 \pm 0.87 (13.86) | 11.75 \pm 1.11 (18.87) | 11.25 \pm 1.25 (22.22) | 11.00 \pm 1.47 (26.76) | 11.25 \pm 1.65 (29.37) |
| High | 13.50 \pm 1.32 (19.60) | 13.75 \pm 1.60 (23.28) | 13.25 \pm 1.31 (19.85) | 12.50 \pm 1.19 (19.04) | 12.25 \pm 1.49 (24.38) |
| (b) Density | | | | | |
| Control | 1.96 \pm 0.48 (49.33) | 1.61 \pm 0.56 (69.75) | 1.66 \pm 0.61 (73.64) | 1.24 \pm 0.59 (94.92) | 0.85 \pm 0.31 (71.95) |
| Low | 3.26 \pm 1.46 (89.35) | 2.37 \pm 1.28 (108.09) | 2.38 \pm 1.28 (107.75) | 2.43 \pm 1.64 (134.89) | 2.17 \pm 1.51 (138.62) |
| Medium | 2.95 \pm 1.34 (91.20) | 2.39 \pm 1.21 (101.63) | 2.51 \pm 1.48 (118.16) | 2.14 \pm 1.31 (122.61) | 2.02 \pm 1.20 (118.29) |
| High | 2.58 \pm 0.95 (73.93) | 2.09 \pm 0.85 (80.75) | 2.39 \pm 0.87 (72.55) | 2.17 \pm 0.70 (64.66) | 2.12 \pm 0.79 (74.32) |
| (c) Crown volume | | | | | |
| Control | - | 426.05 \pm 32.95 (15.47) | 570.17 \pm 111.82 (39.22) | 494.00 \pm 60.99 (24.69) | 607.95 \pm 90.90 (29.91) |
| Low | - | 467.29 \pm 155.19 (66.42) | 815.11 \pm 293.09 (71.92) | 626.85 \pm 165.99 (52.96) | 605.14 \pm 136.03 (44.96) |
| Medium | - | 539.54 \pm 161.31 (59.79) | 402.69 \pm 153.12 (76.05) | 507.29 \pm 118.84 (46.85) | 490.97 \pm 89.76 (36.56) |
| High | - | 604.01 \pm 46.94 (15.54) | 624.14 \pm 187.16 (59.97) | 510.07 \pm 61.25 (24.01) | 445.95 \pm 58.61 (26.29) |

Density

Density showed a similar pattern to number of species, in that there was a slight decline over time in some of the treatment levels, but very little difference between the treatments, except for the fact that the control paddocks had less variation than any of the others (Fig. 21, Table 19b). Apart from an apparent increase in the low and medium treatment levels over time, there were no treatment level-dependent patterns visible in the coefficient of variation (Table 19b). The regression of time on density was significant for control ($y=2244.86-259.48x$, $p=0.01$; $r^2=0.92$, $p=0.01$) and medium ($y=3028.43-209.49x$, $p=0.01$; $r^2=0.84$, $p=0.01$) treatment levels. Again there were no significant differences between any of the regression coefficients ($F=1.29$, $p=0.32$).

The effect of treatment level and survey number was highly significant when tested with two-way ANOVA without replication ($F=38.98$, $p<0.001$). Control differed from all the other treatments, but there were no significant differences between any of the others (Tukey's HSD; $msd_{\text{sapling density}} = 358.69$). There were no significant differences between treatment level within the individual survey cycles (all $F\text{-values}\leq 0.36$, all $p\text{-values}>0.05$).

Crown volume

Crown volume increased slightly in control and low, stayed very much at the same average level in the medium treatment level and decreased slightly in the high treatment level (Fig. 22, Table 19c). The coefficient of variation, unlike the case in number of species per paddock, decreased in all treatment levels over time after an initial increase from the second to the third survey (Table 19c). Although a two-way Kruskal-Wallis test showed the effect of treatment level to be highly significant overall ($X^2 = 43.809$, $p < 0.001$), there were no significant differences within any of the individual surveys (all $H\text{-values}\leq 3.46$, all $p\text{-values}>0.05$).

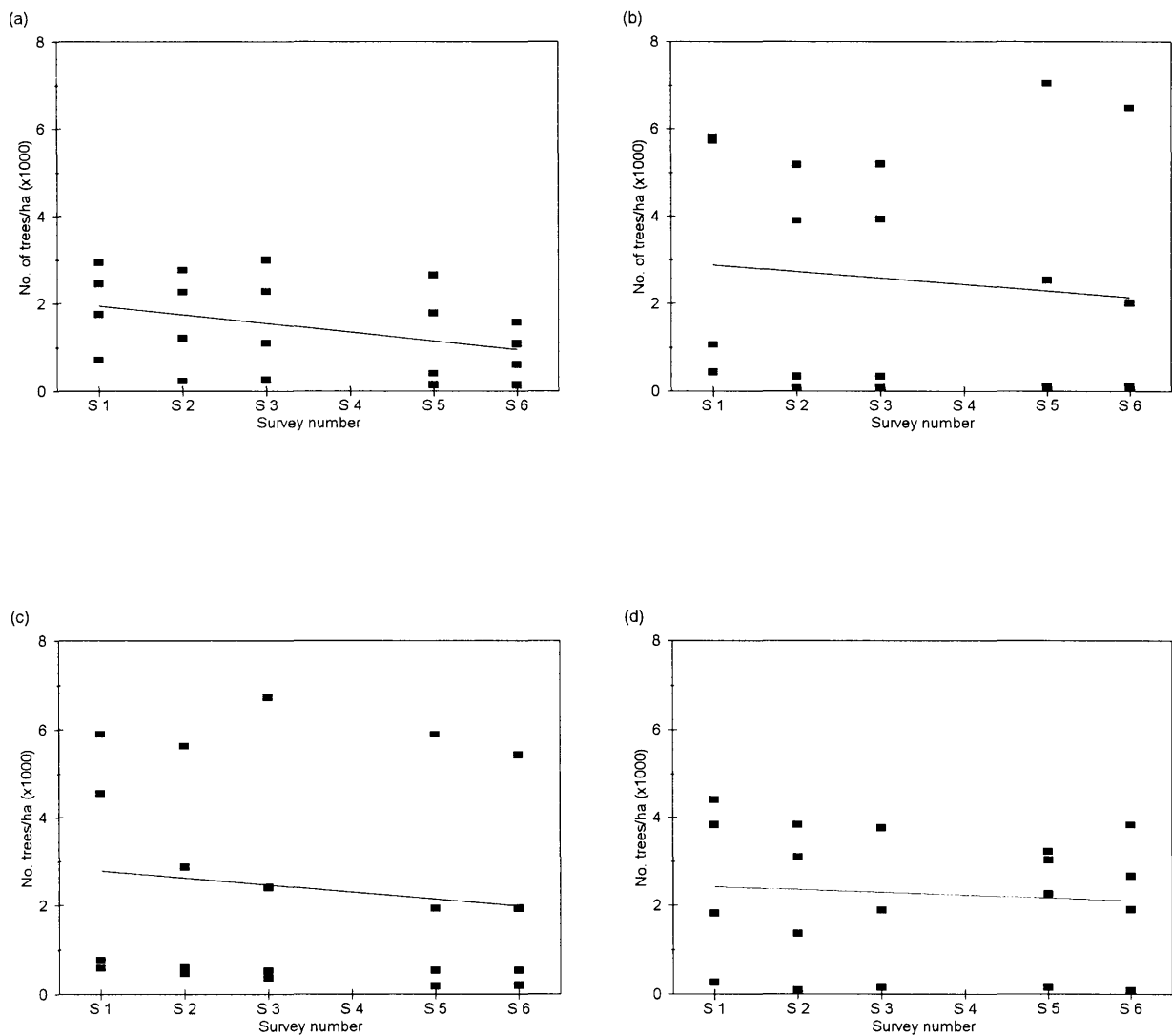


Figure 21. The density of saplings (individual trees/ha) over 6 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. For logistic reasons the density of saplings was not recorded during survey 4. The lines were fitted on the mean values per survey through least squares linear regression and can be described by (a): $y = 2244.86 - 259.48x$ ($p=0.01$), $r^2 = 0.92$ ($p=0.01$); (b): $y = 3154.09 - 210.15x$ ($p=0.11$), $r^2 = 0.62$ ($p=0.11$); (c): $y = 3028.43 - 209.49x$ ($p=0.03$), $r^2 = 0.84$ ($p=0.03$) and (d): $y = 2525.17 - 85.31x$ ($p=0.24$), $r^2 = 0.42$ ($p=0.24$).

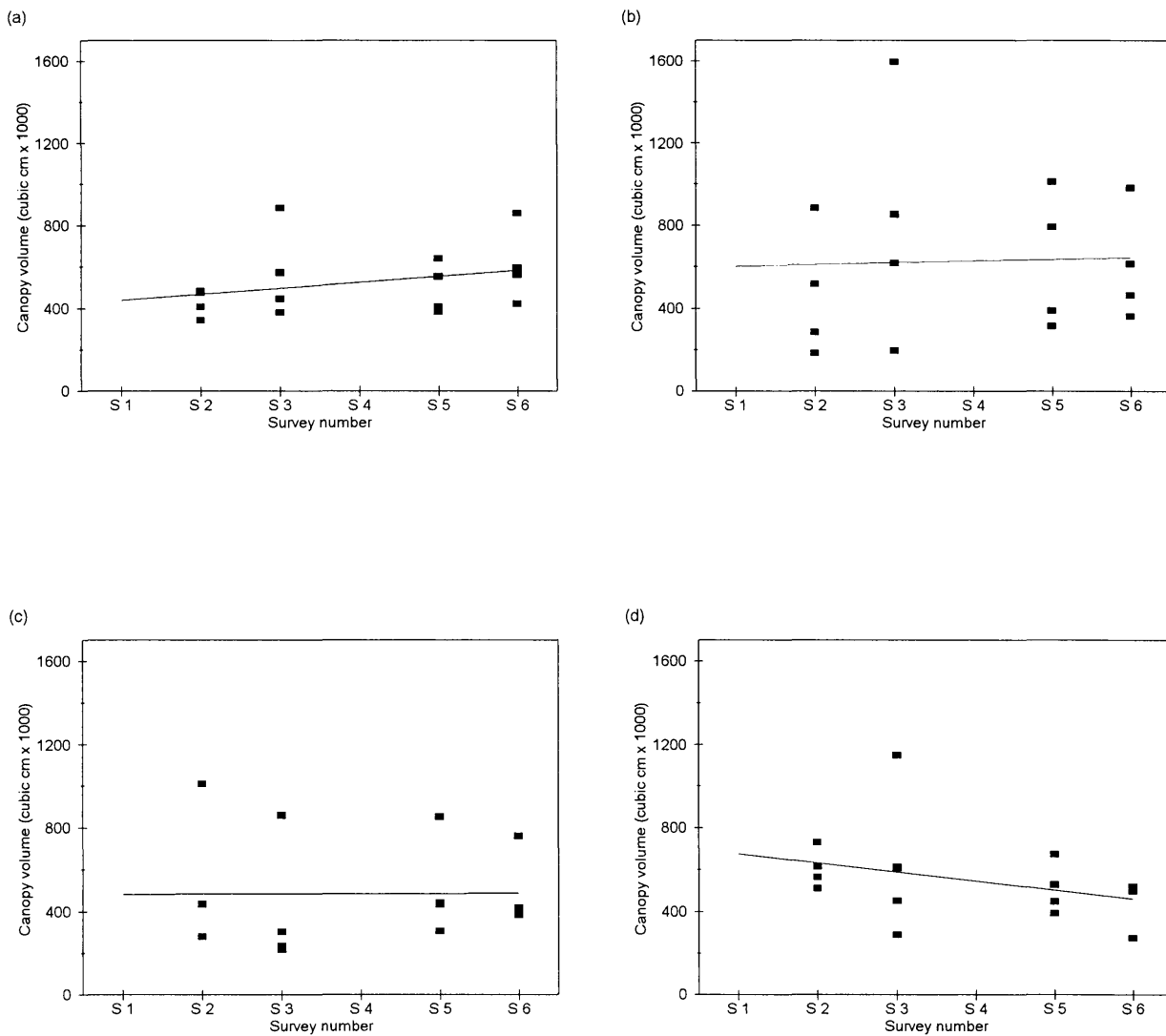


Figure 22. The crown volume (cm^3) of saplings over 4 plant surveys in control (a), low (b), medium (c) and high (d) treatment paddocks. For logistic reasons crown volume was not measured during surveys 1 and 4. The lines were fitted (for descriptive purposes only) on the mean values per survey through least squares linear regression and can be described by (a): $y = 2.34 + 1.51x$, $r^2 = 0.68$; (b): $y = 5.72 + 2.25x$, $r^2 = 0.04$; (c): $y = 4.95 - 4.11x$, $r^2 = 0.01$ and (d): $y = 6.93 - 5.88x$, $r^2 = 0.83$. (All values except r^2 multiply with 10000).

Replacement, direction of changes in height and rate of loss from group

With the exception of the medium treatment, the largest number of changes per treatment level were due to trees growing taller than the upper boundary (Fig. 23a). When taken together with the number of trees entering the group from below (ie. growing taller than the lower boundary), it is clear that most trees were increasing in height, with only relatively few being adversely affected by the cattle. This was supported by the finding that by far the most trees also increased in height between the first and the last survey cycles (Fig. 23b). Multiple G-tests for goodness of fit showed that the treatment levels did not differ significantly in the percentage of trees that increased in height, decreased in height or stayed the same (G-test; all G-values ≤ 3.00 , using a Bonferroni adjusted critical p-value of 0.008).

The total number of changes varied considerably between treatments, but without any pattern (Fig. 23a). In general trees more often increased in height than either decreased in height or were destroyed. This was apparently independent of treatment level, and there were no significant differences between treatment levels when tested with a Kolmogorov-Smirnov two-sample test using a Bonferroni-adjusted probability of 0.008 (all maximum differences ≤ 0.31).

The rate of loss from the original cohort of trees (which was identified before any grazing had taken place), was very similar for all treatments (Fig. 23c). The regressions (time on percentage of original cohort left) were highly significant for all treatments (control: $y=106.56-13.23x$, $p=0.008$, $r^2=0.93$, $p=0.008$; low: $y=109.48-15.52x$, $p=0.005$, $r^2=0.95$, $p=0.005$; medium: $y=111.04-14.17x$, $p=0.002$, $r^2=0.97$, $p=0.002$; high: $y=108.44-14.27x$, $p=0.004$, $r^2=0.96$, $p=0.004$), but there were no significant differences between the regression coefficients ($F_s=0.26$, $p=0.86$).

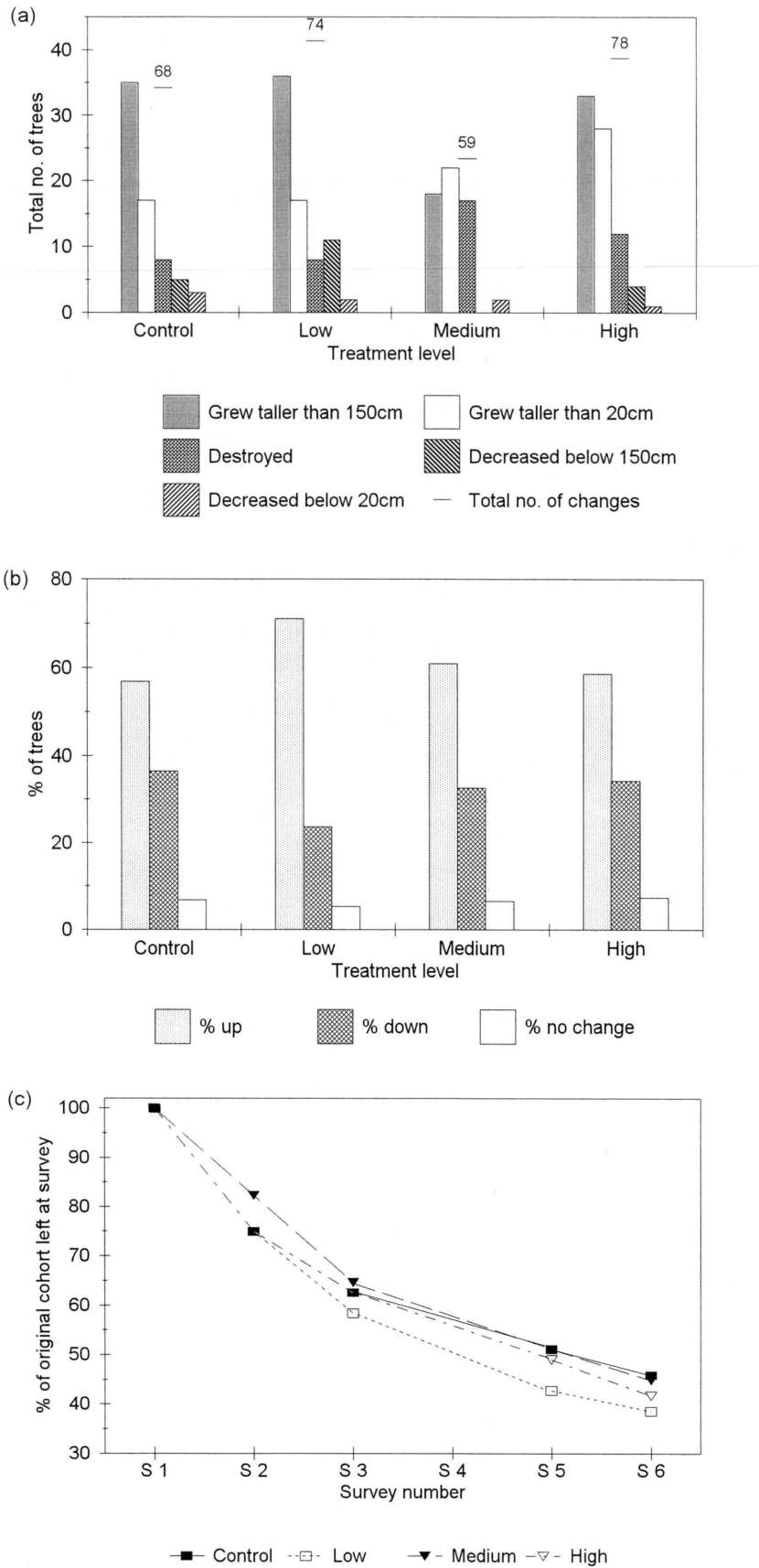


Figure 23. Factors responsible for either a loss from or gain of saplings to the original cohort in four treatment levels - underlined figures are total number of changes (losses and gains) per treatment level (a). Direction of changes in height of saplings in four treatment levels, calculated over all surveys (b). Loss of saplings over six surveys from the original cohort (for four treatment levels) (c).

Height class distribution

The frequency distribution of saplings were much the same between all treatment levels (Fig. 24), with no significant differences between treatment levels, either before or after the application of grazing. However, some of the treatment levels after grazing did differ significantly from before grazing, both within the same level as well as between different levels (Kolmogorov-Smirnov two-sample test; Table 20). In general here it was the high treatment level which tended to differ from the others.

Table 20. Maximum difference and significance output from multiple Kolmogorov-Smirnov two sample tests for goodness of fit between all possible combinations of four treatment levels before (=survey 1) and after (=survey 6) grazing, testing for significant differences in the height class distribution of saplings. There were no significant differences between treatment levels within either survey 1 or survey 6.

| | Control Before | Low Before | Medium Before | High Before |
|---------------|----------------|------------|---------------|-------------|
| Control After | 0.17 | 0.11 | 0.13 | 0.21* |
| Low after | 0.14 | 0.08 | 0.11 | 0.24* |
| Medium after | 0.10 | 0.08 | 0.12 | 0.14 |
| High after | 0.25** | 0.19 | 0.22* | 0.28** |

*=significance at $p=0,05$, **=significance at $p=0.01$

Species composition

Seventy-six woody species (between 20cm and 150cm in height) were identified in all the paddocks over all surveys. A multi-dimensional scaling of all the paddocks over all surveys shows the relationship between change in community composition over time and change due to treatment level (Fig. 25). The stress value of 0.24 is relatively high, suggesting that the two-dimensional representation is not so good (best three-dimensional stress was 0.16). Even so, it is obvious that the pattern is very similar to the MDS of herbaceous species in a 1m² quadrat (see Fig. 15). In general site differences dominated almost to the same extent as in the herbaceous

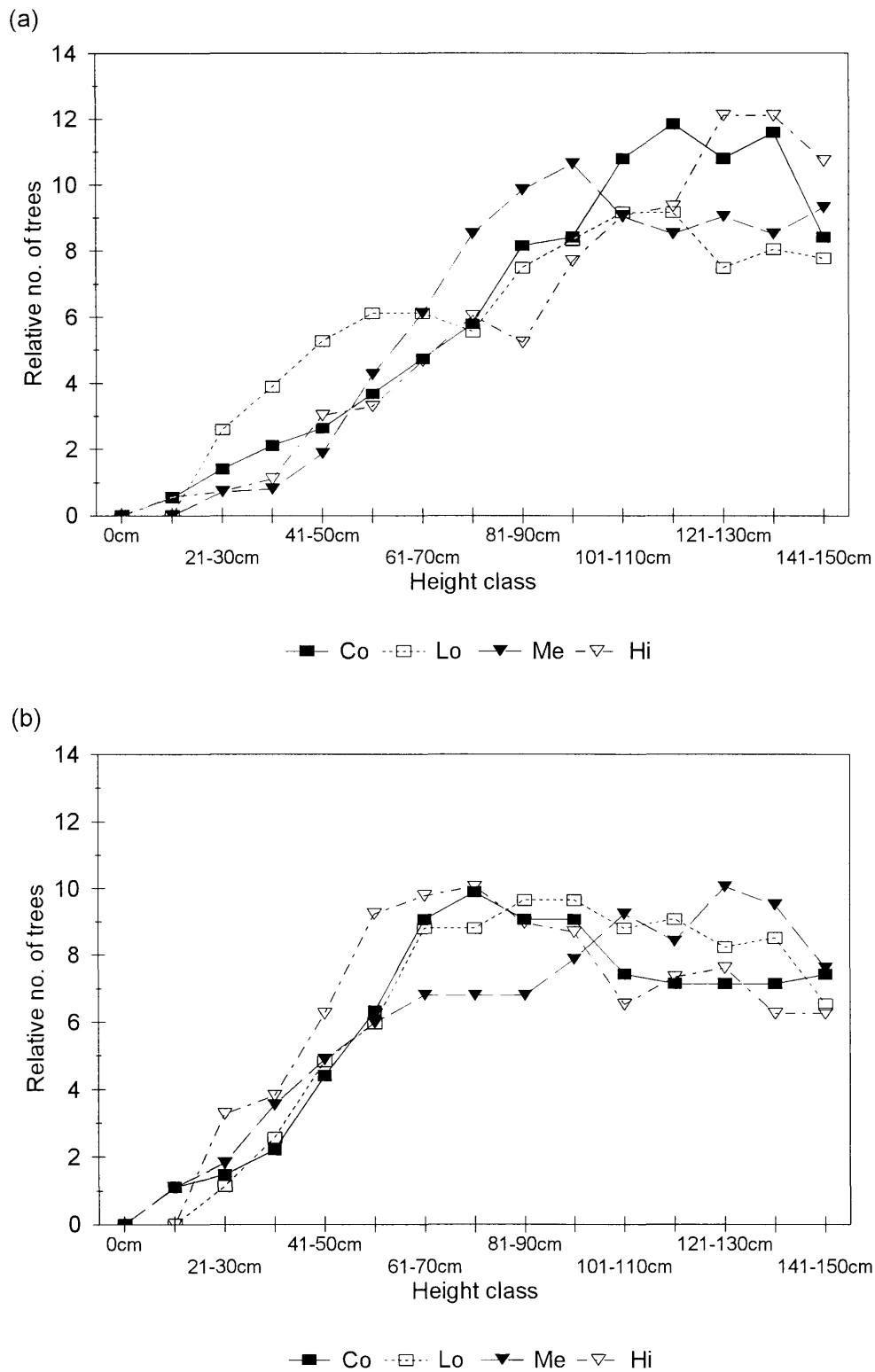


Figure 24. Height class distribution of saplings in four treatment levels before grazing had begun (a) and after the end of the application of grazing (b).

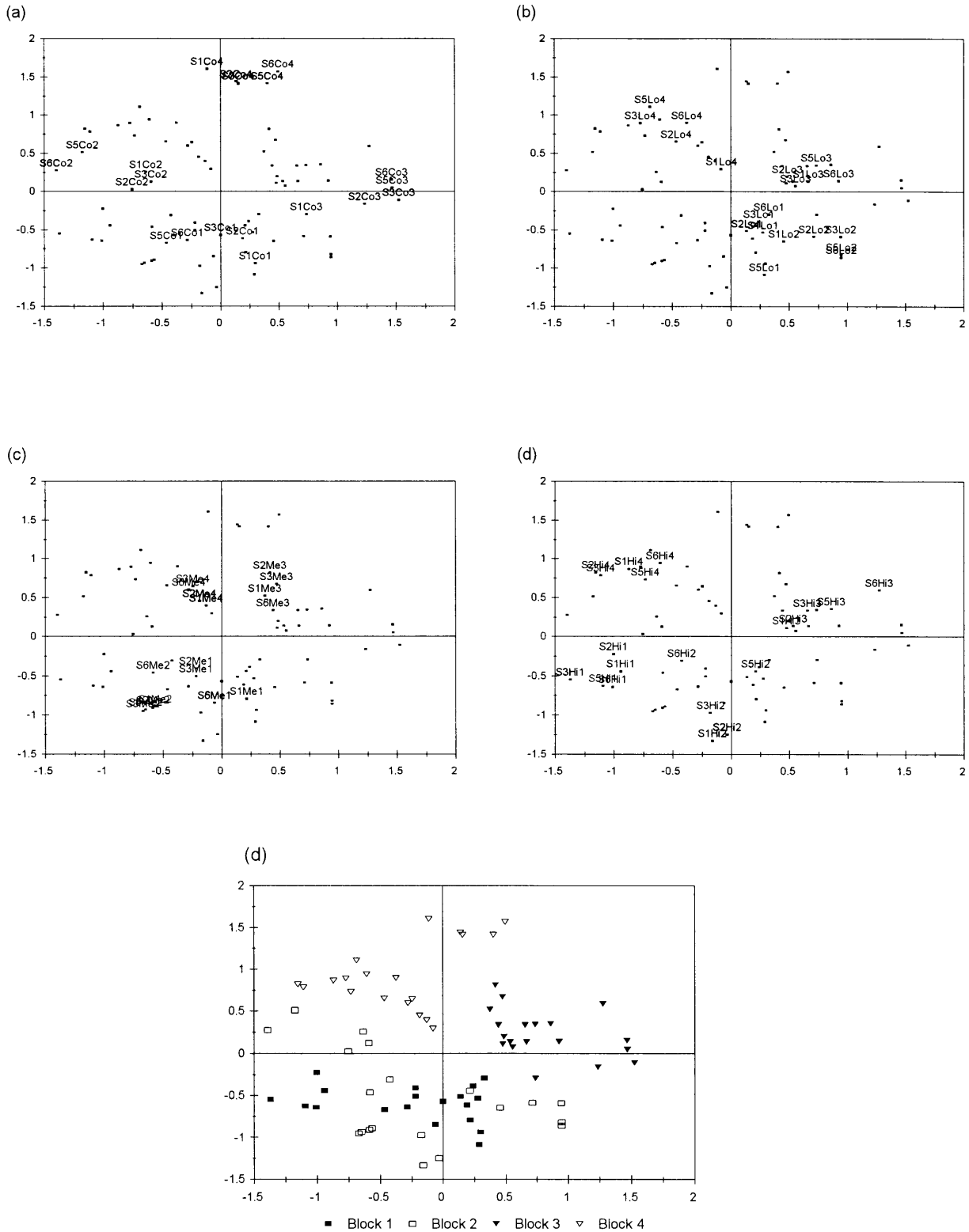


Figure 25. Multiple dimensional scaling (MDS), of all paddocks over all surveys, with the control, low, medium and high paddocks labelled in figures (a), (b), (c) and (d) respectively. Figure (e) represents the same MDS with the paddocks labelled according to the block in which it was situated. Stress = 0.24. Based on sapling presence at a point. The letter "S" followed by a number is the survey number; Co = control, Lo = low, Me = medium and Hi = high (treatment level codes). The number following the treatment-level code is the block number.

species community, although the paddocks from blocks 1 and 2 were much more similar to each other in terms of sapling-species composition than in herbaceous species composition (Fig. 25d). The site-dominance is also apparent in the MDS of each survey (Fig. 26). Paddocks from each block of treatment paddocks continually group closer together than paddocks from the same treatment level, but from different blocks.

Analysis of similarity supported the MDS. There were no significant differences between either survey or treatment level (two-way crossed ANOSIM, Survey: Global $R=-0.24$, $p=0.99$; Treatment level: Global $R=-0.13$, $p=0.99$). There were also no significant differences between the treatment levels within any of the surveys when tested with one-way ANOSIM ® ranged from -1.12 to -0.09, $p>0.05$ in all cases).

PLOT SURVEY OF WOODY PLANTS IN TREATMENT AND CONTROL PADDOCKS

Treatment level had no consistent effect on any of the variables (mean density, mean diameter, mean crown volume, mean number of species per survey block, mean height and mean number of stems) which were measured (Fig. 27). Data were heteroscedastic and were therefore tested with the non-parametric Kruskal-Wallis test. None of the variables showed significant differences between treatment levels in any of the height categories (canopy, sub-canopy, sapling and seedling) (all H -values ≤ 6.90 , all p -values > 0.05). Data on all variables are given in Appendix 9.

The general lack of pattern in the species composition of the woody plants is also reflected in Figure 28. Apart from two paddocks from each treatment level which grouped closer together than expected, there was no real association between either treatment level or site. This was substantiated by one-way ANOSIM which could not show any significant differences in the species composition of the different treatment levels, for any of the classes (sub-canopy: global $R=-0.09$, sapling: global $R=-0.03$, seedling: global $R=0.20$; all p -values > 0.05).

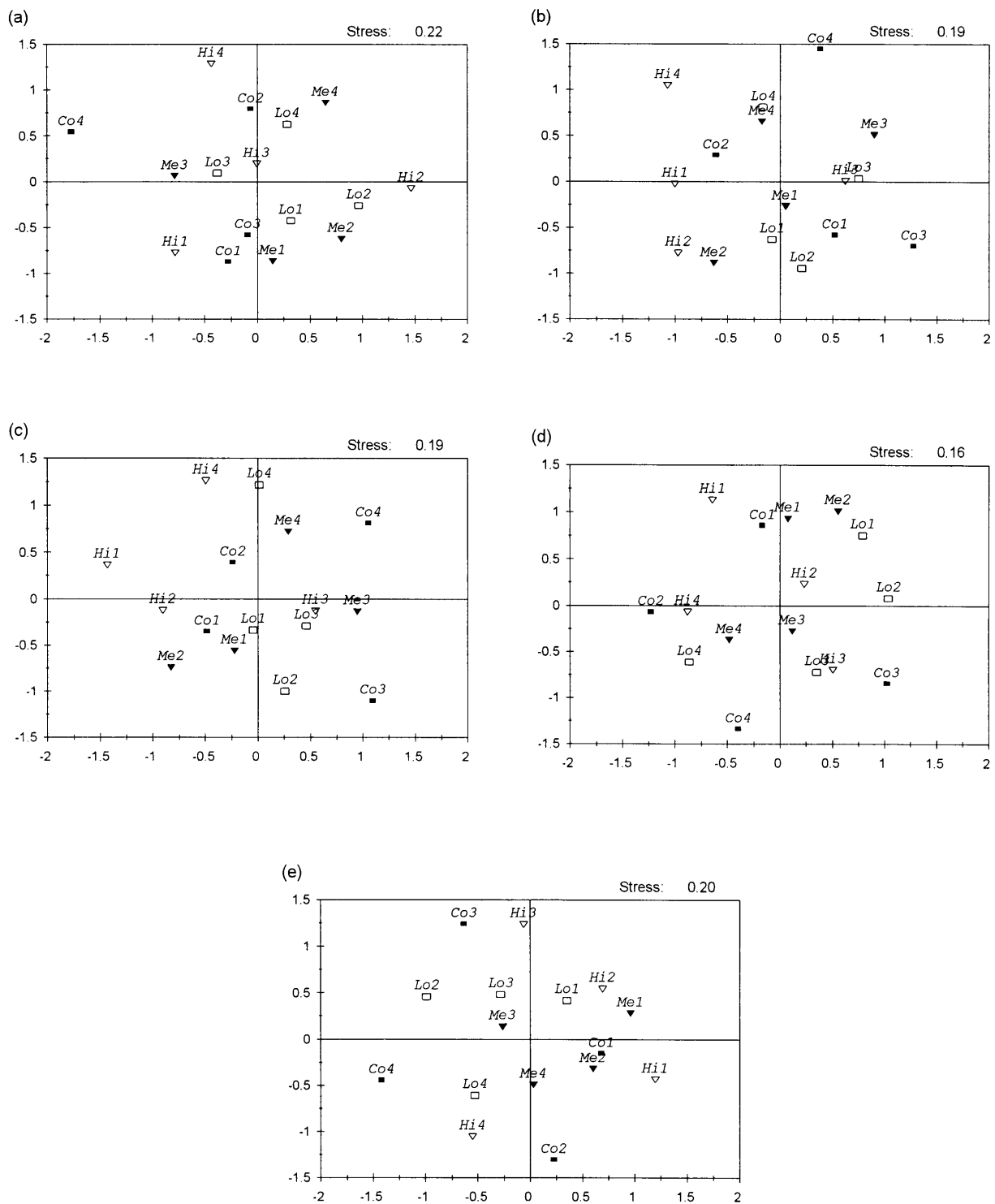


Figure 26. Multiple dimensional scaling (MDS) of all paddocks for each survey: survey 1 (a), survey 2 (b), survey 3 (c), survey 5 (d) and survey 6 (e). Based on sapling presence at a point. Treatment level codes: Co = control, Lo = low, Me = medium and Hi = high treatment level. The number following the treatment-level code is the block number.

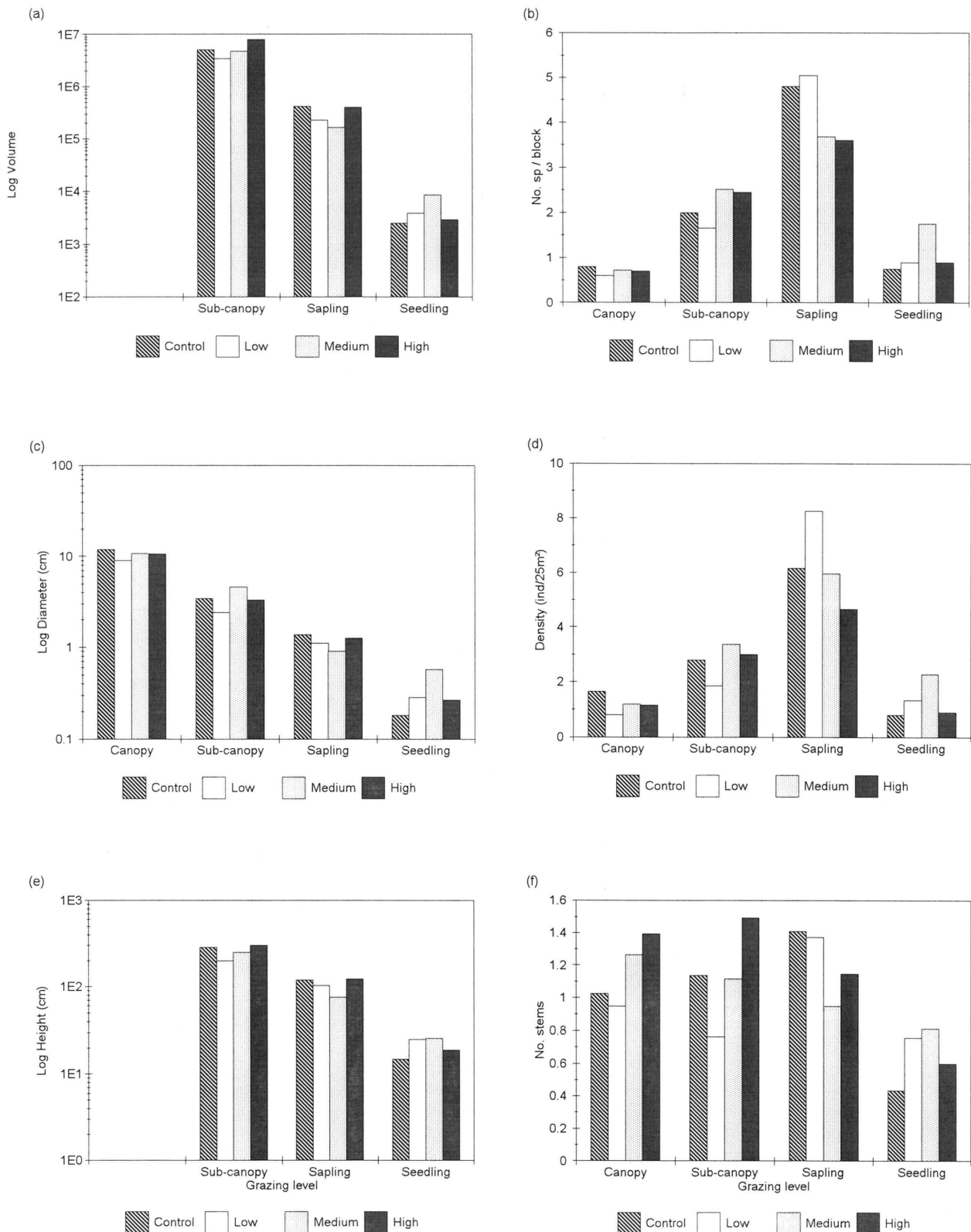


Figure 27. Differences between four treatment levels in the crown volume (a), number of species per 25m² plot (b), stem diameter (c), density (individual trees/ha) (d), height (cm) (e) and number of stems (f), for four height categories: canopy, sub-canopy, sapling and seedling - see text for explanation of categories. The variables crown volume and height were not measured for the canopy class.

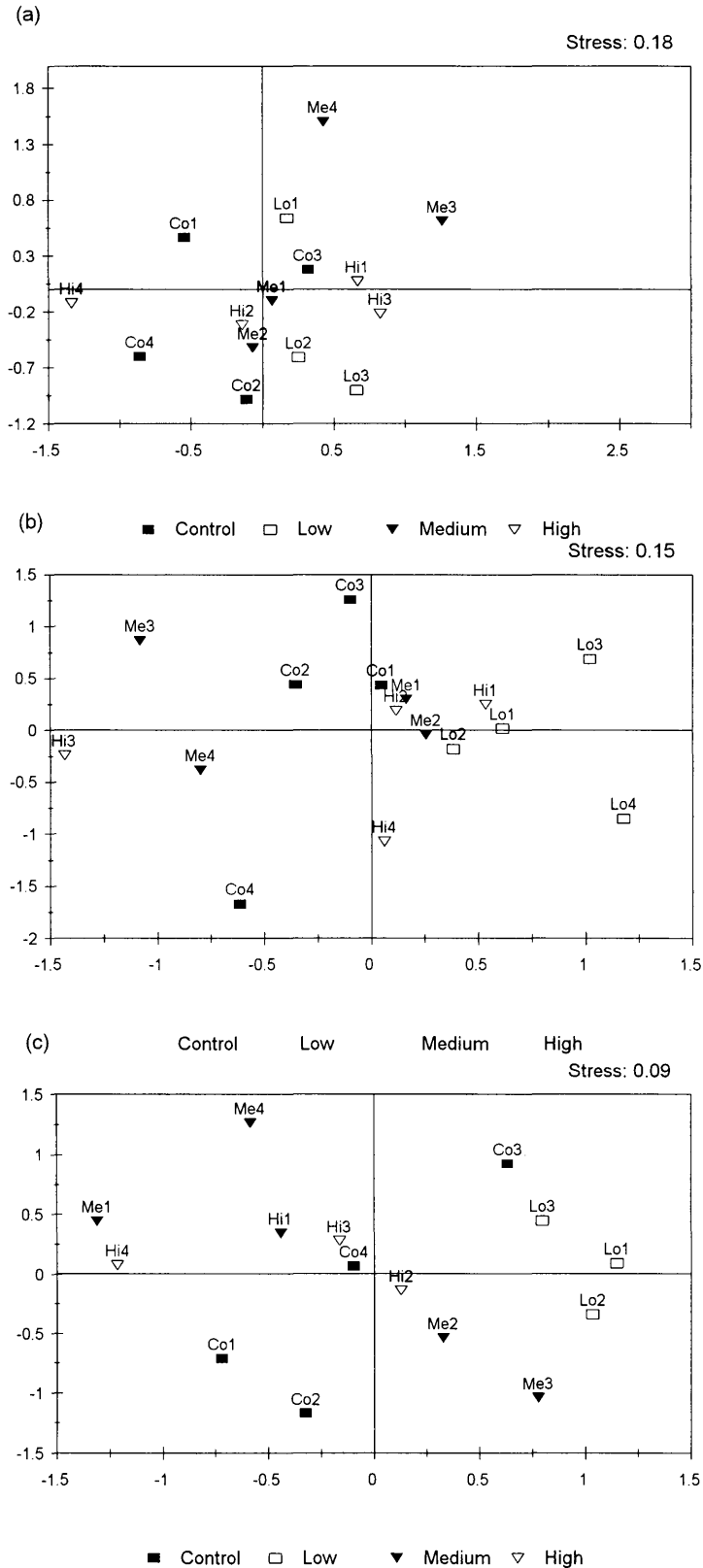


Figure 28. Multiple dimensional scaling (MDS) of woody plant species in four treatment levels and in three height categories: sub-canopy (a), sapling (b) and seedling (c) - see text for explanation of categories. Treatment codes: Co = control, Lo = low, Me = medium, Hi = high treatment levels. Block number follows the treatment code.

BIOMASS PRODUCTION OF TREATMENT AND CONTROL PADDOCKS

There were no significant differences between treatment levels (one-way Kruskal-Wallis, $H=6.82$, $p=0.08$) in the mean dry mass of plant material two months after the last grazing cycle (Table 21). Data on vegetation dry mass are given in Appendix 10.

Table 21. The mean dry mass and standard error (per treatment level) of plant material harvested from one 25m² plot in each paddock. Only plant material below 1m in height was harvested. Based on data in Appendix 10.

| | Treatment level | | | |
|----------------|-----------------|------|--------|------|
| | Control | Low | Medium | High |
| Mean | 2.16 | 3.14 | 2.02 | 1.14 |
| Standard error | 0.19 | 0.68 | 0.37 | 0.38 |

CHAPTER 5

DISCUSSION

DETERMINISTIC AND STOCHASTIC FACTORS WHICH COULD INFLUENCE THE EXPERIMENT

Rainfall, light, canopy tree structure and density

Several abiotic and biotic variables affecting the survey sites were measured to ensure that the applied disturbance by cattle was the main effect, or at the very least that all other effects were taken into account. The analysis shows that abiotic and biotic conditions were similar for all sites. There were no significant differences between paddocks in the light intensity 50cm above ground level, percentage branch and/or leaf cover, and canopy tree structure and density. The different grazing cycles also did not differ in the ratios of total metabolic mass applied to the three different treatment paddocks.

Rainfall seems to have been an important factor determining the response of the vegetation to the disturbance created by the cattle. The rainfall for the period leading up to survey 3 was below the daily average for most of the time and the short, dry period immediately preceding survey 3 could explain the obvious change in values at that time, an effect that is visible in almost all variables recorded as part of this study. By the time of survey 4 much more rain had fallen and most vegetation variables regained their previous levels.

Cattle diet preferences and habits

Analysis of cattle diet preferences showed some interesting responses by the cattle to a dwindling food supply. They spent most of their time feeding while inside the treatment paddocks, but there was a definite difference between the treatment levels in the relative time spent feeding and on other activities. This difference was not statistically significant, but it is quite possible that it would have been amplified had the observation period (treatment period) been longer. It is certainly explainable in terms of the experiment being conducted - cattle with a limit to their food

supply (as in the high treatment level paddocks where they had to spend exponentially more time) will spend more of their time looking for food and less time on other activities.

The effect of food limitation at the end of the high treatment application is also reflected in their diet and diet preferences. The mean number of species that they were eating per day decreased significantly with treatment level, probably because they had finished the most preferred and most available plants in the first few days of the grazing cycle and were forced to switch to less preferred and rarer species. The increase in the total number of species utilised in a specific treatment level appears to be non-linear, again suggesting that they had removed the bulk of the available plants in the initial stages of grazing. Seen the other way around, it means that initially (in the first two days of the grazing cycle) they were selecting from a variety of plants, some of which were rare (those plants with high selection values), but later on were forced to spend more time grazing on the less preferred ones. This is also evident from the number of species with a negative selection value which increased with treatment level while the number of positively selected species remained about the same. This suggests that the cattle initially had some choice, but later on were forced to eat less preferred species.

The most preferred species was the grass *Dactyloctenium australe*. Given that this species seems to be a dominant part of the forest floor of other, younger parts of the rehabilitating area (own unpublished data), it may be that it, as well as one or two of the other highly preferred species, are keystone resources in the sense of Davidson (1993). Even though over 50% of the cattle's diet comprised only three plant species, in all they utilised about one third of the total available pool of species. The cattle used in the experiment preferred grasses, apparently avoided a number of the herbaceous species (climbers and forbs), but utilised woody species at about the same rate as their occurrence in the herb layer. The relatively large percentage of woody plants in their diet is not typical for cattle, although browsing by cattle is not uncommon (Walker 1976). There is not much to be gained from a detailed analysis of the species which they selected for and the selection values of each, but it is interesting to note that *Panicum maximum*, although it has been found to be a palatable and highly nutritious fodder grass species, especially in the dry season

in savannas (Skinner, Monro and Zimmermann 1984, Rethmann, pers. comm.)*, it was one of the least preferred species in all the treatment levels.

An MDS of their diet preferences reflects two aspects. First of all the cattle were forced by a dwindling food supply in the high treatment level to concentrate on less preferred and less available plants, which probably tended to be the same species in all the paddocks of the specific treatment level. That is probably why the treatment levels do not separate as well in the MDS on the first two days as in an MDS of the last two days of each treatment, where the low treatment level completely separates from the other two.

Secondly the three grazing levels were applied systematically, i.e. they started in the low level paddocks for two days, moved onto the medium ones for 4 days and ended in the high treatment level paddocks where they stayed for 8 days. This obviously included some sort of learning period for the cattle, so that by the time they arrived in the high treatment paddocks, they knew what was available to them and which species were the really tasty ones. This could explain why, in spite of some overlap in the paddocks from different treatment levels in the MDS on the first two days of grazing, paddocks from a specific treatment level still tended to cluster together. The clear distinction between treatment levels (if data on all days of treatment level are included), is probably first and foremost the result of a limiting food supply towards the end of especially the high and medium treatment levels (experienced in all paddocks of a specific treatment level to more or less the same degree) and secondly the learning effect of moving from the one treatment level to the next sequentially. This means that the distinction seen between treatment levels as far as cattle diet preferences are concerned is unlikely to have influenced the results of the vegetation analysis in an unpredictable manner.

Evaluation of treatment levels

The differences in the selected treatment levels do not imply a direct relationship between the levels of mass as applied and a specific level of disturbance as seen in the field. There is very little

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information on specific levels of disturbance in the coastal dune forests of anywhere, let alone the northern parts of KwaZulu-Natal. Some information is available, mostly of an anecdotal nature, on human disturbance in the area, but no studies have been conducted on disturbance intensity. This made it very difficult to decide what is a light, a moderate and a heavy disturbance intensity. In the end the most expedient solution was to stagger the intensity of disturbance between the three treatment levels in a more or less exponential fashion. To some extent this was confounded by variability in the mass of available cattle as well as by the fact that the cumulative mass applied to a specific treatment level did not increase exponentially. However, the total disturbance applied (as measured by metabolic mass) to the high treatment paddocks was in effect about twice that applied to the medium, which was about twice that applied to the low treatment paddocks.

There is bound to be a vast difference between the effects of a disturbance of a given level applied as a number of short and intense disturbances and that same level applied as a continuous, low grade disturbance (Miller 1982). At the start of the project it was decided, for logistic reasons, to apply the grazing disturbance as a number of short intense grazing cycles (varying the number of grazing days per treatment level in a grazing cycle to simulate different disturbance levels), rather than a single continuous one with different stocking rates. It is quite conceivable that the two approaches would have had different effects and all conclusions drawn from the results of the present study have to take this into account.

VEGETATION VARIABLES

Factors determining the response of vegetation variables to disturbance

Three main factors determined the response of the vegetation to the disturbance created by cattle. The first factor was the rainfall pattern over the study period and its effect was visible as a change in magnitude in almost all variables around the time of survey 3 (see for instance Figs. 8,9,12). It is well known that rainfall (and climate in general) has a dominant influence on plant community variables (e.g. Walker & Knoop 1987, O'Connor 1991), at least in seasonally dry

systems. Also, apart from the general effect of rainfall on plant growth and reproduction, it will affect the rates of all kinds of herbivory (Coley & Barone 1996). Although this was not investigated further, there were some indications of a possible interaction between treatment level and rainfall effect, since a MANOVA for multiple response variables could find differences between treatment levels only in the survey conducted at the end of a period of below-normal rainfall. This was also the case with Kruskal-Wallis tests for differences between treatment levels in the percentage herbaceous cover.

Rainfall was below the daily average for quite some time and was still decreasing before the start of the experiment (Fig. 4). The brief increase during survey 2 was apparently not enough to negate the effect of the sharp decrease immediately after that (which is in effect a second type of disturbance). During grazing cycle 3 it was for instance difficult to ensure that the cattle had enough food while inside the grazing paddocks. This was due to a recent short-term drought and the drop in for e.g. cover values at that time is not surprising. Most variables were affected by this period of low rainfall, either directly or in their response to it afterwards. Some variables (e.g. similarity to initial species composition) lagged in their response and only showed the effects of low rainfall by the time of survey 4.

The second main factor affecting the response of vegetation to disturbance by cattle, is the site of the specific paddock. The method used to determine species number (as well as cover) is dependent on biomass present, rather than individuals present. A species which can lose all or part of their above ground parts without being adversely affected in the long term, could be counted as absent, while its absence is really only the result of a specific response type and not an absolute decrease in abundance. This means that the species composition of a specific site at the start of the experiment will be crucial in determining the response of the site/area to the disturbance. For instance a site which is dominated by a highly resilient species like the stoloniferous grass *Dactyloctenium australe*, may have a smaller decrease in species richness under the influence of cattle than sites which are dominated by more fragile species like *Aneilema aequinoctiale*. It is also intuitively obvious that the same site or sites close to each other will be more highly correlated in time (with regard to species composition/species richness) than sites separated in space (Von Ende 1993).

Dependence of community composition on site history is one of the main tenets of community assembly theory (Lockwood 1997) and the findings from MDS in the present study tend to confirm it. Paddocks from the same block, but from different treatment levels, clustered together closer than paddocks from different blocks, but from the same treatment level. Most importantly, this happened through all surveys. The blocks of paddocks, which started out with a difference in species composition, stayed different, in spite of being disturbed by cattle at levels which were replicated amongst the blocks. The cumulative nature of the disturbance by cattle did eventually have an effect on species composition, albeit only a minor one. By the time of survey 6, the control paddocks were much closer to each other on an MDS plot than to other treatment paddocks in each block. This could be a spurious result (control paddocks were becoming equally more dissimilar to the other paddocks, rather than becoming more similar to each other), since mean similarity between control paddocks did not increase with time, if anything it slightly decreased.

Figure 17 illustrates the dominant effects of both site and rainfall on mean similarity. If the cattle had any significant treatment - level dependent effect in the short term on species composition of the herb layer, one would have expected these two lines to cross or diverge at some stage.

The third main factor affecting the response of the vegetation to a disturbance was the interaction of time with treatment level, which manifested itself mostly as an increase in variation around the mean in the low, medium and high treatment levels for almost all variables. With one exception (vegetation height), there were no significant differences between treatment levels within any specific survey. On the other hand the overall differences between treatment levels, when tested over time and treatment level, were significant for all of the univariate variables. Regression analysis, which in a sense takes account of changes over time, was unduly influenced by the increased variation in values with time, leading to few significant differences between regression coefficients. The question of a treatment - level dependent increase in variation around the mean for all variables with time will be considered later.

Response of herbaceous layer vegetation variables to disturbance by cattle

Species richness (species per treatment level, per paddock, per quadrat and per pin)

During the present study species numbers per paddock and per quadrat decreased in the control paddocks, but increased somewhat over time under the influence of grazing (Figs 9,10). There is no information on the effects of disturbance on specifically the species richness of the herbaceous layer in the coastal dune forest, but Gibson, Watt & Brown (1987) (moist grassland) and Pandey & Singh (1992) (seasonally dry savanna) recorded an increase in species richness with grazing. However, the increase in species numbers in the present study was not significant for any of the treatment levels, nor was it dependent on the level of treatment, but it was associated with increased variability over time. Since it is quite possible that the increase in numbers was an artefact of the higher variability rather than an absolute increase (at the very least some of the treatment paddocks had even fewer species than the control), it is probably less important than the increased variability.

In the control paddocks on the other hand, species numbers decreased over time and also showed less variation (see Figs. 9,10). This apparent decrease in the control paddocks, when compared to the treatment paddocks, begs explanation. First of all, the question is whether species are lost from the control paddocks because of the exclusion of grazing, or whether the herbaceous layer in the study area was undergoing a loss of species, independent of the experimental grazing, over the study period.

A certain level of disturbance may be a natural part of the successional process in the herb layer. The history of disturbance at a site has implications for the rates and patterns of succession there (Denslow 1985) and we know that the rehabilitating area had experienced varying amounts of disturbance by cattle before the present experiment. In such a case one would expect the pattern outside the experimental paddocks to be different from the pattern inside the control paddocks, but similar to the pattern in the treatment paddocks. However, it may be that the herbaceous layer, quite independent of the disturbance by cattle, is heading towards a developmental stage when the numbers of earlier successional as well as later successional species will be relatively

low - a sort of species poor intermediate stage between seres. (Very few of the species present in the herbaceous layer of the rehabilitating area are present in unmined coastal dune forest (Venter 1972, Van Aarde *et al.* 1996 and own unpublished data), but there is no information on intermediate stages, since the oldest rehabilitating areas are still only relatively early successional stages). In this case one would expect the pattern outside the experimental paddocks to be the same as in the control paddocks but different to the treatment paddocks.

When explaining or comparing the recorded patterns of species richness, it has to be kept in mind that species richness is a function of the available species as well as the history of a particular site (Sheil 1997) and that it very often cannot be explained in terms of current conditions. Nevertheless, there seems to have been a downward trend in the total number of species in the control paddocks, while numbers tended to increase in all the other treatment levels (Fig. 11). A survey of four unfenced sites in the same area (similar in size to the paddocks used in the present study and surveyed at the same time as the experimental paddocks) showed a pattern of decrease in species numbers over time which was very similar to that of the control paddocks, except that there was more variability per survey (own unpublished data, see also Appendix 11). Also, at least the highest levels of grazing applied in the experiment was higher than the background disturbance by cattle, so one would expect treatment paddocks to be different from areas outside the experimental paddocks. It is therefore reasonable to assume that the decrease in species numbers in the control was at least partly the result of succession - the exclusion of grazing caused at most a decrease in the amount of variation in species richness over time. Various intensities of grazing therefore resulted in an increase in mean species richness, strongly associated with an increased variability in species numbers in a specific paddock.

The second question is how the changes in species numbers occurred (both the decrease in numbers in control, and the relative increase in treatment paddocks). Without a specific disturbance by cattle, or with very low levels of disturbance, the patch size of species which naturally tend to occur in a local patch (typically species with short-distance dispersal strategies or a vegetative growth form that enhances a patchy distribution, like clonal plants (Lavorel & Chesson 1995) and creepers) gradually increases. The chance of finding a rarer species (which may or may not have another growth form) while using a specific scale of measurement therefore

decreases over time. Conversely a disturbance created by cattle would, by causing more heterogeneity in the herbaceous stratum and by decreasing the patch size of clonal plants and creepers, increase the chances of these rarer species to occupy sites and to be found (see for instance Burke & Grime 1996). This is effectively a reversal of the competitive abilities of plants *sensu* Crawley (1983), although the mechanism probably includes not only the consumption of plants, but also all other ways in which cattle disturb plants. Theoretically a complete lack of disturbance could make it difficult for rarer species to survive in the area, but in the present study it is not easy to make unqualified statements about rarer species' response to disturbance since the scale of measurement is critical for this [patterns of change in the species richness of a site are to a large extent determined by the scale of measurement (Bellehumeur, Legendre & Marcotte 1997)].

If one considers the small scale patchiness caused by the activities of cattle, and that biotic and abiotic disturbances at various scales quite likely drive the development of the coastal dune forest, as it does in most forests (Denslow 1985, White & Pickett 1985, Whitmore 1989 and Keddy & MacLellan 1990), the ability of a species to exploit a patchy resource-environment (and hence its relative competitive ability) becomes important. For instance Dushyantha & Hutchings (1997) found that clonal plants displayed a scale dependent (highest biomass at highest scales of heterogeneity) ability to locate the most nutrient-rich patches. Larger resource patches will therefore favour clonal plants and since disturbance by cattle decreases the scale of heterogeneity (cattle activity results in small-scale patchiness, as opposed to a larger scale spatial heterogeneity assumed for the herb layer), a lack of disturbance will favour clonal plants. Creepers also have a distinct disadvantage in an environment disturbed by cattle, since their growth form (stems creeping horizontally along the ground surface) exposes them to direct injury. An injury to a stem anywhere along the line of growth will therefore damage a significant part of the plant (pers. obs.). The exclusion of grazing will therefore also favour creepers. These observations are borne out by the fact that clonal plants and creepers apparently increased in relative abundance over time in the control, while they either fluctuated or stayed at about the same levels in the other treatment paddocks (see Appendix 12 - not statistically analysed). The proposed mechanisms involved in changes in species numbers have not been tested, so they remain conjectural. However, the observed pattern in species richness could be explained if the mechanism of

disturbance by cattle involves a change in (plant- and resource-) patch size and therefore a reversal of competitive abilities amongst plant species.

Ground and herbaceous cover

Cover values tended to be strongly influenced by treatment level, much more so than species richness. Ground and herbaceous cover is dependent more on biomass presence than on species presence and will therefore be influenced by mechanical removal of vegetation, which is the main mechanism through which cattle disturb the vegetation. Vegetation cover is a prerequisite for soil stability (Cumming 1982), especially so in a high rainfall area. A decrease in the mean cover, together with an increase in the amount of variation around the mean, could therefore have far-reaching effects on the development of a community.

Vegetation height

Cattle decreased vegetation height with treatment level and with time. The significant differences between treatment level in surveys 3, 4 and 5 emphasise the cumulative effect of the grazing treatment. Although variation seemed to increase with time, it was not as obvious as with the other variables. Of all the variables measured, vegetation height was the most sensitive to rainfall and a large part of the variation, both within and between surveys, was probably in response to variation in rainfall. This is apparent in the almost cyclical rise and fall in mean height of vegetation, where the increases in height generally corresponded with the growing season and with rainfall.

Species composition and similarity measures

Total species numbers

In a once-off survey of all rehabilitating areas I recorded 61 species in the area where the experiment was situated (own unpublished data). During the same survey I recorded 73 species in an unmined area south of Mapelane Forest Reserve. These figures are markedly lower than the

total number of species found over all surveys in all treatment levels, but very similar to the total number of species found per survey (see Fig. 11), suggesting that the survey method was at least repeatable. It is also somewhat higher than the total number of species (40) that was found by Lubke *et al.* (1992) in five 100m² plots in the oldest stand.

Species composition and similarity

The results from an MDS on species composition have already been discussed (see under “Factors determining the response of vegetation to disturbance”), but it is important to note that the species composition of the site at the start of the experiment was the major determinant of species composition of a specific treatment level over time, at least at the time scale of the experiment. It is quite possible that major effects of a disturbance by cattle (at the grazing levels applied in the experiment) on the species composition of the herb layer in rehabilitating areas will only become apparent over a longer time scale than the present study. There were indications of this in the MDS of the individual surveys (Fig. 16), for instance, where there seems to have been a movement of a specific treatment level’s paddocks in the MDS multi-dimensional space closer to each other and further away from other paddocks in the same block.

Similarity values showed up a few interesting responses of the vegetation to disturbance (Figs. 17,18,19). Given the variability in species composition (i.e. patchiness) of the herbaceous layer the levels (or hierarchy) of similarity one would logically expect are: same paddock over time (within time frame of study) most similar to itself (i.e. temporal similarity - history dependence of site dictates this); paddocks closest to each other next similar (i.e. close spatial similarity); and paddocks from different sites (blocks) least similar (i.e. far spatial similarity). Any exception to this pattern would mean that the cattle had an effect over and above site and environment. The layout of the experiment in a randomized block design meant that paddocks from the same treatment level were situated in different blocks and each block consists of four treatment levels. One would therefore expect paddocks from different treatment levels, but within a single block to be more similar to each other than paddocks from the same treatment level. This was the case through all surveys (see for instance Fig. 17), leading one to conclude that a disturbance by cattle had no effect on the species composition of the herbaceous layer.

However, some paddocks showed movement over time on an MDS plot (Fig. 15). Although it is not apparent from the MDS plot, this movement could have been in response to a specific treatment level and the similarity of treatment level at each survey with its original species composition certainly supports this. Although the slope of the regression line (similarity of paddocks to their initial species composition) in control is not significantly different from the other treatment levels, it is steeper, which suggests that change in species composition may be faster in the absence of disturbance. This could be an artefact of the general decrease in species numbers in control as opposed to the other treatment levels. If the decrease in numbers is the result of a gradual increase in patch size as proposed earlier, it would mean that the most patch-dominant species will tend to push out other species, most likely the rarer species first. This in turn means that the change in similarity might be the result of a loss of species, and not necessarily a gain at the same time. Whatever the reason for such a change in species composition, it means that a disturbance by cattle will effectively retard the rate of succession. This of course answers key question 2 set at the beginning of the study, although not as unequivocally as one would have hoped.

Increased variability in response to disturbance by cattle

The most striking treatment-level dependent effect of the cattle on the vegetation was an increase in variation around the mean for several variables. Vegetation height and the number of species per pin were the only variables that did not show this to any great extent. The increased variability was particularly obvious in number of species per paddock and in herbaceous cover (Figs. 10,12). Disturbance by the cattle may have caused an increase in spatial heterogeneity, which in turn somehow gave rise to more variable species numbers / cover values. However, increased variation around the mean over time with little change in the mean value of the variable itself implies that during each survey there were some paddocks where the values increased and others where it decreased. While a more patchy environment may lead to more species (Denslow 1985), it is difficult to explain the proximate cause of an increase in for instance species numbers per paddock in some paddocks, *together* with a decrease in others. It is unlikely that the increases were the result of new colonisations, since this would have been reflected in the MDS which then would have showed more consistent treatment level-dependent change.

The answer has to lie in the differential response of specific plant types and species to disturbance. A paddock which happened to consist of a few patch-dominant plant species before grazing had begun, might become more heterogenous in response to grazing and consequently allow a more even spread of species. In a similar vein vegetation cover may increase if a species which is competitively at a disadvantage without disturbance, is suddenly released from this competition. On the other hand paddocks which were more heterogenous before the start of grazing may react in exactly the opposite way in that a few robust clonal plants may become dominant at the cost of a number of more fragile plants. Also, a differential response of the woody and herbaceous components of the herbaceous layer to a disturbance by cattle as well as their effects on correlated, not-measured factors, may lead to increases or decreases in species numbers. Any of the above factors may explain the increase in variation, but it remains highly conjectural.

The concept of variability (or heterogeneity, or variance, or variation) in nature approaches a paradigm in ecology. Most aspects of ecological research implicitly or explicitly deals with variation in some form and most often as a cause or correlate of some biological factor (e.g. Dushyantha & Hutchings 1997, Thomson, Weiblen, Thomson, Alfaro & Legendre 1997). However, there is very little information on functional mechanisms involved in the creation and maintenance of variability or its implications (but see Warwick & Clarke 1993). This may be a promising field of research in determining the role which disturbance plays in coastal dune forests, whether they are relatively undisturbed or still in a developing phase.

Response of woody plant variables to disturbance by cattle

Woody plants (trees and woody shrubs) are quite likely the key structural step in the development of the rehabilitating areas into coastal dune forest (see also earlier in description of materials and methods). It is for this reason that they were chosen to be investigated in the present study. However, it proved to be very difficult to isolate the effects of disturbance to woody plants from the effects on the herbaceous layer, as a result of the high density of the herbaceous layer and the patchy distribution of emerging woody plants.

With a few notable exceptions (the number of sapling species per paddock, which differed significantly between treatment levels over time, for instance) there were no differences which could unequivocally be ascribed to either disturbance by cattle or the level of that disturbance. Either the temporal and/or spatial scale of measurement in the present study was insufficient to pick up any changes, or woody plants as a functional group are highly resistant to the disturbance by cattle. In this context Tiver & Andrew (1997) found that the negative effects of herbivory (by rabbits, sheep and goats) on recruited juveniles must exceed natural thinning before overall regeneration is affected. Although regeneration was only studied indirectly in the present study, the principle is most likely the same. Furthermore the woody plants as a group were very dynamic, with a lot of changes unrelated to treatment level happening between surveys.

Coefficient of variation did not consistently increase with treatment level to the same degree as in other herbaceous variables, nor did rainfall have such a visible effect (except maybe for the pattern in CV of mean crown volume - see Table 19c). The difference between the before grazing and after grazing surveys in height class distribution (see Fig. 24) could be the result of the division of height classes into arbitrarily chosen 20cm units, which do not necessarily have any relation to the growth pattern of sapling trees. There may be more active growth in the upper height classes than in the middle ones, leading to a loss of trees from the group before they could be replaced from the lower height classes. In any case, there were no differences between treatment levels within a survey, only between before (survey 1) and after (survey 2) distributions, so it is not possible to ascribe this effect to the presence of the cattle. Species composition analysis (ANOSIM and MDS) supports the general pattern found in the univariate analyses. With one or two exceptions, there was very little movement of paddocks over time in the MDS, and no significant differences.

CHAPTER 6

SYNTHESIS

The aim of the present study has been to determine whether a disturbance caused by cattle would have an effect on plant succession in rehabilitating coastal dune forests at Richards Bay. Disturbance by cattle as defined in the present study included all aspects of the effect of a large mammalian herbivore on vegetation, namely trampling, defecating and urinating on the vegetation, eating the plant, as well as serving as dispersal agents for plants through their faeces and hair coat. Change in species composition (a multivariate variable) of the herbaceous layer as well as of the woody component of the forest understorey was identified as the main factor that would indicate an effect of cattle on succession of the herb layer. Closely related to species composition are other emergent properties of the plant community, namely species richness and vegetation cover. Growth parameters in woody plants are indicators of the effect of cattle on the performance of juvenile trees, which indirectly also has an effect on the species composition of the woody plant community in the sense that plants that either decrease in size or grow very slowly probably have a larger chance of eventually disappearing from the community than plants which grow vigorously. The variables were used to test the null hypothesis that cattle would not have an effect on the process of plant succession in the rehabilitating forest, as well as the related, secondary null hypothesis that any effect of cattle on these variables were independent of treatment level.

Disturbance by cattle (i.e. treatment level) could have caused either a decrease or increase in the value of any given variable, there could have been a decrease or increase in a variables' value over time unrelated to the disturbance caused by the cattle, or there could have been an interaction between treatment level and the change over time. An interaction between time and treatment would have precluded any further investigation into the possible effects of treatment or time alone. In the context of the hypothesis that cattle would have an effect on plant succession in the herb layer, the differences between any one time period and the next were irrelevant, but those between treatment levels were relevant. Subtle effects of disturbance on a variable were elucidated by analysing the relationship between time and the given variable and testing for differences between treatment levels in these relationships.

Rainfall had a dominant effect on vegetation, causing a drop in values of most variables and in all treatment levels around the time of the third plant survey. Because this effect was the same for all treatment levels, it was implicitly incorporated into the statistical analyses as part of the background variation. Although this was not investigated further, there were some indications of a possible interaction between treatment level and rainfall effect, since a MANOVA could find differences between treatment levels only in the survey conducted at the end of a period of below-normal rainfall.

There were a number of significant effects of cattle on the selected univariate variables. However, species composition (of both the herbaceous and woody components) was not affected more than what could have been expected in the absence of grazing. Although there was apparently a trend for paddocks in the same treatment level to become more similar to each other under the influence of grazing, this was never very obvious or significant. Cattle had almost no effect on the species composition of the woody plant community. Results like these have to be qualified in terms of the time period over which the measurements were done, since it is highly unlikely that significant changes in species composition of long-lived plants will develop over a short time period. In the case of the present study, where the recording of data occurred over a period of 18 months, some effects were possible, especially in the herb layer. On the other hand, although seedlings and to a lesser extent saplings could have been affected, woody plants probably still had a smaller chance of reacting to the disturbance caused by cattle than plants which complete their life cycle within a year.

The null hypothesis that cattle do not have an effect on plant succession (through their effect on species composition, species richness and vegetation cover of the herb layer) is rejected for the univariate variables of the herbaceous community because there were significant overall effects (time-treatment interaction) in number of species per quadrat and vegetation height. However, this hardly constitutes an unambiguous statement about the effect of cattle on plant succession, since there were no treatment-dependent changes in species composition of either the herb layer or woody component. The most striking effect of the cattle on the herb layer (as well as to a lesser extent on the woody plants), was a treatment-dependent increase in the amount of variation around the mean for almost all variables. Increased variation in the abundances of

species is a reliable indicator of environmental or other stress (Warwick & Clarke 1993). Cattle therefore probably cause a significant amount of environmental stress in the herbaceous layer of the rehabilitating coastal dune forest.

This has important consequences for the dynamics of the herbaceous layer in a rehabilitating dune forest. Vegetation cover for instance is important for the stabilisation of soil structure and in providing a suitable environment for later successional species to germinate and establish (Van de Koppel, Rietkerk & Wiessing 1997). In the same vein the number of species per quadrat reflects on the 'structural' species diversity at any point (Whittaker 1977), which affects the germination conditions of other species (Johnstone 1986). Grazing causes increased variability in all of these variables, leading to an increased variability in the conditions that any species can expect to find when it arrives there. Community assembly theory predicts that the timing of arrival of a specific propagule is important in determining the composition of a community - if a later successional species arrives too early, it probably won't establish (Lockwood 1997). But it also matters what the micro-climatic conditions at the spot of arrival is. A late successional species arriving at the "right" time still won't establish if conditions are not suitable. The process of rehabilitating a coastal dune forest is completely dependent on the dynamic development of a succession of plant communities (although these successional communities are not always clearly defined and are sometimes interchangeable to an extent). It is therefore conceivable that a disturbance by cattle will in the long term, through its effect on the amount of variability in species numbers and vegetation cover, significantly affect the rehabilitation process.

Cattle may increase species richness by causing more heterogeneity in the herb layer and therefore increasing the possible number of micro-habitats. The number of species did indeed increase (or at least stayed the same) in paddocks where grazing was allowed, while in grazing-excluded control paddocks, number of plant species decreased over time. However, considering that the similarity of the control paddocks to their initial composition decreased faster than in the case of the grazed paddocks, it becomes clear that the cattle will most probably slow down the rate of succession. Any increase in species richness will likely be unwanted in terms of the rehabilitation of the coastal dune forest. On the other hand, there are indications that coastal dune forests undergo a high rate of disturbance, both exogenous and endogenous and probably at all

stages of successional development. It is quite possible that the characteristic species composition and structure of coastal dune forests in KwaZulu-Natal depend on a certain level of disturbance (see for e.g. Everard 1992).

The aim of the present study was not mainly to deliver a judgement on whether the effect of cattle will be “bad” or “good” for the developing coastal dune forest (which is a value judgment made *a posteriori*), but to determine whether they would have a (measurable) effect on selected variables representing aspects of plant community succession. To that extent it has succeeded, which means that there are management implications and it means also that management applications has to be based on these results. However, the number of unclear results suggests that the total effect of cattle are probably more complex than could be determined in a study over this time scale.

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OPSOMMING

Die effek van beeste op ontwikkelende kusduinwoud-plantgemeenskappe is ondersoek deur middel van die toepassing van eksperimentele beweiding in 'n 16-jaar oue stand van rehabiliterende kusduinwoud naby Richardsbaai, Suid-Afrika. Beweiding is oor 'n periode van 18 maande in vyf weidingsiklusse toegepas waarvan elkeen ongeveer 16 dae geduur het. Drie vlakke beweidingsdruk is gesimuleer deur die aantal dae wat beeste in 'n gegewe eksperimentele kampie gespandeer het, te varieer. Kampies is in 'n ewekansige blok-patroon toegewys aan 'n behandelingsvlak (beweidingsvlak) voor die begin van beweiding. 'n Aantal strukturele plantgemeenskapsveranderlikes wat verband hou met die plantbedekking, spesie-rykheid en spesiesamestelling van die kruidlaag-gemeenskap, asook die spesiesamestelling en groei van breëblaar houtagtige plante is gemeet gedurende ses plantopnames. Plantopnames is gedoen voor die begin van elke beweidingsiklus, asook twee maande na die laaste weidingsiklus.

Alhoewel reënval en tydsgebonde veranderinge 'n oorheersende invloed op alle veranderlikes gehad het, was die effek daarvan dieselfde vir alle behandelingsvlakke. Die beeste het min betekenisvolle behandelings-afhanklike effekte gehad op die geselekteerde kruidlaag-veranderlikes. MANOVA (met aantal spesies per pen, per vierkant en per kampie, asook kruid- en grondbedekking as veelvuldige respons-veranderlikes) het gewys dat daar slegs tydens 'n plantopname wat op 'n tydperk van droogte gevolg het en slegs in die geval van aantal spesies per pen en kruidbedekking, 'n betekenisvolle verskil tussen behandelingsvlakke was. In albei gevalle was dit die kontrole wat beduidend van die hoë behandelingsvlak verskil het. Daar was betekenisvolle oorkoepelende effekte (Friedman se ewekansige blok nie-parametriese toets) in die aantal spesies per kampie en in kruidbedekking. Geen *post-hoc* vergelykings kon gemaak word nie aangesien die steekproefgoottes te klein was om dit toe te laat. Veelvoudige Kolmogorov-Smirnov toetse het gewys dat daar betekenisvolle verskille bestaan tussen kontrole en alle ander behandelingsvlakke sover dit die aantal spesies per behandelingsvlak betref. MANOVA vir herhaalde metings het betekenisvolle tyd-behandeling interaksies gewys vir die aantal spesies per vierkant (met betekenisvolle kwadratiese tyd-effek en liniêre tyd-behandeling interaksie) en planthoogte (met 'n betekenisvolle liniêre tyd-effek en tyd-behandeling interaksie), asook 'n betekenisvolle tyd-effek in die aantal spesies per pen (met betekenisvolle liniêre tyd-

effek) en grondbedekking (met 'n betekenisvolle kwadratiese tyd-effek). Die kleinste-kwadratiese liniêre regressie van tyd teenoor veranderlike was beduidend slegs vir aantal spesies per vierkant en grondbedekking en in beide gevalle slegs vir die kontrole. Behalwe in die geval van persentasie grondbedekking was daar geen betekenisvolle verskille tussen die hellings van enige van die regressielyne vir enigteen van die veranderlikes nie.

ANOSIM het gewys dat daar geen betekenisvolle verskille in die spesiesamestelling van die kruidlaag tussen behandelingsvlakke binne elke plantopname bestaan nie. Dit was die geval afgesien daarvan of die toets gedoen is op die teenwoordigheid van spesies in 'n 1m² vierkant of by 'n pen van die puntbrug. Daar was geen betekenisvolle verwantskappe tussen tyd en die soortgelykheid ("similarity") van elke kampie met ander kampies van dieselfde behandelingsvlak in elke opname vir óf spesie-teenwoordigheid by 'n pen óf in 'n 1m² vierkant nie. Die regressie van tyd op gemiddelde ooreenkoms van elke kampie met sy oorspronklike spesie-teenwoordigheid was betekenisvol vir die kontrole en lae behandelingsvlak in die geval van spesie-teenwoordigheid in 'n 1m² vierkant en vir die kontrole in die geval van spesie-teenwoordigheid by 'n pen van die puntbrug.

Daar was oorkoepelende betekenisvolle verskille tussen behandelingsvlak in die aantal jongboompie spesies per kampie (hoë behandeling verskil betekenisvol van alle ander), digtheid van jongboompies (kontrole verskil betekenisvol van al die ander) en die kruinvolume van jongboompies (geen *post-hoc* vergelykings). Die regressie van tyd teen aantal spesies per kamp was betekenisvol in die kontrole, lae en hoë behandelingsvlakke, terwyl die regressie van tyd teenoor digtheid betekenisvol was vir kontrole en medium behandelingsvlakke. Daar was geen betekenisvolle verskille tussen behandelingsvlak of opname in enigteen van die res van die veranderlikes vir beide die jongboompies en alle houtagtige plante. Die biomassa opbrengs van die behandelingskampies was ook nie betekenisvol verskillend nie.

Die nulhipotese dat die beeste geen invloed op die gekose veranderlikes het nie word dus verwerp. Die sekondêre nulhipotese dat die invloed van die beeste onafhanklik is van die vlak van behandeling, kan nie verwerp word nie, omdat daar geen betekenisvolle verskille was tussen die laag, medium of hoë behandelingsvlakke nie.

Alhoewel die beeste wel 'n betekenisvolle invloed gehad het op 'n paar van die gekose veranderlikes kon geeneen van die effekte sonder enige twyfel toegeskryf word aan die vlak van beweiding nie. In alle betekenisvolle gevalle was daar ook 'n interaksie tussen tyd en behandelingsvlak. Dit kan dus nie onowonde uit die resultate van hierdie studie gestel word dat die beeste die proses van plantgemeenskapsuksesie in ontwikkelende kusduinwoude betekenisvol affekteer nie. Aan die ander kant het die beeste 'n opvallende invloed gehad op die hoeveelheid variasie, sigbaar in die behandelings-afhanklike verhoging in koëffisient van variasie in alle veranderlikes. Hierdie verhoging in variasie was waarskynlik die rede dat daar slegs twee betekenisvolle regressies tussen tyd en die gegewe veranderlike was (in beide gevalle was dit die kontrole waar die koëffisient van variasie ook die laagste was) en ook geen betekenisvolle verskille tussen die hellings van die onderskeie behandelingsvlakke was nie. Heelwaarskynlik was dit ook die oorsaak van die betekenisvolle tyd-behandeling interaksies in sommige veranderlikes.

Verhoogde variasie in die gekose veranderlikes kon die gevolg van verskeie faktore gewees het, maar die mees waarskynlike is 'n differensiële reaksie van plantspesies en plantgroeitipes op die versteuring wat deur die beeste veroorsaak is. Variasie in plantbedekking mag belangrike langtermyn implikasies vir die stabiliteit van grondstruktuur hê, asook vir die toestand nodig vir die ontkieming en vestiging van later-suksessionele spesies. In dieselfde trant dui die aantal spesies per 1m²-vierkant op die "strukturele" spesie-diversiteit op enige punt, wat ook die ontkiemingstoestand van ander spesies beïnvloed. Aangesien die rehabilitasie van 'n kusduinwoud totaal afhanklik is van die ontwikkeling van 'n suksesie van (goed- en minder goedomskrewe) plantgemeenskappe, is dit denkbaar dat 'n versteuring deur beeste in die lang termyn rehabilitasie van hierdie plantgemeenskappe betekenisvol kan beïnvloed.

SUMMARY

The effects of cattle on developing coastal dune forest plant communities were investigated using an experimental application of grazing in a 16-year old stand of rehabilitating coastal dune forest at Richards Bay, South Africa. Grazing was applied over a period of 18 months in five grazing cycles, each lasting about 16 days. Three levels of grazing pressure were simulated by varying the number of days per grazing cycle that cattle spent in a designated paddock. Paddocks were assigned in a randomized block pattern to treatment (grazing) levels before the start of grazing. A number of plant community structural variables relating to the vegetation cover, species richness and species composition of the herbaceous community, as well as the species composition and growth of emerging broad-leaved woody plants were measured during six plant surveys. Plant surveys were done before the start of each grazing cycle and also two months after the last grazing cycle.

Although rainfall and temporal changes had an overriding effect on all variables, the effect was the same for all treatment levels. The cattle had very few significant treatment-level dependent effects on the selected herbaceous layer variables. MANOVA, using species per pin, per quadrat and per paddock, as well as herbaceous and ground cover as multiple response variables, showed that there was a significant overall effect only during a plant survey that followed a period of drought and only in the number of species per pin and herbaceous cover. In both cases it was the control which differed from the high treatment level. There were significant overall effects (Friedman's randomized block non-parametric test) only in the number of species per paddock and herbaceous cover. No *post-hoc* comparisons could be made due to small sample sizes. Multiple Kolmogorov-Smirnov tests showed that there were significant differences between the control and all other treatment levels in the number of species per treatment level. Repeated measures MANOVA showed significant time-treatment interactions for number of species per quadrat (with a significant quadratic time effect and linear time-treatment interaction) and vegetation height (with a significant linear time effect and time-treatment interaction) and a significant time effect in number of species per pin (with a significant linear time effect) and ground cover (with a significant quadratic time effect). The least squares linear regression of time against variable was significant only for the control in the number of species per quadrat and

ground cover. Except in the case of percentage ground cover, there were no significant differences between the slopes of any of the regression lines in any of the selected variables.

ANOSIM showed that there were no significant differences between treatment levels within each survey in the species composition, regardless of whether the test was based on species presence at a pin of the point-bridge or a 1m² quadrat. There was no significant relationship between time and similarity of each paddock to others in the same treatment level in a survey. This was the case in both the analysis based on species presence at a pin and species presence in a quadrat. The relationship between time and similarity to others in treatment level as well as to initial composition was significant only for the control in the case of species presence at a pin and for control and low treatment levels in the case of species presence in a quadrat

Number of sapling species per paddock, density of saplings and sapling crown volume were significantly different overall, but there were no significant differences between treatment level within each survey. The regression of time against sapling species per paddock was significant in the control, low and high treatment levels, while the regression of time against density was significant for the control and medium treatment levels. None of the other variables (both uni- and multivariate and for both the saplings and all woody plants) were significantly different between treatment level or survey and neither was the biomass yield of the herbaceous layer.

The null hypothesis that cattle would not have a significant effect on the selected variables is therefore rejected. However, the secondary null hypothesis that the effects of cattle are independent of treatment level could not be rejected because there were no significant differences between the low, medium or high treatment levels in those cases where a significant overall effect was detected.

Although the cattle did have a significant overall effect on a few of the selected variables, none of these effects could without any doubt be ascribed to the level of grazing and in all significant cases there was an interaction of time with treatment level. It can therefore not be unequivocally stated from the results of the present study that cattle would affect the process of plant community succession in rehabilitating coastal dune forest. However, cattle had a striking effect

on the amount of variability, evident in a treatment-level dependent increase in the coefficient of variation in the selected variables. The increase in coefficient of variation was probably the reason why there were only two significant regressions of time with the given variable (in both cases it was the control) and no significant differences between slopes of regression lines for the different treatment levels. It was probably also the cause of the significant time-treatment interactions in some variables.

Increased variability in the selected variables could have been caused by a variety of factors, but the most likely is a differential response of plant species and growth-types to the disturbance caused by cattle. Variability in vegetation cover may have important long-term consequences for the stability of soil structure and conditions for later successional species to germinate and establish. In the same vein the number of species per quadrat reflects on the 'structural' species diversity at any point, which affects the germination conditions of other species. Since the process of rehabilitating a coastal dune forest is completely dependent on the development of a succession of (clearly and sometimes not so clearly circumscribed) plant communities, it is conceivable that a disturbance by cattle will in the long term significantly affect the rehabilitation of these plant communities.

Appendix 1. List of all plant species recorded in experimental grazing paddocks over all treatment levels in six surveys.

| Family | Name | Survey | | | | | |
|----------------|---|--------|----|----|----|----|----|
| | | S1 | S2 | S3 | S4 | S5 | S6 |
| Unknown | sp. (B255) | - | - | - | - | - | 1 |
| Unknown | sp. (R75) | - | 1 | - | - | - | - |
| POLYPODIACEAE | <i>Microsorium scolopendrium</i> (Burm. f.) Copel. | 1 | 1 | 1 | 1 | - | 1 |
| CYPERACEAE | <i>Cyperus albostrigatus</i> Schrad. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Mariscus dregeanus</i> Kunth | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Mariscus macrocarpus</i> Kunth | - | - | 1 | 1 | - | 1 |
| ARECACEAE | <i>Phoenix reclinata</i> Jacq. | 1 | - | - | - | - | - |
| COMMELINACEAE | <i>Commelina benghalensis</i> L. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Commelina eckloniana</i> Kunth | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Aneilema aequinoctiale</i> (Beauv.) Loudon | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Coleotrype natalensis</i> C.B. C.L. | 1 | 1 | 1 | 1 | 1 | 1 |
| ASPHODELACEAE | <i>Anthericum saundersiae</i> Bak. | 1 | - | - | - | - | - |
| HYACINTHACEAE | <i>Ornithogalum tenuifolium</i> Delaroche subsp. <i>tenuifolium</i> | - | - | - | 1 | - | - |
| ASPARAGACEAE | <i>Protasparagus africanus</i> (Lam.) Oberm. | 1 | 1 | 1 | 1 | 1 | 1 |
| AMARYLLIDACEAE | <i>Scadoxus puniceus</i> (L.) Friis. & Nordal | 1 | 1 | 1 | 1 | 1 | 1 |
| DIOSCOREACEAE | <i>Dioscorea sylvatica</i> (Kunth.) Eckl. | 1 | 1 | - | - | - | - |
| ULMACEAE | <i>Celtis africana</i> Burm. f. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Chaetacme aristata</i> Planch. | - | - | 1 | - | 1 | 1 |
| URTICACEAE | <i>Laportea peduncularis</i> (Wedd.) Chew subsp. <i>latidens</i> Friis. | 1 | 1 | 1 | 1 | 1 | 1 |
| AMARANTHACEAE | <i>Amaranthus thunbergii</i> Moq. | - | - | - | 1 | 1 | 1 |
| | <i>Pupalia lappacea</i> (L.) A. Juss. var. <i>lappacea</i> | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Achyranthes aspera</i> (L.) * | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Achyroopsis avicularis</i> (E. Mey. ex Moq.) Cooke & Wright | 1 | 1 | 1 | 1 | 1 | 1 |
| NYCTAGINACEAE | <i>Commicarpus chinensis</i> L. Heimerl subsp. <i>natalensis</i> Meikle | 1 | 1 | 1 | 1 | 1 | 1 |
| MENISPERMACEAE | <i>Cissampelos torulosa</i> E. Mey. ex Harv. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Tinospora caffra</i> (Miers) Troupin | 1 | 1 | - | - | 1 | 1 |
| CAPPARACEAE | <i>Maerua</i> Forssk. sp. | 1 | 1 | - | - | - | - |
| FABACEAE | <i>Acacia karroo</i> Hayne | 1 | 1 | 1 | 1 | 1 | 1 |
| OXALIDACEAE | <i>Oxalis corniculata</i> L. | - | 1 | - | 1 | 1 | 1 |

* Exotic species

| Appendix 1. (continued) | | S1 | S2 | S3 | S4 | S5 | S6 |
|-------------------------|--|----|----|----|----|----|----|
| RUTACEAE | <i>Zanthoxylum capense</i> (Thunb.) Harv. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Vepris lanceolata</i> (Lam.) G. Don | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Teclea gerrardii</i> Verdoorn | - | - | 1 | - | 1 | - |
| | <i>Clausena anisata</i> (Willd.) Hook. f. ex Benth | 1 | 1 | 1 | 1 | 1 | 1 |
| MELIACEAE | <i>Trichilia emetica</i> Vahl | 1 | 1 | 1 | 1 | 1 | 1 |
| EUPHORBIACEAE | <i>Phyllanthus burchellii</i> Muell. Arg. | 1 | - | - | - | - | - |
| | <i>Tragia glabrata</i> (Mull. Arg.) Pax & K. Hoffm. var. <i>glabrata</i> | 1 | 1 | 1 | - | - | - |
| ANACARDIACEAE | <i>Rhus natalensis</i> Bernh. ex Krauss | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Rhus nebulosa</i> Schonl. | 1 | 1 | 1 | 1 | 1 | 1 |
| CELASTRACEAE | <i>Maytenus nemorosa</i> (Eckl. & Zeyh.) Marais | - | 1 | 1 | 1 | 1 | 1 |
| | <i>Maytenus procumbens</i> (L. f.) Loes. | 1 | 1 | - | 1 | 1 | 1 |
| ICACINACEAE | <i>Apodytes dimidiata</i> E. Mey. ex Arn. subsp. <i>dimidiata</i> | 1 | 1 | 1 | 1 | 1 | 1 |
| SAPINDACEAE | <i>Allophylus natalensis</i> (Sond.) De Winter | 1 | 1 | 1 | 1 | 1 | 1 |
| RHAMNACEAE | <i>Scutia myrtina</i> (Burm. f.) Kurz | 1 | 1 | 1 | 1 | 1 | 1 |
| VITACEAE | <i>Rhoicissus digitata</i> (L. f.) Gilg & Brandt | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Cyphostemma flaviflorum</i> (Sprague) Desc. ex Wild & Drum. | - | - | 1 | 1 | 1 | 1 |
| TILIACEAE | <i>Grewia caffra</i> Meisn. | 1 | 1 | 1 | 1 | 1 | 1 |
| PASSIFLORACEAE | <i>Adenia gummifera</i> (Harv.) Harms var. <i>gummifera</i> | 1 | 1 | 1 | 1 | 1 | 1 |
| THYMELAEACEAE | <i>Peddiea africana</i> Harv. | - | - | - | 1 | 1 | 1 |
| MYRTACEAE | <i>Eugenia capensis</i> (Eckl. & Zeyh.) Harv. ex Sond. | 1 | 1 | 1 | 1 | 1 | 1 |
| SAPOTACEAE | <i>Sideroxylon inerme</i> L. subsp. <i>inerme</i> | - | 1 | 1 | 1 | 1 | 1 |
| | <i>Mimusops caffra</i> E. Mey. ex A. DC. | 1 | 1 | 1 | 1 | 1 | 1 |
| ASCLEPIADACEAE | <i>Cynanchum ellipticum</i> (Harv.) R.A. Dyer | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Sarcostemma viminale</i> (L.) R. Br. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Secamone alpini</i> Schultes | 1 | - | - | - | - | - |
| | <i>Secamone filiformis</i> (L.f.) J.H. Ross | 1 | 1 | 1 | 1 | 1 | 1 |
| CONVOLVULACEAE | <i>Ipomoea ficifolia</i> Lindl. | - | - | - | 1 | 1 | 1 |
| VERBENACEAE | <i>Clerodendrum glabrum</i> E. Mey. var. <i>glabrum</i> | - | 1 | 1 | 1 | 1 | 1 |
| SOLANACEAE | <i>Solanum</i> L. sp. | - | 1 | - | 1 | 1 | - |
| ACANTHACEAE | <i>Asystasia gangetica</i> (L.) T. Anders. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Isoglossa woodii</i> C.B. C.L. | - | 1 | - | - | 1 | 1 |

Appendix 1. (continued)

| | | S1 | S2 | S3 | S4 | S5 | S6 |
|---------------|---|----|----|----|----|----|----|
| RUBIACEAE | <i>Catunaregam spinosa</i> (Thunb.) Tirvengadam subsp. <i>spinosa</i> | - | - | 1 | - | - | - |
| | <i>Tricalysia sonderiana</i> Hiern. | - | - | - | 1 | - | 1 |
| | <i>Kraussia floribunda</i> Harv. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Canthium inerme</i> (L. f.) Kuntze | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Psydrax obovata</i> (Eckl. & Zeyh.) Bridson | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Psychotria capensis</i> (Eckl.) Vatke | - | - | - | - | - | 1 |
| | <i>Rubia cordifolia</i> L. subsp. <i>conotricha</i> (Gand.) Verdc. | - | - | - | 1 | - | - |
| CUCURBITACEAE | <i>Zehneria parvifolia</i> (Cogn.) J.H. Ross | 1 | 1 | - | 1 | 1 | 1 |
| | <i>Momordica balsamina</i> L. | - | 1 | - | - | - | - |
| | <i>Coccinia variifolia</i> A. Meeuse | 1 | 1 | 1 | 1 | 1 | 1 |
| ASTERACEAE | <i>Vernonia angulifolia</i> DC. | - | - | 1 | 1 | 1 | 1 |
| | <i>Vernonia aurantiaca</i> (O. Hoffm.) N.E. Br. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Chromolaena odorata</i> (L.) R.M. King & H. Robson | 1 | - | - | - | - | - |
| | <i>Mikania natalensis</i> DC. | - | - | - | - | 1 | - |
| | <i>Conyza albida</i> Spreng. * | 1 | - | - | - | 1 | 1 |
| | <i>Brachylaena discolor</i> DC. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Helichrysum decorum</i> DC. | - | 1 | - | 1 | - | - |
| | <i>Bidens pilosa</i> L. | - | - | 1 | 1 | 1 | 1 |
| | <i>Crassocephalum crepidoides</i> (Benth) S. Moore | - | - | - | 1 | - | - |
| | <i>Senecio</i> L. sp. | - | 1 | - | 1 | 1 | 1 |
| | <i>Senecio</i> cf. <i>helminthoides</i> (Sch. Bip.) Hilliard | - | - | - | 1 | 1 | 1 |
| | <i>Senecio deltoideus</i> Less. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Senecio helminthoides</i> (Sch. Bip.) Hilliard | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Senecio oxyodontus</i> DC. | - | - | - | 1 | - | 1 |
| | <i>Senecio quinquelobus</i> (Thunb.) DC. | 1 | 1 | 1 | - | - | - |
| POACEAE | <i>Imperata cylindrica</i> (L.) Raeuschel | 1 | - | - | - | - | - |
| | <i>Digitaria diversinervis</i> (Nees) Stapf | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Brachiaria chusqueoides</i> (Hack.) Clayton | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Panicum laticomum</i> Nees. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Panicum maximum</i> Jacq. | 1 | 1 | 1 | 1 | 1 | 1 |
| | <i>Dactyloctenium australe</i> Steud. | 1 | 1 | 1 | 1 | 1 | 1 |

* Exotic species

Appendix 2. The total mass (kg) of cattle in three treatment levels over five grazing cycles. Cattle were weighed each morning before being put into the treatment paddocks.

| Treatment level | Grazing cycle | | | | |
|-----------------|---------------|------|------|------|------|
| | 1 | 2 | 3 | 4 | 5 |
| Low | 1020 | 1160 | 980 | 845 | 1165 |
| | 1020 | 1200 | 955 | 880 | 1105 |
| | 1020 | 1165 | 950 | 870 | 1165 |
| | 1020 | 1235 | 985 | 865 | 1140 |
| Medium | 2040 | 2330 | 1920 | 1710 | 2885 |
| | 2040 | 2350 | 1670 | 1745 | 2910 |
| | 2040 | 2505 | 1375 | 1710 | 2815 |
| | 2040 | 2405 | 1920 | 1755 | 2980 |
| High | 3060 | 4865 | 4070 | 3530 | 5970 |
| | 3060 | 4800 | 4090 | 3405 | 5930 |
| | 3060 | 4565 | 4085 | 3450 | 5970 |
| | 3060 | 4870 | 4045 | 3455 | 5540 |

Appendix 3. The relative number of records in three treatment levels (=levels of grazing pressure) for each activity of cattle while inside the treatment paddocks.

| Treatment level | Activity | | | | | | | |
|-----------------|----------|----------|----------|--------------|------------------|------------|---------|-----------------|
| | Eating | Foraging | Sleeping | Resting down | Resting standing | Ruminating | Walking | Social activity |
| Low | 0.56 | 0.04 | 0.00 | 0.02 | 0.08 | 0.15 | 0.02 | 0.13 |
| | 0.40 | 0.12 | 0.00 | 0.12 | 0.15 | 0.00 | 0.12 | 0.10 |
| | 0.50 | 0.02 | 0.00 | 0.00 | 0.12 | 0.00 | 0.19 | 0.17 |
| | 0.69 | 0.04 | 0.00 | 0.00 | 0.10 | 0.00 | 0.06 | 0.12 |
| Medium | 0.86 | 0.06 | 0.00 | 0.00 | 0.00 | 0.01 | 0.07 | 0.01 |
| | 0.61 | 0.03 | 0.00 | 0.09 | 0.06 | 0.14 | 0.03 | 0.05 |
| | 0.61 | 0.02 | 0.00 | 0.01 | 0.15 | 0.06 | 0.07 | 0.09 |
| | 0.93 | 0.01 | 0.00 | 0.00 | 0.03 | 0.01 | 0.02 | 0.00 |
| High | 0.75 | 0.01 | 0.00 | 0.01 | 0.03 | 0.14 | 0.02 | 0.02 |
| | 0.76 | 0.05 | 0.00 | 0.01 | 0.03 | 0.01 | 0.04 | 0.09 |
| | 0.89 | 0.01 | 0.00 | 0.02 | 0.00 | 0.01 | 0.01 | 0.06 |
| | 0.87 | 0.02 | 0.00 | 0.00 | 0.00 | 0.05 | 0.01 | 0.04 |

Appendix 4. The density (individuals/ha), stem diameter (cm), number of stems per tree and height (cm) of canopy-class trees growing inside paddocks of four treatment levels (=levels of grazing pressure).

| Treatment level | Variable | | | |
|-----------------|----------|---------------|----------------|---------|
| | Density | Stem diameter | Stems per tree | Height |
| Control | 100.00 | 27.30 | 1.67 | 1000.00 |
| | 104.66 | 42.35 | 2.55 | 977.50 |
| | 110.80 | 30.53 | 1.66 | 950.00 |
| | 110.80 | 32.26 | 2.13 | 950.00 |
| Low | 101.56 | 27.75 | 1.79 | 992.31 |
| | 102.14 | 38.88 | 1.53 | 989.47 |
| | 86.65 | 29.93 | 1.29 | 1074.29 |
| | 99.41 | 28.73 | 1.97 | 1002.94 |
| Medium | 103.32 | 26.87 | 1.65 | 983.82 |
| | 98.55 | 31.85 | 1.65 | 1007.35 |
| | 79.72 | 30.83 | 2.65 | 1120.00 |
| | 113.54 | 23.33 | 2.54 | 938.46 |
| High | 98.21 | 26.11 | 1.64 | 1009.09 |
| | 110.44 | 37.10 | 1.78 | 951.56 |
| | 94.09 | 27.00 | 1.86 | 1030.95 |
| | 108.13 | 20.06 | 2.40 | 961.67 |

Appendix 5. The number of species per pin (a), number of species per quadrat (b), number of species per paddock (c), percentage herbaceous cover (d), percentage ground cover (e) and vegetation height in cm (f) in paddocks of four treatment levels (=levels of grazing pressure).

| Treatment level | Survey | | | | | |
|--------------------------------------|--------|------|------|---|------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(a) Number of species per pin</i> | | | | | | |
| Control | 1.45 | 1.80 | 1.33 | - | 1.65 | 1.54 |
| | 1.81 | 2.45 | 1.76 | - | 1.58 | 1.64 |
| | 1.91 | 2.17 | 1.55 | - | 1.69 | 1.56 |
| | 2.02 | 2.23 | 1.77 | - | 2.10 | 1.54 |
| Low | 1.48 | 1.73 | 1.28 | - | 1.83 | 1.86 |
| | 1.57 | 2.36 | 1.46 | - | 2.23 | 1.94 |
| | 1.90 | 2.08 | 1.17 | - | 1.70 | 1.67 |
| | 2.10 | 2.56 | 1.59 | - | 1.91 | 1.39 |
| Medium | 1.83 | 1.97 | 1.36 | - | 1.80 | 1.63 |
| | 1.64 | 1.61 | 1.11 | - | 1.51 | 1.33 |
| | 1.81 | 2.02 | 1.14 | - | 1.53 | 1.60 |
| | 2.07 | 2.59 | 1.56 | - | 2.16 | 1.77 |
| High | 1.78 | 2.18 | 1.18 | - | 1.18 | 1.36 |
| | 1.73 | 1.92 | 0.85 | - | 0.81 | 1.02 |
| | 1.48 | 1.92 | 1.37 | - | 1.70 | 1.48 |
| | 1.61 | 2.52 | 1.08 | - | 1.77 | 1.42 |

Appendix 5. (continued)

| Treatment level | Survey | | | | | |
|---|--------|-------|------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(b) Number of species per 1m² quadrat</i> | | | | | | |
| Control | 6.50 | 7.50 | 6.67 | 7.33 | 6.33 | 6.33 |
| | 10.67 | 9.83 | 8.83 | 10.00 | 7.50 | 7.00 |
| | 7.67 | 9.00 | 7.67 | 8.67 | 7.00 | 6.00 |
| | 9.33 | 8.17 | 7.33 | 7.83 | 8.17 | 6.50 |
| Low | 9.50 | 10.67 | 6.67 | 12.33 | 11.83 | 9.33 |
| | 12.17 | 10.67 | 8.83 | 14.17 | 15.17 | 12.17 |
| | 8.00 | 9.67 | 7.67 | 9.83 | 9.00 | 7.50 |
| | 9.17 | 8.50 | 7.33 | 8.67 | 8.67 | 5.50 |
| Medium | 11.00 | 11.00 | 9.83 | 10.50 | 12.50 | 10.50 |
| | 8.50 | 10.50 | 8.67 | 12.17 | 11.33 | 8.50 |
| | 7.33 | 8.17 | 7.00 | 7.83 | 7.17 | 7.50 |
| | 8.83 | 11.33 | 9.33 | 10.50 | 10.33 | 7.83 |
| High | 9.67 | 11.83 | 8.33 | 12.83 | 11.33 | 10.33 |
| | 12.00 | 12.67 | 8.83 | 14.83 | 14.00 | 11.00 |
| | 7.67 | 9.00 | 5.83 | 7.33 | 7.00 | 5.67 |
| | 9.50 | 9.00 | 7.67 | 10.17 | 10.17 | 7.67 |

Appendix 5. (continued)

| Treatment level | Survey | | | | | |
|--|--------|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(c) Number of species per paddock</i> | | | | | | |
| Control | 19 | 17 | 19 | 20 | 19 | 18 |
| | 20 | 21 | 20 | 19 | 18 | 15 |
| | 17 | 19 | 19 | 19 | 17 | 14 |
| | 22 | 21 | 19 | 20 | 19 | 14 |
| Low | 25 | 24 | 27 | 28 | 31 | 29 |
| | 26 | 26 | 25 | 32 | 33 | 29 |
| | 17 | 22 | 19 | 23 | 23 | 20 |
| | 21 | 24 | 22 | 24 | 20 | 14 |
| Medium | 26 | 28 | 28 | 30 | 31 | 31 |
| | 21 | 24 | 22 | 30 | 25 | 21 |
| | 19 | 21 | 19 | 20 | 19 | 18 |
| | 24 | 24 | 22 | 21 | 25 | 21 |
| High | 21 | 26 | 20 | 27 | 28 | 27 |
| | 27 | 34 | 27 | 37 | 37 | 34 |
| | 18 | 21 | 15 | 18 | 17 | 17 |
| | 18 | 19 | 17 | 21 | 23 | 17 |

Appendix 5. (continued)

| Treatment level | Survey | | | | | |
|-----------------------------|--------|--------|-------|---|--------|--------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(d) Herbaceous cover</i> | | | | | | |
| Control | 93.94 | 100.00 | 98.48 | - | 100.00 | 100.00 |
| | 90.91 | 99.24 | 97.73 | - | 97.73 | 95.45 |
| | 96.21 | 96.97 | 93.18 | - | 99.24 | 96.21 |
| | 98.48 | 98.48 | 96.21 | - | 99.24 | 100.00 |
| Low | 95.45 | 91.67 | 81.82 | - | 96.97 | 95.45 |
| | 85.61 | 100.00 | 82.58 | - | 96.97 | 94.70 |
| | 99.24 | 97.73 | 82.58 | - | 95.45 | 95.45 |
| | 93.94 | 100.00 | 93.18 | - | 100.00 | 98.48 |
| Medium | 90.91 | 93.94 | 82.58 | - | 94.70 | 91.67 |
| | 90.15 | 93.94 | 79.55 | - | 91.67 | 86.36 |
| | 93.94 | 100.00 | 87.88 | - | 90.15 | 93.18 |
| | 96.97 | 99.24 | 87.88 | - | 100.00 | 98.48 |
| High | 86.36 | 97.73 | 70.45 | - | 75.00 | 84.85 |
| | 87.12 | 92.42 | 59.09 | - | 52.27 | 74.24 |
| | 92.42 | 100.00 | 94.70 | - | 99.24 | 96.97 |
| | 94.70 | 99.24 | 76.52 | - | 96.97 | 93.18 |

Appendix 5. (continued)

| Treatment level | Survey | | | | | |
|-------------------------|--------|-------|-------|---|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(e) Ground cover</i> | | | | | | |
| Control | 67.42 | 68.18 | 78.03 | - | 73.48 | 87.88 |
| | 59.85 | 66.67 | 68.94 | - | 66.67 | 79.55 |
| | 64.39 | 48.48 | 47.73 | - | 75.00 | 80.30 |
| | 74.24 | 71.21 | 71.97 | - | 79.55 | 78.79 |
| Low | 45.45 | 45.45 | 48.48 | - | 52.27 | 64.39 |
| | 47.73 | 65.91 | 41.67 | - | 50.00 | 44.70 |
| | 72.73 | 62.88 | 35.61 | - | 59.09 | 75.00 |
| | 78.03 | 62.88 | 64.39 | - | 75.00 | 81.06 |
| Medium | 72.73 | 50.00 | 34.09 | - | 56.06 | 55.30 |
| | 61.36 | 39.39 | 35.61 | - | 37.88 | 40.91 |
| | 59.85 | 67.42 | 46.97 | - | 68.18 | 66.67 |
| | 73.48 | 59.85 | 55.30 | - | 59.09 | 67.42 |
| High | 54.55 | 48.48 | 31.82 | - | 20.45 | 36.36 |
| | 57.58 | 42.42 | 21.21 | - | 12.88 | 24.24 |
| | 75.76 | 61.36 | 67.42 | - | 81.82 | 87.88 |
| | 64.39 | 65.15 | 32.58 | - | 46.97 | 53.79 |

Appendix 5. (continued)

| Treatment level | Survey | | | | | |
|-------------------|--------|----|----|---|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(f) Height</i> | | | | | | |
| Control | 25 | 35 | 40 | - | 45 | 40 |
| | 25 | 40 | 35 | - | 45 | 45 |
| | 30 | 55 | 35 | - | 55 | 45 |
| | 30 | 50 | 30 | - | 45 | 50 |
| Low | 30 | 30 | 30 | - | 45 | 50 |
| | 25 | 45 | 35 | - | 40 | 45 |
| | 30 | 40 | 30 | - | 35 | 40 |
| | 30 | 60 | 25 | - | 45 | 40 |
| Medium | 25 | 30 | 30 | - | 35 | 40 |
| | 30 | 35 | 30 | - | 35 | 35 |
| | 30 | 35 | 25 | - | 30 | 40 |
| | 35 | 45 | 25 | - | 45 | 40 |
| High | 25 | 40 | 25 | - | 25 | 30 |
| | 25 | 30 | 15 | - | 25 | 25 |
| | 20 | 30 | 25 | - | 35 | 30 |
| | 25 | 40 | 20 | - | 30 | 30 |

Appendix 6. Bray-Curtis similarity of each paddock in a treatment level to other paddocks of the same treatment level, within each survey. Species presence at a pin was not recorded during survey 4.

| Treatment level | Survey | | | | | |
|-----------------------|--------|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Control 1 : Control 2 | 62.57 | 63.20 | 63.92 | 70.53 | 63.14 | 53.68 |
| Control 1 : Control 3 | 42.15 | 43.33 | 50.72 | 59.67 | 58.95 | 47.51 |
| Control 1 : Control 4 | 54.62 | 51.25 | 62.80 | 59.92 | 55.13 | 43.37 |
| Control 2 : Control 3 | 57.27 | 66.96 | 64.53 | 68.91 | 67.13 | 60.19 |
| Control 2 : Control 4 | 69.75 | 68.93 | 64.52 | 63.63 | 67.19 | 55.63 |
| Control 3 : Control 4 | 62.10 | 68.07 | 61.94 | 68.18 | 66.48 | 69.38 |
| Low 1 : Low 2 | 61.62 | 49.08 | 46.96 | 63.54 | 65.16 | 51.22 |
| Low 1 : low 3 | 51.43 | 51.49 | 51.45 | 61.43 | 60.74 | 46.89 |
| Low 1 : Low 4 | 51.64 | 46.52 | 51.73 | 50.78 | 49.42 | 27.52 |
| Low 2 : Low 3 | 55.99 | 57.48 | 53.10 | 62.10 | 64.89 | 62.56 |
| Low 2 : Low 4 | 59.79 | 50.50 | 53.80 | 53.67 | 51.89 | 29.24 |
| Low 3 : Low 4 | 64.82 | 69.08 | 59.32 | 65.06 | 64.69 | 34.87 |
| Medium 1 : Medium 2 | 75.82 | 70.05 | 61.52 | 71.68 | 72.22 | 66.41 |
| Medium 1 : Medium 3 | 56.00 | 55.83 | 53.36 | 60.82 | 52.72 | 58.96 |
| Medium 1 : Medium 4 | 59.54 | 53.17 | 53.69 | 53.33 | 57.81 | 53.72 |
| Medium 2 : Medium 3 | 56.35 | 50.99 | 42.72 | 53.29 | 50.31 | 49.65 |
| Medium 2 : Medium 4 | 66.04 | 62.75 | 64.49 | 58.09 | 62.87 | 50.49 |
| Medium 3 : Medium 4 | 53.87 | 59.72 | 48.07 | 55.62 | 48.64 | 51.84 |
| High 1 : High 2 | 62.61 | 60.68 | 62.33 | 74.08 | 65.95 | 67.90 |
| High 1 : High 3 | 67.85 | 72.49 | 66.58 | 69.25 | 61.22 | 65.18 |
| High 1 ; High 4 | 66.33 | 65.60 | 57.32 | 65.20 | 56.41 | 51.30 |
| High 2 : High 3 | 56.43 | 54.44 | 51.46 | 54.85 | 52.76 | 53.15 |
| High 2 : High 4 | 60.52 | 52.22 | 53.43 | 58.53 | 60.74 | 50.05 |
| High 3 : High 4 | 65.48 | 66.25 | 62.04 | 59.95 | 64.45 | 60.06 |

Appendix 7. Bray-Curtis similarity of each paddock in four successive surveys to its own species composition in survey 1, in four treatment levels. Species presence at a pin was not recorded during survey 4.

| Treatment level | Survey | | | | |
|-----------------|--------|-------|-------|-------|-------|
| | 2 | 3 | 4 | 5 | 6 |
| Control | 79.85 | 82.08 | 80.18 | 78.05 | 69.59 |
| | 85.67 | 83.76 | 83.68 | 78.41 | 65.45 |
| | 87.73 | 88.58 | 77.37 | 84.61 | 69.32 |
| | 82.19 | 80.73 | 69.64 | 80.07 | 66.45 |
| Low | 75.96 | 78.18 | 78.10 | 80.74 | 77.43 |
| | 86.18 | 76.67 | 83.65 | 80.95 | 81.60 |
| | 78.48 | 72.49 | 73.46 | 69.74 | 66.45 |
| | 82.36 | 81.25 | 78.95 | 71.97 | 50.40 |
| Medium | 84.74 | 83.68 | 83.81 | 78.77 | 78.55 |
| | 79.19 | 82.72 | 72.09 | 83.15 | 79.62 |
| | 84.29 | 86.13 | 72.85 | 78.84 | 80.76 |
| | 88.87 | 90.48 | 78.48 | 76.20 | 73.39 |
| High | 84.42 | 80.84 | 74.05 | 73.64 | 72.88 |
| | 81.81 | 79.32 | 74.53 | 77.03 | 70.88 |
| | 86.69 | 71.29 | 77.67 | 72.55 | 71.67 |
| | 90.05 | 79.37 | 76.91 | 77.21 | 74.62 |

Appendix 8. Number of sapling species per paddock (a), density of saplings as individuals/ha (b) and crown volume in cm³ (c) in four treatment levels and in five surveys. Saplings were not surveyed during survey 4 and crown volume was not measured during survey 1.

| Treatment level | Survey | | | | | |
|--|---------|---------|---------|---|---------|---------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(a) Number of sapling species per paddock</i> | | | | | | |
| Control | 11 | 12 | 13 | - | 12 | 12 |
| | 12 | 12 | 13 | - | 11 | 11 |
| | 13 | 12 | 10 | - | 10 | 11 |
| | 11 | 10 | 10 | - | 12 | 10 |
| Low | 13 | 13 | 13 | - | 12 | 12 |
| | 12 | 11 | 10 | - | 10 | 10 |
| | 12 | 12 | 12 | - | 11 | 10 |
| | 11 | 9 | 10 | - | 9 | 9 |
| Medium | 13 | 11 | 11 | - | 12 | 12 |
| | 13 | 13 | 14 | - | 14 | 15 |
| | 14 | 14 | 12 | - | 11 | 11 |
| | 10 | 9 | 8 | - | 7 | 7 |
| High | 17 | 17 | 15 | - | 14 | 13 |
| | 14 | 16 | 16 | - | 15 | 16 |
| | 11 | 11 | 11 | - | 10 | 9 |
| | 12 | 11 | 11 | - | 11 | 11 |
| <i>(b) Density of saplings</i> | | | | | | |
| Control | 2941.68 | 2764.02 | 2995.60 | - | 2652.47 | 607.91 |
| | 2453.78 | 2258.60 | 2276.60 | - | 1779.09 | 1573.66 |
| | 707.96 | 236.26 | 252.15 | - | 143.88 | 147.92 |
| | 1754.34 | 1201.11 | 1098.87 | - | 403.08 | 1079.40 |
| Low | 5804.99 | 3896.10 | 3926.67 | - | 2531.55 | 2019.95 |
| | 5731.97 | 5178.82 | 5194.38 | - | 7041.91 | 6486.19 |
| | 1054.71 | 345.12 | 341.93 | - | 104.77 | 114.78 |
| | 437.90 | 56.41 | 72.22 | - | 55.61 | 77.03 |
| Medium | 4544.88 | 2863.50 | 2413.76 | - | 1932.13 | 1932.13 |
| | 5898.24 | 5631.12 | 6723.42 | - | 5897.42 | 5434.34 |
| | 756.64 | 587.70 | 365.18 | - | 184.84 | 200.06 |
| | 582.51 | 469.12 | 523.10 | - | 529.69 | 529.69 |
| High | 3836.00 | 3093.58 | 3767.64 | - | 3027.63 | 2659.41 |
| | 4407.64 | 3836.00 | 3758.02 | - | 3219.15 | 3826.12 |
| | 258.44 | 91.16 | 153.87 | - | 159.51 | 77.93 |
| | 1810.77 | 1359.13 | 1883.53 | - | 2258.60 | 1900.67 |

Appendix 8. (continued)

| Treatment level | Survey | | | | | |
|-------------------------------------|--------|------------|------------|---|------------|------------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>(c) Crown volume of saplings</i> | | | | | | |
| Control | - | 407339.39 | 570816.75 | - | 637886.48 | 561529.81 |
| | - | 340817.81 | 380873.11 | - | 381719.87 | 420862.97 |
| | - | 480582.58 | 444949.40 | - | 551786.83 | 592890.83 |
| | - | 475460.41 | 884055.63 | - | 404595.30 | 2238805.28 |
| Low | - | 285762.21 | 616693.00 | - | 387741.26 | 461589.14 |
| | - | 183664.54 | 195952.75 | - | 314891.49 | 362755.78 |
| | - | 883496.10 | 853821.71 | - | 792106.77 | 613428.69 |
| | - | 516239.11 | 1593975.39 | - | 1012646.92 | 982798.17 |
| Medium | - | 434169.74 | 301376.09 | - | 433981.57 | 418674.49 |
| | - | 277814.15 | 233316.43 | - | 439683.89 | 382505.98 |
| | - | 435646.45 | 217299.18 | - | 304257.00 | 403359.97 |
| | - | 1010542.79 | 858785.94 | - | 851237.73 | 759328.30 |
| High | - | 613723.21 | 1149880.18 | - | 674100.70 | 517896.46 |
| | - | 509011.64 | 450908.54 | - | 447681.04 | 498187.87 |
| | - | 563939.26 | 286929.15 | - | 526524.68 | 270697.29 |
| | - | 729385.37 | 608851.29 | - | 391983.22 | 497005.68 |

Appendix 9. The crown volume in cm³ (a), number of species per survey plot (b), density (individual trees/25m²) (c), tree height in cm (d), number of stems per tree (e) and stem diameter in cm (f) of all woody plants in paddocks of four treatment levels. This survey was done once only after grazing had been applied.

| Treatment level | Height class | | | |
|------------------------------|--------------|-------------|-----------|----------|
| | Canopy | Sub-canopy | Sapling | Seedling |
| <i>(a) Volume</i> | | | | |
| Control | - | 11751031.25 | 377859.24 | 7875.00 |
| | - | 6590900.00 | 298441.15 | 2158.33 |
| | - | 9072665.42 | 212324.19 | 878.80 |
| | - | 4855642.33 | 703844.08 | 928.05 |
| Low | - | 3750530.73 | 353590.56 | 3492.27 |
| | - | 2676514.03 | 257019.28 | 5346.70 |
| | - | 9206310.83 | 425231.34 | 1228.80 |
| | - | 4434601.25 | 641129.29 | 0.00 |
| Medium | - | 4251332.50 | 284719.71 | 3565.30 |
| | - | 4438600.00 | 313944.71 | 8970.33 |
| | - | 3618720.00 | 102951.58 | 494.40 |
| | - | 1271310.00 | 216001.30 | 2568.93 |
| High | - | 2476606.58 | 256751.86 | 5810.69 |
| | - | 6619851.13 | 231518.37 | 8493.97 |
| | - | 9863320.00 | 37774.25 | 11794.50 |
| | - | 4382819.96 | 297977.35 | 17179.28 |
| <i>(b) Species per block</i> | | | | |
| Control | 0.60 | 1.60 | 6.00 | 1.00 |
| | 0.80 | 2.40 | 3.60 | 1.60 |
| | 0.80 | 2.60 | 3.00 | 0.20 |
| Low | 0.60 | 3.20 | 1.80 | 0.80 |
| | 0.80 | 2.80 | 6.80 | 0.60 |
| | 0.80 | 2.00 | 8.00 | 2.20 |
| | 0.80 | 1.60 | 2.00 | 0.20 |
| Medium | 0.80 | 1.60 | 2.40 | 0.00 |
| | 1.00 | 3.40 | 7.60 | 1.20 |
| | 0.60 | 2.00 | 7.20 | 1.40 |
| | 0.40 | 0.60 | 2.40 | 0.20 |
| High | 0.40 | 0.60 | 3.00 | 0.80 |
| | 1.00 | 4.20 | 5.20 | 2.20 |
| | 1.00 | 3.60 | 7.80 | 4.00 |
| | 0.60 | 1.60 | 1.80 | 0.80 |
| | 1.00 | 3.20 | 3.60 | 1.80 |

Appendix 9. (continued)

| Treatment level | Height class | | | |
|--------------------|--------------|------------|---------|----------|
| | Canopy | Sub-canopy | Sapling | Seedling |
| <i>(c) Density</i> | | | | |
| Control | 0.80 | 2.00 | 8.40 | 1.00 |
| | 0.80 | 2.80 | 4.00 | 1.60 |
| | 2.00 | 3.80 | 3.60 | 0.20 |
| | 1.00 | 3.40 | 2.60 | 0.80 |
| Low | 1.60 | 3.80 | 8.40 | 0.80 |
| | 2.40 | 2.80 | 11.40 | 2.20 |
| | 1.60 | 2.60 | 2.00 | 0.20 |
| | 1.00 | 2.00 | 2.80 | 0.00 |
| Medium | 1.40 | 4.20 | 10.60 | 1.40 |
| | 1.00 | 2.00 | 11.40 | 1.80 |
| | 0.40 | 0.60 | 2.40 | 1.00 |
| | 0.40 | 0.60 | 8.60 | 1.20 |
| High | 1.00 | 5.20 | 6.40 | 2.60 |
| | 2.00 | 5.40 | 13.40 | 5.20 |
| | 0.80 | 2.40 | 2.00 | 0.80 |
| | 2.20 | 3.80 | 8.00 | 2.80 |
| <i>(d) Height</i> | | | | |
| Control | 600.00 | 270.50 | 115.10 | 34.60 |
| | 860.00 | 303.33 | 126.83 | 19.33 |
| | 903.33 | 314.88 | 124.00 | 9.60 |
| Low | 640.00 | 310.87 | 126.50 | 11.60 |
| | 795.00 | 279.75 | 132.13 | 13.87 |
| | 793.33 | 200.45 | 111.97 | 36.85 |
| | 820.00 | 346.60 | 104.75 | 8.40 |
| Medium | 900.00 | 310.80 | 128.10 | 0.00 |
| | 1040.00 | 245.97 | 119.47 | 20.67 |
| | 620.00 | 303.33 | 112.13 | 43.73 |
| | 360.00 | 139.00 | 86.33 | 7.92 |
| High | 400.00 | 106.00 | 96.30 | 27.60 |
| | 1140.00 | 285.07 | 108.63 | 26.89 |
| | 990.00 | 322.20 | 114.73 | 31.63 |
| | 460.00 | 334.50 | 42.00 | 30.40 |
| | 1016.67 | 298.03 | 112.86 | 39.79 |

Appendix 9. (continued)

| Treatment level | Height class | | | |
|----------------------------|--------------|------------|---------|----------|
| | Canopy | Sub-canopy | Sapling | Seedling |
| <i>(e) Number of stems</i> | | | | |
| Control | 1.10 | 2.48 | 1.15 | 1.00 |
| | 2.20 | 1.47 | 1.23 | 0.80 |
| | 1.07 | 0.94 | 1.00 | 0.20 |
| | 1.20 | 1.08 | 1.20 | 0.40 |
| Low | 0.80 | 1.31 | 1.33 | 0.53 |
| | 1.10 | 0.87 | 1.20 | 1.00 |
| | 1.00 | 1.36 | 1.60 | 0.20 |
| | 1.20 | 1.00 | 1.50 | 0.00 |
| Medium | 1.40 | 0.99 | 1.33 | 0.70 |
| | 0.60 | 1.27 | 1.77 | 1.07 |
| | 1.00 | 0.40 | 1.00 | 0.20 |
| | 0.80 | 0.40 | 1.39 | 1.07 |
| High | 2.00 | 1.23 | 1.35 | 0.80 |
| | 1.40 | 1.18 | 1.42 | 1.47 |
| | 1.00 | 1.26 | 0.60 | 0.80 |
| | 1.92 | 1.90 | 1.36 | 1.00 |
| <i>(f) Stem diameter</i> | | | | |
| Control | 7.20 | 2.40 | 1.24 | 0.50 |
| | 13.40 | 3.05 | 1.39 | 0.37 |
| | 13.60 | 4.17 | 1.37 | 0.08 |
| | 8.24 | 3.61 | 1.01 | 0.11 |
| Low | 10.22 | 2.48 | 1.26 | 0.23 |
| | 14.59 | 2.02 | 1.22 | 0.41 |
| | 10.65 | 4.90 | 1.19 | 0.08 |
| | 11.88 | 4.22 | 1.78 | 0.00 |
| Medium | 12.43 | 2.46 | 1.15 | 0.23 |
| | 10.20 | 3.40 | 1.20 | 0.56 |
| | 4.58 | 2.12 | 0.99 | 0.07 |
| | 8.40 | 1.61 | 1.09 | 0.27 |
| High | 13.48 | 2.95 | 1.24 | 0.69 |
| | 17.59 | 9.43 | 1.37 | 0.50 |
| | 11.60 | 8.06 | 0.68 | 0.94 |
| | 10.83 | 2.30 | 1.17 | 0.72 |

Appendix 10. Dry mass (g) per treatment level of plant material harvested from one 25m² plot in each paddock.

| | Treatment level | | | |
|---------|-----------------|------|--------|------|
| | Control | Low | Medium | High |
| Block 1 | 1.95 | 2.37 | 2.29 | 0.67 |
| Block 2 | 1.83 | 2.09 | 1.33 | 0.42 |
| Block 3 | 2.67 | 3.01 | 1.54 | 2.10 |
| Block 4 | 2.20 | 5.10 | 2.93 | 1.35 |

Appendix 11. The number of species per pin (a), number of species per quadrat (b), and number of species per plot (c) recorded in four survey plots in a 16-year-old rehabilitating stand over a period of ± 18 months (June 1994 to December 1995).

| | Survey 1 | Survey 2 | Survey 3 | Survey 4 | Survey 5 |
|--------------------------------|----------|----------|----------|----------|----------|
| <i>(a) Species per pin</i> | | | | | |
| | 1.89 | 1.30 | - | 1.27 | 1.30 |
| | 1.95 | 1.38 | - | 1.51 | 1.65 |
| | 2.45 | 1.92 | - | 1.64 | 1.74 |
| | 2.02 | 1.48 | - | 1.56 | 1.73 |
| <i>(b) Species per quadrat</i> | | | | | |
| | 8.83 | 10.50 | 8.50 | 8.30 | 6.10 |
| | 6.33 | 7.17 | 7.60 | 6.20 | 5.60 |
| | 9.00 | 7.83 | 6.80 | 8.40 | 7.70 |
| | 6.83 | 4.83 | 5.10 | 5.50 | 5.20 |
| <i>(c) Species per plot</i> | | | | | |
| | 23 | 28 | 25 | 25 | 18 |
| | 18 | 20 | 18 | 11 | 11 |
| | 22 | 21 | 19 | 22 | 19 |
| | 16 | 14 | 18 | 18 | 14 |

Appendix 12. The percentage of plants in four growth forms over six plant surveys in the control (a), low (b), medium (c), and high (d) treatment levels.

| | Survey 1 | Survey 2 | Survey 3 | Survey 4 | Survey 5 | Survey 6 |
|--------------------|----------|----------|----------|----------|----------|----------|
| <i>(a) Control</i> | | | | | | |
| Other growth forms | 17.56 | 10.14 | 14.75 | 12.81 | 12.07 | 10.32 |
| Clonal | 16.59 | 16.43 | 15.85 | 16.75 | 18.97 | 21.94 |
| Creeper | 35.12 | 36.23 | 37.16 | 37.93 | 39.08 | 46.45 |
| Climber | 30.73 | 37.20 | 32.24 | 32.51 | 29.89 | 21.29 |
| <i>(b) Low</i> | | | | | | |
| Other growth forms | 22.32 | 21.94 | 24.15 | 21.56 | 21.27 | 20.29 |
| Clonal | 18.03 | 20.68 | 20.29 | 16.36 | 17.16 | 22.22 |
| Creeper | 27.47 | 27.85 | 29.47 | 27.88 | 27.61 | 33.82 |
| Climber | 32.19 | 29.54 | 26.09 | 34.20 | 33.96 | 23.67 |
| <i>(c) Medium</i> | | | | | | |
| Other growth forms | 25.23 | 21.14 | 26.79 | 21.95 | 21.77 | 21.84 |
| Clonal | 17.29 | 16.26 | 17.22 | 16.67 | 17.34 | 20.87 |
| Creeper | 24.77 | 24.80 | 22.97 | 27.64 | 25.00 | 32.04 |
| Climber | 32.71 | 37.80 | 33.01 | 33.74 | 35.89 | 25.24 |
| <i>(d) High</i> | | | | | | |
| Other growth forms | 23.18 | 24.31 | 28.26 | 29.15 | 26.67 | 28.85 |
| Clonal | 14.16 | 12.94 | 16.85 | 12.18 | 16.08 | 17.79 |
| Creeper | 32.62 | 27.84 | 30.98 | 31.37 | 27.06 | 32.69 |
| Climber | 30.04 | 34.90 | 23.91 | 27.31 | 30.20 | 20.67 |