

**VEGETATION SUCCESSION
AND
SOIL PROPERTIES
FOLLOWING THE REMOVAL OF PINE
PLANTATIONS ON THE EASTERN SHORES
OF LAKE ST LUCIA, SOUTH AFRICA**

by

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ABSTRACT

Pine plantations have been established on secondary grassland on the dune systems of the Eastern Shores of Lake St Lucia, KwaZulu-Natal, South Africa for the past 40 years. These plantations have been progressively felled for the past six years, and will continue to be felled until the year 2011, by which time they will be eliminated.

Space-for-time substitution was used to determine the direction of both woody and herbaceous vegetation succession and to predict possible future management implications for the Eastern Shores. Soil samples were taken from undisturbed grassland, grassland with trees, dune forest, pine plantations, and clearfelled areas at various successional stages. To determine the effects of the pine plantations on the soils of the area, soils were subjected to particle size analysis, and determination of pH, organic carbon, phosphorus, exchangeable bases, iron and aluminium.

Minimal modification of the sandy soils by the pine plantations was found to have occurred. That which did occur was shown to be short-term, and to be ameliorated by the establishment of an indigenous woody understorey, resembling pioneer dune forest. Soil under plantations was shown to have a lower pH and cation exchange capacity than under opposite indigenous vegetation but no other direct effects were observed. The direction of succession was determined by the nature of the indigenous vegetation adjacent to the plantation. Pine plantations were shown to facilitate succession towards dune forest by the exclusion of fire, provision of perches and refugia for forest-dwelling animals, and creation of a forest environment for the establishment of trees. However, the extent of re-establishment of indigenous dune forest under pine plantations was shown to be directly related to the nature of the adjacent indigenous vegetation, be it grassland, grassland with trees or dune forest.

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DECLARATION

I hereby certify that this research is the result of my own investigation, except as acknowledged herein, and that it has not been submitted for a higher degree in any other university.

A handwritten signature in black ink that reads "B James". The signature is written in a cursive style with a horizontal line underneath the name.

B M JAMES

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1 INTRODUCTION

Lake St Lucia is an estuarine lake on the east coast of South Africa, in the province of KwaZulu-Natal (Figure 1.1, p.4). It is part of a large conservation area known as the Greater St Lucia Wetland Park, which extends from the marine reserve in the Indian Ocean to the Mkuzi Game Reserve in the west. The Eastern Shores of Lake St Lucia (Mfabeni Section) comprises the dune system between the Lake and the sea. The entire Greater St Lucia Wetland Park has been subject to much man-induced disturbance, the most important, for the purposes of this study, being the afforestation of the Eastern Shores with exotic pine plantations (*Pinus elliotii* and *P. caribea*). These plantations were established on land reported to be secondary grasslands, in the late 1950's, on land that had originally been cleared for slash-and-burn agriculture and iron smelting (Hall and Vogel, 1978; Hall, 1984; Weisser, 1978).

There has been much debate about the presence of the pine plantations on the Eastern Shores and their short and long-term effects on the hydrology, soils and the vegetation of the system, but only effects on hydrology have been studied in any detail (Lindley and Scott, 1987). Nevertheless, it was decided that all of the pine plantations are to be progressively felled and no more planted on the Eastern Shores, until their complete eradication by the year 2011, at which time the land will be used purely for conservation and ecotourism purposes (Blackmore, 1993; Department of Forestry, unpublished data).

The Eastern Shores has also been the subject of much debate and lobbying with regard to proposed opencast dune mining by Richards Bay Minerals, who are presently mining for heavy metals on the dunes north of Richards Bay. For the time being, a detailed Environmental Impact Assessment (1993) and public sentiment has resulted in mining being disallowed by Government, but future economic exigencies might change this.

The establishment of pine plantations has been reported to be accompanied by lowering of soil pH, reduction in soil fertility and inhibition of decomposition of organic matter (Barbour *et al.*, 1987; Killham, 1994; Hill and Wallace, 1989). The effects on indigenous vegetation are varied and often depend on the period of establishment of the plantations, sometime even facilitating the establishment of the indigenous vegetation (Chiarucci and de Dominicis, 1985;

Sturges and Atkinson, 1993; Chiarucci, 1996; Nakamura, 1996). In some areas, pine plantations have been used as nursery crops for more desirable indigenous trees (Chiarucci and de Dominicis, 1985; Hamilton, 1990; Chapman and Chapman, 1996; Chiarucci, 1996).

The ongoing clear-felling of the pine plantations on the Eastern Shores provides the impetus for the re-establishment of indigenous vegetation by secondary succession. Successive logging has taken place over a period of six years at different sites in the area. As a result, the opportunity was provided for space-for-time substitutions to establish the pattern and direction of succession during the years since clearing, and to determine direct effects of the pine plantations on the soils of the coastal dune system.

The successional patterns developing could indicate the type of vegetation that is likely to establish in future years, and could help with future management decisions. Studies on the effects of the pine plantations on the soils and the vegetation dynamics of the area may provide useful information for management of other similar areas and for direct application to practical rehabilitation of dune vegetation. In the unforeseen event that the area is eventually mined, an understanding of successional processes could enhance rehabilitation efforts.

In the light of the above, questions considered in this study were:

- i) Have soil physical and chemical characteristics, specifically pH, cation exchange capacity, organic carbon, exchangeable phosphorus and particle size, changed significantly as a result of the pine plantations?
- ii) Are changes to the above soil physical and chemical characteristics permanent?
- iii) In what way has the presence of pine plantations affected successional patterns?
- iv) How do the indigenous plant species establish under pines and subsequently in cleared areas? Are they already in the soil? Do they depend on the proximity of an indigenous seed source? Are they wind dispersed or dispersed by animals or birds?
- v) Is any form of active human intervention in vegetational processes called for?
- vi) Which is more important, knowledge of the vegetation structure and physiognomy during succession in this area, or actual species composition? Whatever the successional climax after removal of the pine trees, be it grassland or forest, is this "final product" comparable to adjacent intact forest or grassland?

As a result of a review of the literature and after direct observation of the vegetation within pine plantations and clearfelled areas, the following hypotheses were generated and tested in this study:

- H1: The nature of adjacent undisturbed vegetation determines the initial floristic composition, and the direction of succession after clearfelling.
- H2: The number of rotations of pine plantations affects soil characteristics and the initial floristic composition (i.e. type of seeds persisting and indigenous species established under the pine canopy).
- H3: Pine plantations create a favourable micro-habitat for the establishment of a dune forest understorey.
- H4: Soil under pine plantations, relative to the soil under adjacent indigenous sites, has lower pH and reduced fertility (in terms of major cations) and reduced extractable phosphorus.
- H5: Soil pH, fertility and extractable phosphorus continue to decline with increased time under pines.
- H6: Pine-induced soil acidity changes texture through increased weathering of particles.
- H7: Pine-induced acidity causes aluminium and iron toxicity.
- H8: The presence of the pine plantations causes podzolisation of the soil.

In the following chapters, the general theory of disturbance, succession and rehabilitation is examined, along with documented effects of pine plantations, and literature on forest rehabilitation. A detailed description of the study area is then given, followed by the actual mechanics of the study.

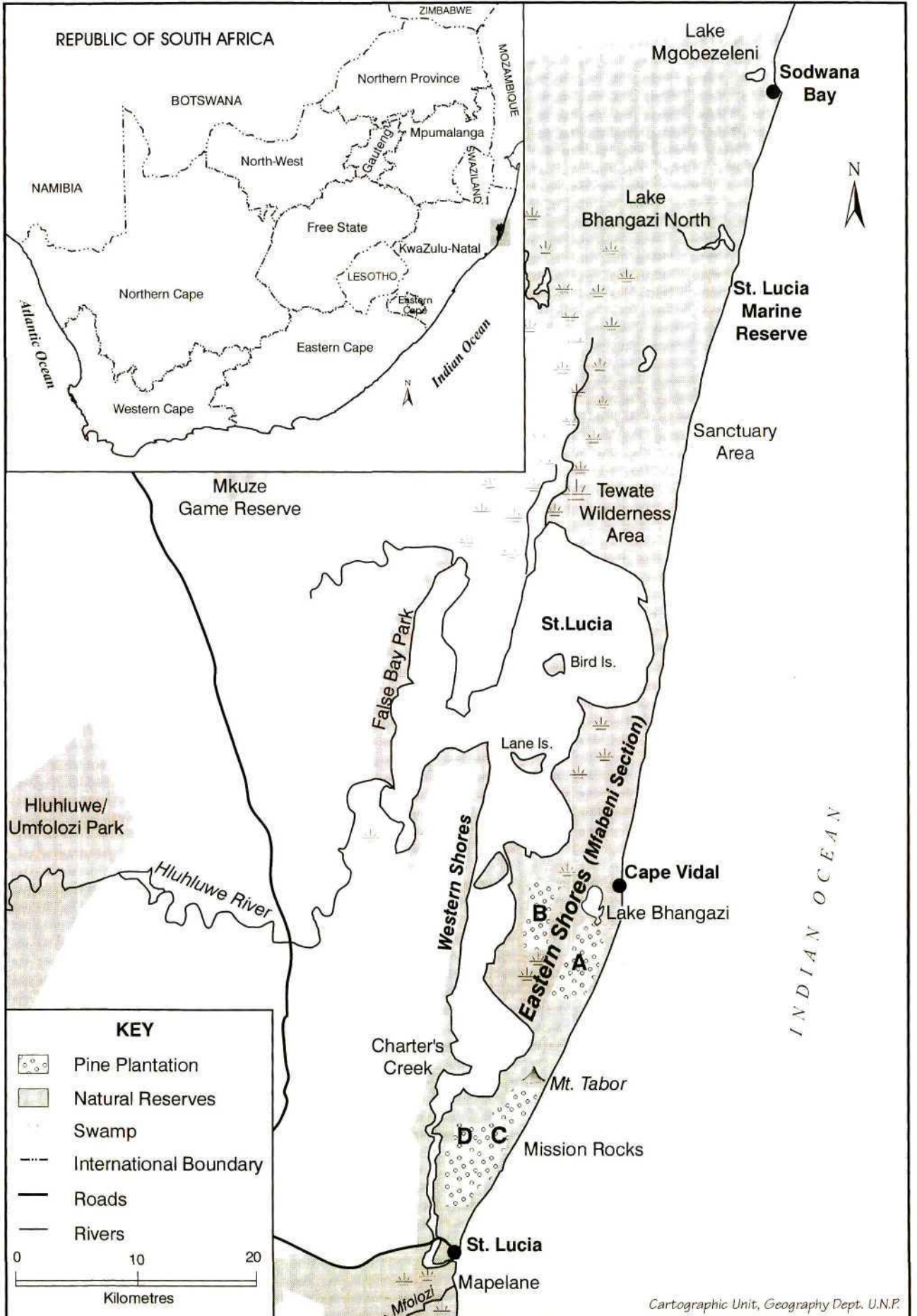


Figure 1.1: Location of the Greater St Lucia Wetland Park.

Cartographic Unit, Geography Dept. U.N.P.

2 LITERATURE REVIEW

The title “Succession and soil properties following the clearfelling of [exotic] pine plantations...” implies a number of factors:

- i) An alien monoculture (pine plantation) has been introduced into a system which is at a certain successional stage.
- ii) This alien is mechanically removed after a period of time.
- iii) Different suites of indigenous plant species begin to re-establish sequentially and to move towards a dynamic stable state.

The suite of plant species in the system before planting is dependent on historical events affecting the area and reactions of the species to those events (disturbance and succession). Establishment of the alien monoculture could dramatically alter vegetation and soil dynamics of the area (disturbance). Indigenous vegetation could establish within the plantations and, over time, species composition could change (succession). Mechanical removal of the alien monoculture alters or disturbs the *status quo* once more, and re-establishment of the indigenous vegetation in clearfelled areas causes further, gradual change (succession), or eventual rehabilitation of the natural system.

It is, therefore, necessary to examine the theoretical aspects of disturbance and succession. Due to the potential practical relevance of this project to rehabilitation, an understanding of rehabilitation is also necessary.

2.1 DISTURBANCE AND STABILITY

In this discussion, the terms disturbance and perturbation are synonymous, with either term being used according to the usage of the author being discussed.

A disturbance has traditionally been viewed as an uncommon, irregular event that causes abrupt structural changes in natural communities, and moves them away from static, near equilibrium conditions (Sousa, 1984). It has also been defined as a significant change in the

character of interest. If, for example, the characteristic was biomass or energy flow, then a perturbation would be a significant change in this variable (McNaughton, 1974, 1977; Connell and Sousa, 1983).

There are some difficulties in defining disturbance in terms of equilibrium conditions, namely: (i) few natural populations or communities persist at or near an equilibrium condition on a local scale, although they might appear so on a macro-scale; and (ii) the extent of change caused by any force depends on the intensity of the force and the vulnerability of the target organisms, and this can vary from negligible to extreme (Sousa, 1984).

All organisms are subject to periodic seasonal and cyclical changes which vary in intensity. Usually the organisms adapt physiologically and morphologically to these changes, but if these changes are too severe, some, or all of the individuals in the population will die. The difficulty is in defining the threshold point at which periodicity becomes a disturbance. Sousa (1984) argued that in the initial stages of an organism's evolutionary history, environmental periodicity probably constituted a greater hazard than it does at present. Over time, the species would have evolved homeostatic mechanisms to cope with the environmental fluctuations but it would never be able to track these fluctuations perfectly. Certain species even depend on environmental disruption for completion of their life cycles and persistence of their populations.

Disturbance is both a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and an agent of selection in the evolution of life histories. Differing life history patterns under different conditions produce much of the spatial and temporal heterogeneity observed in natural communities and, similarly, biological and physical environmental heterogeneity induced by disturbance will be a major factor in selecting different life history variants (Sousa, 1984).

Habitat situations that reduce adult survival and, therefore, favor the annual life cycle may be related to disturbance and the existence of temporary habitats. Disturbance removes competing vegetation, makes resources readily available, creates temporary habitats and, thus, favours growth and reproduction. Species adapted to temporary habitats are commonly described as

weeds because they are well adapted to life in habitats disturbed by human activity. Thus, they are usually *r*-selected “pioneers” (MacArthur and Wilson, 1967; Barbour *et al.*, 1987).

Maintenance of high species diversity appears to require episodic, random (stochastic) disturbances. Very stable, regionally extensive and homogenous communities exhibit lower species diversity than communities composed of a mosaic of patches disturbed at various times by wind-throw, fire, disease, or other factors. Following disturbance, diversity increases with time up to a point where dominance by a few long-lived, large size species reverses the trend and diversity decreases thereafter (Sousa, 1984; Barbour *et al.*, 1987).

Disturbance has, thus, in recent times been seen less as a rare and unpredictable event and more as a natural process (Pickett *et al.*, 1989). Therefore, a natural “disaster”, although disastrous in human terms, may be merely another natural event which opens gaps, allows colonization and increases biodiversity (Horn, 1974, 1975a). Diversity is higher for intermediate degrees of extrinsic disturbance than for high or low disturbance. By inference, the same pattern should occur for intermediate successional stages compared with early or late stages (Horn, 1975a). Species diversity increases initially and decreases with late succession, therefore, disturbance maintains diversity (Barbour *et al.*, 1987). The extent to which diversity changes during succession will be considered during this study.

Since diversity is generally lower in later succession, disturbance before late succession can prevent a reduction in diversity. But, frequent disturbances that maintain early successional conditions reduce diversity, leading to dominance by fast-growing species (Connell and Sousa, 1983).

Equilibrium species, or MacArthur and Wilson’s (1967) *K*-selected species, are always at a competitive advantage over opportunists (*r*-selected), but in natural systems the temporal and spatial frequency of disturbances has always been great enough to maintain opportunistic species as well as equilibrium species. The mature equilibrium species inhibit recruitment by propagules of another species via a variety of mechanisms. Propagules may be consumed, or the residents may simply have used up all available space. Site conditions may be modified in ways that inhibit germination or metamorphosis of propagules that reach the substratum.

They may reduce resources such as light, water, food and nutrients, or they may release toxic chemicals (allelopathy) (Sousa, 1984).

Frank (1968) warns against calling mature communities stable when the reason for their constancy is that they are composed of long-lived individuals. Thus, the minimum time period considered must be one complete turnover of all individuals, including colonies or clones (Connel and Sousa, 1983). The time scale of a disturbance (or perturbation) is also important. Appropriate time scales must be specified for observations of responses of populations to disturbance before meaningful judgements can be made (Connel and Sousa, 1983).

Full understanding of the dynamics of populations within habitats subject to disturbance requires knowledge of the regime of disturbance, such as areal extent, magnitude, frequency and predictability, as well as subsequent patterns of recolonization and succession in the undisturbed patches. These patterns are a product of certain characteristics of the original disturbance and the life histories of the species available to reoccupy the disturbed site (Sousa, 1984).

A term associated with disturbance is stability. A system is stable if it persists despite perturbations. The strategy is either to give way and recover quickly, or not to give way at all (Connel and Slatyer, 1977; Connel and Sousa, 1983; Barbour *et al.*, 1987). Other terms for giving way and recovering quickly are; *Adjustment* (Margalef, 1969); *Elasticity* (Orians, 1974) and *Resiliency* (Boesch, 1974). *Amplitude* (Hurd *et al.*, 1971; Orians, 1974) refers to the distance from which the system is capable of returning. Terms for remaining in equilibrium or not giving way when disturbed are; *Inertia* (Murdoch, 1970; Orians, 1974); *Persistence* (Margalef, 1969; Boesch, 1974); *Resistance* (Boesch, 1974; Margalef, 1969); *Constancy* (Orians, 1974; Whittaker, 1974; Golley, 1977); *Conservatism* (Margalef, 1969) and *Endurance* (Margalef, 1969). Other terms associated with stability are; *Maleability*, the extent of alteration of the stable state from the original, and; *damping*, the extent and duration of oscillation in an ecosystem parameter following disturbance (Westman & O'leary, 1986).

Whether stability increases or decreases with succession depends on the definition of stability. If stability is lack of change and resistance to minor changes or invasion, then stability

increases with succession. If stability is the ability to return rapidly to a homeostasis following a major recurring disturbance such as fire or windstorm, then stability decreases with succession (Horn, 1974, 1975a). Lack of change only becomes important in the presence of a disturbing force. A system cannot be described as resistant or resilient if it has not been exposed to external stress.

There is a growing realisation that disturbance may play as great a role in community dynamics as do biological interactions such as competition and predation, which have received far more empirical and theoretical attention from ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organisation and spatial patterning of natural communities (Sousa, 1984).

Thus, it is clear that any study concerned with disturbance or succession should discuss the terminology associated with disturbance and perturbation in order that a clear understanding of the mechanisms involved can be achieved and ambiguity can be avoided. An additional factor is to determine whether the goal of managing a protected area such as the Eastern Shores, should be towards a climax community dominated by a few long-lived species, or towards maximum biodiversity. Thus, in the Eastern Shores context, should Management allow clearfelled areas to continue along a successional pathway to an inevitable stable, though relatively species-poor climax, or is it desirable to disturb this successional process? If man-induced disturbance is desirable, what will be an acceptable disturbance regime?

2.2 SUCCESSION

In many ecology textbooks and university undergraduate courses in ecology, succession is presented, mostly for pedagogical purposes, as a fairly simple, straightforward concept (McIntosh, 1980). This is certainly not the case and, therefore, this section will attempt to outline some of the major schools of thought on the subject. The confusion and contradictions surrounding the concept and associated problems may be better understood with reference to the philosophical history of ecology.

There were, and still are, several divergent positions in ecology specifically concerned with succession. Many of the historical schools of thought in ecology had clearly defined 'intellectual leaders' who were followed by 'disciples', and adherence to these schools of thought reflected the fashions of the time and so-called 'invisible colleges' (Crane, 1972; McIntosh, 1980). To an extent these invisible colleges still exist today.

To understand the concept of succession, a discussion of definitions and terminology will be presented, followed by a review of some of the better known authors who have studied and written about the subject.

2.2.1 Definitions and Terminology of Succession

Ecological succession refers to the progressive, directional, cumulative change in plant or animal community composition in a given area over time. These changes may be observed over a broad range of space and time, from the microscopic to the continental, and from seconds to millennia. However, this definition of succession does not include seasonal or cyclical changes (Krebs, 1985; Barbour *et al.*, 1987). Connell and Slatyer (1977) define succession as the changes observed in an ecological community following a perturbation that opens up a relatively large space. A universal general cause for succession is unlikely, since numerous aspects of historical and environmental circumstances will impinge on the process in a unique manner (McCook, 1994).

The occurrence of periodic natural disturbance ensures that succession never stops. After a

disturbance there is usually a burst of regeneration that, once established, suppresses later regeneration. Thus, a single age class may emerge and dominate for a long period. Without major perturbations the successional process will reach a stage of an assemblage of long-lived individuals and will be regarded as late successional or climax (Connell and Slatyer, 1977).

Communities are usually referred to as *mature* or *climax* communities when no significant changes occur within a time frame from 1 to 500 years. This does not mean that changes do not occur, but that the community is in a state of dynamic equilibrium, similar to a chemical balance in a solution (Barbour *et al.*, 1987). This concept has been the source of much confusion and confounded arguments (McCook, 1994) and the idea (Clements, 1938) that the inevitable endpoint of any undisturbed succession was a particular stable and mature climax composition has been sharply criticized by a number of authors (Drury and Nisbet, 1973; Pickett and McDonnell, 1989).

A community exhibiting some directional, cumulative, non-random change is called a *successional* or *seral community*. It is often possible to estimate a community's future composition by extrapolating from changes measured in a short time, by comparing other communities that have plants of different ages, or by noting differences between overstory plants and understory seedlings. This study attempts to describe succession on the Eastern Shores of Lake St Lucia by recording plant species composition of plots clearfelled at different times and using space-for-time substitution to infer successional trajectories. Seral communities will replace one another until a climax is reached. The entire process from the first seral stage to occupy bare ground to the climax community is called a *succession* or *sere* (Krebs, 1985; Barbour *et al.*, 1987).

A distinction is made between primary and secondary succession. The establishment of new plants on land not previously vegetated is called *primary succession* and the invasion of land that has been previously vegetated is called *secondary succession*. Secondary succession occurs when pre-existing vegetation has been partially or completely destroyed by some form of disturbance such as fire, logging, cultivation or wind-throw. Primary succession occurring with the establishment of a pioneer community on a wet substrate is called *hydrarch primary succession*, and that occurring on a dry substrate is called *xerarch primary succession*. In both

cases, the direction of succession is usually towards the most mesophytic community possible, given the limitations of regional climate, topography and soil parent material. Secondary succession occurring on abandoned cropland is called *old-field succession* (Krebs, 1985; Barbour *et al.*, 1987).

Some blurring of the distinction between primary and secondary succession does occur because at the ecosystem level very few successions are primary, for what appears a bare surface may contain a well-developed community of micro-organisms (Goodal, 1977). One of the problems with studying secondary succession as opposed to studying primary succession is that sites undergoing secondary succession have a residue from the previous plant community (seed bank, soil characteristics) that may be difficult to match across sites (Johnson, 1997). This would be one of the problems inherent in the present study.

Succession that is driven by changes in the habitat caused by plants themselves is called *autogenic (biotic)* succession. In this type of succession, both the environment and the community change and the metamorphosis is due to the activities of the organisms themselves. *Allogenic* succession occurs as a result of environmental changes beyond the control of the organisms themselves (Krebs, 1985; Barbour *et al.*, 1987).

Progressive succession is usually defined as a move to communities with greater complexity and biomass and to habitats that are progressively more mesic. *Retrogressive* succession would lead to simpler, more depauperate communities (fewer species) and towards either a more hydric or a more xeric habitat (Krebs, 1985; Barbour *et al.*, 1987).

The pattern of diversity in succession results from a balance of many mechanisms. In general, some intermediate stage should have a mixture of both early and late species, and, thus, a higher diversity than early or late stages (Horn, 1974, 1975a). With reference to the Zululand coastal area, Bews (1920) formulated the hypothesis that in a sub-tropical region, as the succession advances, the vegetation becomes increasingly tropical.

One climax community does not necessarily cover an entire region. Many plant communities may exist in a complex patchy (mosaic) pattern. Where the patches represent different stages

of recovery (seral stages) from a disturbance, the mosaic is called a *chronosequence*. Where the communities in the mosaic represent topographical rather than successional relationships, they constitute a *toposequence*. Within a toposequence each community can, in fact, be a climax community. A climax community reflecting regional climatic conditions is called a *climatic climax*, one reflecting a prevailing fire regime, a *fire climax* and one reflecting soil conditions is called an *edaphic climax* community. North and south-facing habitats will have different communities dictated by the unique micro-climate of each. Thus, a region can have a regional climatic climax community and can be characterized by a mosaic of climax types, i.e. a *polyclimax* landscape (Krebs, 1985; Barbour *et al.*, 1987).

Whittaker (1951, 1953) saw the landscape pattern as a continuous array of both seral and climax communities of several types, incorporating the idea that something which was climax on one site could be seral on another.

The major constraints on plants in successional habitats are:

- i) access to the disturbed site, i.e. colonization (Drury and Nisbet, 1973; Pickett, 1976; Noble and Slatyer, 1980; Huston and Smith, 1987);
- ii) availability of limiting soil resources (e.g. Clements, 1916);
- iii) the availability of light (Cooper, 1913; Horn, 1971; Shugart, 1984; Tilman, 1985); and
- iv) herbivores, pathogens and other sources of loss and mortality (Connel and Slatyer, 1977; Walker and Chapin, 1987).

Each of these constraints can be overcome by allocation to particular structures or physiological functions, but all such allocation patterns necessarily reduce proportional allocation to other structures or functions, causing trade-offs (Tilman, 1990a & b). The presence of pine plantations on the Eastern Shores could alter all of these factors and thus drive succession in a particular direction.

It is obvious that no natural organism can be simultaneously well-adapted to all environmental conditions, especially when biological interactions such as competition and predation are considered. A plant has to strategically allocate metabolic resources to different physiological functions according to its own particular adaptive strategy. In so doing, trade-offs between the

various functions are made. This adaptive strategy will determine under which set of environmental conditions it will be most competitively successful. Changing environmental conditions will, thus, probably change species composition (McCook, 1994).

A number of authors have discussed the concept of strategic allocation of resources in detail, e.g. MacArthur and Wilson's (1967) single axis r and K -strategies; Grime's (1979) triangular model of competitive, ruderal and stress tolerant populations; Tilman's (1982, 1985, 1988, 1990a) above and below-ground tissue allocation and resource-ratio concepts; Connell and Slatyer's (1977) classification of early and late successional species; and Huston and Smith's (1987) and Smith and Huston's (1989) growth rate/resource availability trade-off.

In most successional studies, the focus is usually on interplant interactions and plant-physical environment interactions, and seldom on the action of herbivores (Connell and Slatyer, 1977). Biological interactions usually considered to be of overriding importance in succession are competition and the actions of micro-organisms and fungi (Connell and Slatyer, 1977). This study considers the actions of herbivores to be an important factor driving succession on the Eastern Shores of Lake St Lucia.

Immediately after disturbance, occupation of that site by a species will cause changes to the conditions at the site. Since different species are adapted to different environmental conditions, sorting of species arriving at a site simultaneously, will take place. The sorting will take place over existing environmental gradients and over time. The sorting may be a result of life history traits or strategies interacting with responses to limited resources (McCook, 1994). There is often an inverse correlation between traits which confer success during early and late succession. Species successful in early succession are described by MacArthur and Wilson (1967) as r -selected species, short-lived species that allocate resources predominantly to quick growth and reproduction. Species, dominant in later succession, are known as K -selected, those that are long-lived and which allocate resources to competitive ability and survival.

The rate and pattern of re-establishment following a disturbance depends on the following (Sousa, 1984):

- i) the morphological and reproductive traits of the species that are present when the

- disturbance occurs. Such traits determine, in part, the likelihood that these species will survive the event and rapidly reoccupy the site;
- ii) the reproductive biology of species that were not present on the site when it was disturbed but have occupied it previously or live within dispersal distance of it;
 - iii) characteristics of the disturbed patch including:
 - a. the intensity and severity of the disturbance that created it;
 - b. size and shape;
 - c. location and degree of isolation from sources of colonists;
 - d. the heterogeneity of its internal environment; and
 - e. the time it was created.

To this list one could add micro-meteorological conditions of the site, proximity to a source of propagules and availability of propagule dispersal vectors, all of which are important to this study.

A mechanistic interpretation of succession given by McCook (1994) goes as follows. Pioneer species, by their very occupancy, will alter the resource levels at the site. If, for instance, shade tolerance and colonization are inversely correlated, then those species will be less able to recruit and grow in the shade that they have produced. Other more shade-tolerant species which grow to a greater height will then emerge but they will, in turn, be replaced sequentially by more and more shade-tolerant, taller and slower-growing species. A number of authors (Egler, 1954; Drury and Nisbet, 1973; Grime, 1974; Noble and Slatyer, 1980; Tilman, 1982, 1990a,b; Huston and Smith, 1987; Smith and Huston, 1989; Pickett and McDonnell, 1989) have indeed observed that these traits are inversely correlated in nature. Species are, thus, often classified by successional timing according to traits such as dispersal mechanisms, responses to disturbance, ability to persist through disturbance by seed bank or vegetative regeneration, maximal height, longevity, resistance to stresses, resistance to small-scale disturbances or herbivory, recruitment, and growth rates at different resource levels. Pioneer species are, by definition, ephemeral, while tracts of the climax remain relatively unchanged for several generations (Horn, 1974, 1975a).

Although this model is an adequate explanation of autogenic succession, it is not an exclusive

explanation, and does not rule out the possibility of other factors or interactions. Factors such as timing of recruitment, availability of propagules, history, and interactions such as competition and predation, could also play a role (McCook, 1994).

Facilitatory or inhibitory effects of species on each other are best understood in terms of these life history interactions, possibly as restrictions on, or as moderators of, these processes (McCook, 1994).

To some extent, patterns of succession or vegetation change can be described at some scale for almost any natural system but, in many respects, individual successional processes appear to be unique and dependent on timing, initial conditions and other factors (McCook, 1994).

The general tendencies in succession involve the appearance and dominance of species with greater maximum size, age and shade tolerance, and progressively lower maximum growth rates (McCook, 1994). The relationships between different models of succession are generally vague, making it difficult to design field studies that make comparisons possible, and there are few field studies that adequately address the reasons for patterns of species abundance during succession (McCook, 1994). All models agree that certain species will usually appear first because they have evolved “colonizing” characteristics discussed earlier, but models differ in the mechanisms that determine how new species appear later in the sequence (Connel and Slatyer, 1977). But different models of succession are not mutually exclusive (Finegan, 1984).

In order to understand the causes of succession at the community level and to focus on models relevant to that understanding, some important questions must be answered (McCook, 1994):

- i) Why do different patterns of species abundance occur during autogenic succession, once a disturbance has freed sites for colonization?
- ii) What can cause one species, or group of species, to be displaced or dominated by another, or others?
- iii) What effects do earlier species have on the success of later species?

The historical development of successional theory is closely related to the development of the science of ecology, therefore an account of this development assists in outlining some of the

difficulties and presuppositions inherent in any successional study.

2.2.2 The Development of Successional Theory

Clements (1928) regarded succession as the growth, development and reproduction of a complex organism or superorganism, with the whole being more than the sum of the parts. His view of succession is also known as *relay floristics*, because succession is assumed to be a series of discrete seral communities, each modifying the habitat in such a way that new species gain a competitive advantage over the previous community. Although recent interpretations have tended to discount much of this early work, Clements' ideas have been perpetuated in textbooks and teaching of ecological principles, possibly due to their pedagogical convenience, even when plant ecologists had rejected most of their substance.

The essence of Clementsian succession is comparison with the development stages of an individual organism that reaches a level of maturity, at which stage it is able to control its own environment and become self-perpetuating. The assumption is that succession moves towards an inevitable and fixed climax. This superorganism concept, or doctrine of order in nature, was a commonly held philosophy amongst scientists at the time (e.g. Forbes, 1880, 1883, 1887; Allee *et al.*, 1949).

Gleason (1917, 1926, 1927, 1939) opposed rigid Clementsian views of orderly, progressive succession. He considered that the nature of changes at a site depended entirely on the species composition of that site, that the species occurring on a site depend on the availability of seed and a favourable environment, and that this resulted in successional courses of a largely individual nature. He argued strongly against the idea that any particular community functions cohesively as an organism, but rather that successional communities are incohesive assemblages, and that patterns of similarity result largely from coincident properties of species and similar environmental conditions. Gleason's major contribution to ecology was his individualistic concept, now one of the most influential ideas in ecology.

Egler (1954) proposed that secondary succession in old fields may be dictated more by the *Initial Floristic Composition* of an area than relay floristics of successively arriving species.

Egler proposed that succession was simply a result of chance and differential longevity of plants. In other words, a certain suite of species are initially present at the site. Over time some species grow rapidly and eclipse the growth of others. Domination occurs due to size, longevity and other life history traits. He does not explain why early successional species disappear, but he does state categorically that the successional trajectory does involve both relay floristics and initial floristic composition processes. There are, however, two critical, usually confounded, differences between the two models. They differ in the timing of arrival of later, dominant species and the nature of the interaction between the species. The fact that organisms within the successional process are not “arriving species” is, in his opinion, the reason for the relatively stable plant communities which change very slowly by resisting invasion by other organisms of the existing populations.

Drury and Nisbet (1973) showed that vegetation patterns of abundance following disturbances include not only successional replacements, but also cycles and divergences. Rather than simply the growth of the ultimately dominant species, they asserted that succession on a single site usually involves a sequence of species, because no one species can dominate the vegetation throughout the period of growth. The critical feature of Drury and Nisbet's (1973) suite of life history characteristics is the tendency towards inverse correlation between traits that confer competitive success in early succession and traits that confer success in late succession (stress tolerance, rapid growth, small size, short life and wide dispersal of seed). According to Drury and Nisbet (1973), there is no such thing as absolute competitive ability, nor any measure that confers competitive ability under all conditions.

Grime (1974, 1979) proposed a classification scheme of plant life history strategies, based on adaptation to particular levels of disturbance and stress, using stress to mean low levels of resources. Unlike Tilman (1982) who gave a relative rank depending on resource levels, Grime aimed to give an absolute and fixed classification to each species. Using the two dimensions of stress and disturbance, Grime classified environment as low disturbance-low stress; high disturbance-low stress; and low disturbance-high stress. He proposed three extreme strategies for these conditions, namely, that of competitor; ruderal (growing on waste ground); and stress tolerator, respectively.

Grime (1974, 1979) postulated that changes in succession alter the environment from high disturbance-low stress (high resources) to low disturbance-high stress, with a concomitant change in dominant plant strategies from ruderal to stress tolerators. In more productive systems there is a middle phase of high competition, with low stress and low disturbance. This theory does not explain changes in species composition, except as the implicitly equilibrium response to unexplained changes in the environment, autogenic or otherwise. It assumes plants have fixed strategies on the two dimensional resource-species gradient and, thus, predicts constant successional relationships between any two species. He suggested that, in addition to competitive interactions between plants or sessile animals, interactions with herbivores, predators and pathogens are of critical importance to the course of succession.

Markovian replacement probability predictive models, advocated in particular by Horn (1975a & b), use estimates of the probabilities of each tree species being replaced by the same or other species. Horn (1975b) estimated the replacement probabilities by counting the relative densities of saplings of each species under mature trees of each species and assuming these proportions represent the likely replacements for each species. He used these techniques quite successfully to describe changes in species composition over time in a forest near Princeton, USA. Similar representation of succession as a plant-by-plant replacement has been done by other workers (Stephens and Waggoner, 1970; Waggoner and Stephens, 1970; Leak, 1970; Botkin *et al.*, 1972).

Although the Markovian model has some potential and is statistically sound, it essentially treats the mechanisms and processes of succession as a black box, examining output only (McCook, 1994). It does not take into account relative importance of life history stages, assumes the constancy of the probabilities, does not allow manipulations to investigate the importance of different factors to community composition, and assumes equilibrium dynamics. An interesting property of the model is that the state of the system converges to a constant outcome, independent of the initial state (species composition). The model, thus, predicts that a single 'climax' state should exist for all successional courses based on the replacement probabilities, and that the initial species composition will make no difference to the stable outcome. This is similar to a class of statistical properties known as "regular Markov chains".

Pickett (1976) attributed major importance to competition, past or present, and in arranging species in spatial and chronological gradients. He, thus, developed an evolutionary population-based interpretation of succession.

Connell and Slatyer (1977) expanded the ideas of Drury and Nisbet (1973) and Egler (1954) to suggest three alternative models of succession: facilitation; tolerance; and inhibition. In these models, early colonists could either facilitate later ones, have no effect on them or inhibit them. All biotic elements (plant interactions, predators and pathogens) were incorporated in their models. They did not endorse the organismic view of the ecosystem and they emphasized the population-centred approach to succession (McIntosh, 1980).

The facilitation model is a modern paraphrasing of Clements' (1928) relay floristics, without the superorganism aspect, although they agreed that the community is a highly integrated, well-adjusted set of species. Whittaker (1975) outlined the steps in facilitation as "one dominant species modified the soil and micro-climate in ways that made possible the entry of a second species, which became dominant and modified the environment in ways that suppressed the first and made possible the entry of a third dominant, which in turn alters the environment." This sequence continues until the resident species no longer modifies the site in ways that facilitate the invasion and growth of a different species.

The tolerance model is a modern paraphrasing of the initial floristic composition approach, i.e. climax species are merely better competitors, more shade-tolerant or resource-tolerant, longer-lived and bigger than seral species, and all may be present together early in succession. However, this model was criticized as lacking in sufficient evidence for application beyond forest vegetation.

The inhibition model is the reverse of relay floristics. Early species inhibit succession by allelopathy and are replaced only when they die or are damaged. This model seems to hold for marine intertidal communities and for some shrub lands, but there is little evidence to show that it might be a universal model (McCook, 1994). Tolerance and inhibition probably relate to secondary succession.

In all three models of Connell and Slatyer (1977), the earlier species cannot invade and grow once the site is fully occupied by their own or later species. The models differ in the way later species become established after their propagules arrive. In facilitation, later ones can become established and grow only after earlier ones have suitably modified the conditions. In the tolerance model, later species are successful whether earlier species have preceded them or not. They can become established and grow to maturity in the presence of other species because they can grow at lower levels of resources than can earlier ones. In the inhibition model, later species cannot grow to maturity in the presence of earlier ones. They appear later because they live longer and so gradually accumulate as they replace earlier ones. Another distinction between the three is the cause of death of early colonists. In the facilitation and tolerance model, they are killed in competition with other species. The latter grow and shade, or deprive them of resources. In the inhibition model, early species are killed by local disturbances caused by physical extremes or natural enemies such as herbivores, parasites or pathogens.

Noble and Slatyer (1980) argued that the qualitative dynamics of species (as persistence or extinction) can be predicted on the basis of certain 'vital attributes', or life history attributes of the population as a whole. This amounts, in part, to classification of plants by similar strategies. The purpose of this model was to describe vegetation dynamics under varying disturbance regimes over longer time scales than individual successions. As such, although the model's dynamics include successions, it does not address the problem of species' abundance during succession.

Tilman's (1982, 1985, 1986a,b, 1988, 1990a,b) resource-ratio hypothesis states that succession results from a gradient through time in the relative availabilities of limiting resources. It assumes that each plant species is a superior competitor for a particular proportion or ratio of limiting resources and that vegetation composition changes as plant consumption, biogeochemical processes and disturbance change the relative availability of limiting resources. It predicts that the local species composition depends on the local rates of supply of limiting resources. To apply this model to a terrestrial plant community, it is necessary to know what the limiting resources are in that community. Important limiting resources can be soil nutrients such as nitrogen, water, phosphorus, potassium, magnesium, and various trace

elements. Light is another important limiting resource. In the St Lucia context, limiting resources may be soil nutrients, protection from salt-laden air and wind and, within pine plantations and mature forests, light.

Johnstone (1986) proposed a concept of succession as a stochastic interaction between invasion, maintenance and decline of species at a location. Succession was observed as the stability or instability in species composition.. He provided a classification of invasion probabilities which he considered to be analogous to the classification of species vital attributes (Noble and Slatyer, 1980), as well as a classification of maintenance probabilities. In each case, the interaction between environmental conditions and plant strategies explains invasion or maintenance potentials. As with Noble and Slatyer (1980), Johnstone's (1986) ideas referred more to generalized vegetation dynamics under various environmental conditions, rather than the vegetation response to specific disturbance. He considered it critical to realise that environmental factors cause invasion, maintenance and decline, but are not the cause of succession.

Huston and Smith (1987) simulated terrestrial forest succession by following individual trees through their lives and modelling birth, growth and death. They argued that species interactions occurred at the level of the individual rather than the population. Competition was not considered in abstract terms but as the effects of species on resource levels and of resource levels on species. Succession is thus a sequential change in relative abundances of the dominant species in a community, where dominance is based on biomass. Sequential implies that a once-dominant species or group of species will not become dominant again unless a disturbance or other environmental change intervenes. Thus, they focused on the intervals between disturbances rather than on the effects of the disturbances themselves. The changes that interested them occur within a time period of the same order of magnitude as the life-span of the longest-lived organism in the successional sequence.

Huston and Smith (1987) derived from first principles, rather than empirically, the conclusion that successional replacements occur when species attributes such as wide dispersal, rapid growth and high rates of sapling establishment are exclusive of traits such as shade tolerance or high maximum size (which gives competitive dominance). Their results portrayed a

baseline model for sequential succession based on competition for light, autogenically decreasing substrate light levels and sequential dominance by species that can grow in progressively lower light levels. This model, however, is not an exclusive explanation for succession but rather the simplest case, which demonstrates that complex, facilitative interactions between species are not necessary to generate sequences of species dominance (McCook, 1994). The model can be expanded to include more species and competition for multiple resources.

Huston and Smith (1987) criticise the Tilman (1982) model for the fact that a population-based approach to succession obscures the central dynamics of plant-succession which are the interactions between individual organisms. The major problem with population models is that they aggregate individuals with different growth rates, reproductive capacities, and mortality probabilities into a single population.

There are a number of critical differences between the resource-based hypothesis (Tilman, 1982) and the individual-based model of succession (Huston and Smith, 1987).

- i) Huston and Smith (1987) base their approach on interactions among individuals rather than among populations.
- ii) Competitive ability is an individual characteristic based on the interaction of a set of life history traits with the individual's environment rather than a set of abstract parameters for an entire population and average environmental conditions.
- iii) The Huston and Smith (1987) model is based on non-equilibrium dynamics of competition rather than on competitive equilibrium for both primary and secondary succession.
- iv) Changes in resource levels that lead to changes in species dominance during primary or secondary succession are a direct result of the plants themselves (autogenic) (Gleason and Tilman, 1992; Tilman, 1982, 1985). The resource-ratio hypothesis is not a model of autogenic succession.

Many successional pathways are found in nature and this frustrates efforts to develop generalisations at the population and ecosystem levels. Huston and Smith (1987) believe that

a focus on individual organisms provides the appropriate level of resolution both for understanding specific successional sequences and for developing a generalised theory of succession.

Huston and Smith (1987) believe that facilitation, tolerance and inhibition have been too narrowly defined and that they have been applied at the population level rather than at the individual level where all three can occur simultaneously. Facilitation, tolerance and inhibition describe processes and properties that are relative, not absolute. They can occur simultaneously, with varying degrees of importance, during every successional sequence.

2.2.3 Conclusion

Much of the current schism in ecology and divergent views of succession are continuations and elaborations of the dichotomy which first became dramatically apparent in the contrasting view of Clements (1916, 1928) and Gleason (1917). Odum (1977) espouses a holistic, integrative new ecology which is a lineal descendent of Clements. The distinction between the population-centred or individualistic position is commonly seen as a dichotomy between reductionist and holistic approaches, although some do not see the distinction (Rosenzweig, 1976).

One pole of the current views of succession is the conceptualisation of an ecosystem as “fundamentally an energy processing system” whose properties “persist even though populations change” (O’Neil, 1976). One of the obvious difficulties in any evaluation of succession is the lack of consistent generalisations which allow any fairly compact overview (McIntosh, 1980). Goodal (1977) stated that it is probably best to regard succession as having no conceptual content differing from dynamic change in general, since there are always difficulties in defining time scales. Changes should be predictable in order to be of interest.

Discussion of succession (and climax) is sometimes confused by consideration of scale or lack of it. The crux of succession is that a species does or does not replace itself on a given site, not that it moves successfully to a new site if disturbance makes one available. The existence of a gradational sequence on the landscape should not be confused with a chronological sequence

on a single site.

The direct observation of succession is usually possible only in the earliest stages of succession when many species are short-lived and amenable to experimentation. As a result of later successional species usually being long-lived, successional processes have to be reconstructed from indirect evidence, by space-for-time substitutions (Oosting, 1942; Keever, 1950), or by dating living and dead trees on one site (Cooper, 1913; Henry and Swan, 1974).

Although the study of succession on the Eastern Shores is essentially a study of forest succession, it suffers from the same problems inherent in any other study of forest succession. To date no direct study of forest succession has so far been possible because of the longevity of the organisms involved (Finegan, 1984). Thus, descriptions of succession are usually inferred from studies of the vegetation of adjacent sites of different known ages, a space-for-time substitution, in which case it is necessary to assume that sites differ only in age and not in substrate material, climatic history, past disturbance or the input of propagules.

There has been some conflict between various authors over the applicability of space-for-time substitutions as used in this study. Some critics of succession studies have argued that only a direct observation of change in time, preferably coupled with experiments, can afford adequate evidence (Swan and Gill, 1970; Austin, 1977; as cited in McIntosh, 1980). The problem of meeting this ideal is the fact that successions do not occur in time scales convenient for human examination (McIntosh, 1980). In the case of the present study, it is feasible and, in fact, desirable, to study succession at fixed locations over a number of years, say ten or twenty. But, since this study is the basis of an MSc thesis and, given the time constraints inherent in such, it is impracticable to do so. Therefore, a space-for-time substitution has, of necessity, been used. Based on the results and conclusions of this study, permanent sample sites could be set up and succession studied over many years, keeping in mind that the successful use of chronosequences relies on the assumption that all sites making up the sequence have identical histories of disturbance, biotic influences and environmental conditions (Luken, 1990).

Descriptive field studies rarely provide much insight into the mechanisms of successional change, which remain hypothetical and are a major concern of the long-standing theoretical

controversy over succession (Finegan, 1984). This study is not a controlled field experiment, so it is not designed to specifically address successional theory, but by observation of the processes, certain inferences can be made.

2.3 REHABILITATION

Ecosystem destruction by mining, quarrying and other processes is an inevitable part of civilisation (Bradshaw, 1982), but this destruction should be limited as far as possible, because preserving ecosystems is far less expensive than restoring them (Cairns, 1993). It is critical that restoration of degraded ecosystems is made a priority, firstly because environmental collapse is a far greater threat to global stability than any national economic deficit and, secondly, the longer restoration is postponed, the less likely that indigenous species will be present to occupy the site (Cairns, 1993).

Restoration requires a knowledge of the nature of the ecosystem, of the nature of the damage and of how to repair it. Land restoration in Bradshaw's (1987) view is an acid test of ecological understanding, but at the same time, discoveries through experience in restoration may contribute to ecological theory. Therefore, the practical implications of this study may provide a better understanding of successional processes and ecosystem functioning so that these can be used and manipulated for use in rehabilitation of damaged or degraded areas.

Firstly, it is important to make a distinction between the terms *restoration*, *rehabilitation*, *revegetation* and *reclamation*. Another term that could be used in this context is *enhanced*. *Restoration* refers to getting a system back to its original condition (Cairns, 1986). *Rehabilitation* refers to restoring some, but not all, of the most desirable features (Cairns, 1986a & b) or restoring a natural dynamic to the ecological communities comprised of strongly or weakly interacting species (Mentis and Ellery, 1994). *Revegetation* refers to establishing a plant cover of any kind (Mentis and Ellery, 1994). *Reclamation* refers to the conversion of desert, marsh, or other so-called "useless" land into land suitable for cultivation. *Enhanced* refers to getting the system back to an acceptable condition, although nothing like the original (Cairns, 1986a). A better term for this is *modified* (Environmental Impact Assessment, 1993). There is probably a blurring of the distinction between *enhanced* and *rehabilitation*, but the end-product of rehabilitation would tend toward the original, whereas the *enhanced* system would be completely different to the original.

Cairns (1986a) noted that small disturbances caused by natural phenomena such as the fall of

a single tree in a large forest result in rapid recovery, but that much human damage is not so rapidly healed. The type of disturbance experienced by a system will dictate the kind of management strategy that will be required to 'repair' the damage.

An illustrative list given by Cairns (1986a) of the types of disturbances is as follows:

- i) Sudden and unexpected disturbances such as nuclear fallout, chemical accidents, and sinking of oil tankers. In these cases, the pre-accident condition is usually not known and because of the unexpectedness of the event, efforts to ameliorate effects are often inadequately recorded.
- ii) Disturbances that have been occurring for a long time, but that have only been detected recently. Examples are industrial discharges that were thought to be harmless, or that were deliberately kept secret until effects on humans, animals or ecosystems were noticed. In these cases, background ecological information is often unknown, and even removal of the source of damage does not immediately rectify the situation.
- iii) Planned disturbance such as mining or dam and highway construction. In cases like these, thorough Environmental Impact Assessments may be undertaken and rehabilitation plans formulated in advance. These situations allow excellent opportunities for applied research into disturbance, succession and rehabilitation (Jordan *et al.*, 1987).

To take effective corrective action after a disturbance, the degree of change, the area in which the change has occurred, the ecological significance of such change and the probability that it will affect adjacent systems must be known. Questions which will assist in this assessment would be:

- i) What was the system like before the disturbance?
- ii) At what rate does normal change occur?
- iii) How does one determine the deviation from the norm?
- iv) What parameters provide early warning of recovery malfunction?

(Cairns,1986).

To these should be added the point that a thorough knowledge of successional processes occurring in similar ecosystems or adjacent comparable vegetation would facilitate a more

rapid and natural return to the desired state of repair.

Jochimsen (1996) stated that the use of natural processes to effect reclamation is the most advantageous course of action. To demonstrate this, she initiated a controlled seeding in virgin mine spoil with a selection of ruderal plant seeds in the proportion equivalent to plants in comparative sites. This seeding was found to accelerate natural succession. The addition of fertilisers facilitated the germination of airborne seeds and fruits. However, different phytosociological communities did not respond identically to different treatments.

Often the overriding problem with restoration is the absence of soil, although soil skeletal materials are present (Bradshaw, 1982). One way to get around this problem is to store topsoil prior to mining or construction and then to replace the stockpiled soil later. But storage of topsoil does not allow for species, especially trees and shrubs, which do not grow well from vegetative fragments or whose seeds do not possess dormancy mechanisms (Bradshaw, 1982). The other problem is that we have been left with a legacy of degraded and derelict areas from times gone by where man gave no thought to the long-term sustainability of his use and abuse of natural resources, and, consequently, no planning was done for eventual reconstruction of the areas.

There is often a conflict between official regulations in judging recovery of damaged ecosystems and criteria based on ecological principles. Sometimes, well-meant clean-up operations are more detrimental than doing nothing would have been. In some cases, time itself heals, provided that the source of disturbance is removed. In the South African context, preconceived ideas of idealised climax conditions on rangelands have resulted in large-scale, misdirected Government intervention and control in situations where equilibrium models do not apply (Mentis *et al.*, 1989). Carefully planned research is the one positive course of action that can take place in each of these cases (Cairns, 1986a). The other problem in the New South Africa is that, although environmental regulations are more enlightened, Government and parastatal organisations do not have the financial or personal resources to adequately police the regulations.

Another source of conflict is how to decide on an acceptable endpoint. This has the two-fold

function of deciding what to aim for and determining when the goal has been reached. Allen and Bastow-Wilson (1991) suggest ways to determine indigenous vegetation growing on a restored site through the relationship between the environment and the composition of remnant native vegetation in that area. They suggest the use of Discriminant Function Analysis and Indicator Species Analysis as tools for estimating extent of vegetation restoration. Practical tests using these methods indicate that successful application in other areas would depend on four conditions:

- i) Indigenous vegetation must survive on sites that represent the range of environments present in the area.
- ii) The vegetation remnants must retain most of their natural flora for the reconstructed vegetation type to be accurate.
- iii) The relationship between the physical environment and the vegetation type must be strong.
- iv) The relationship between environment and vegetation must be definable by factors that are easily obtained by land managers.

Ewel (1990) suggested that the success of restoration can be judged on whether or not the reconstituted community resembles the original, whether it contains the same dominant species and similar structure or physiognomy. He listed five criteria for analysis of success:

- i) Sustainability, i.e. the community must be self-sustaining.
- ii) Productivity - the community must show an increase in abundance or biomass.
- iii) Invasibility. - there must be evidence of invasion of new species into the community.
- iv) Nutrient retention - there must be a satisfactory build-up of a soil system and recycling of nutrients so that there is no nutrient loss.
- v) Biotic interaction - invasion of other species and interaction between species must be evident.

The science of restoration ecology is young and rapidly evolving (Berger, 1990), but so far there is no single overriding principle to be observed in reconstruction of ecosystems (Bradshaw, 1982) and there is unlikely to be in the future. It is well to remember that reconstruction in mined or other destroyed land has little in common with secondary succession in old fields (Bradshaw, 1982). Nevertheless, restoration ecology can provide

powerful techniques to conduct basic ecological research. The ability to reassemble a community and to make it function properly actually represents a critical test of ecological understanding in the most fundamental sense (Jordan *et al.*, 1987). The results of this study would certainly contribute to a better understanding of succession in dune systems so that practical restoration of indigenous communities, particularly dune forests and other dune vegetation, may be enhanced.

A number of factors related to the Eastern Shores of Lake St Lucia contribute towards making this study valuable to the study of rehabilitation ecology, namely that:

- i) The disturbance history is well-documented.
- ii) There are intact, undisturbed communities (grassland, grassland with trees and forest) close to the pine plantations which can serve as benchmarks.
- iii) Post dune-mining rehabilitation is ongoing, within an almost identical system, at Richards Bay Minerals.
- iv) The Eastern Shores is a high-profile area, which has been, and is the subject of a number of different ecological studies, all of which will enhance knowledge about the system and, in turn, about rehabilitation.
- v) The ongoing clearfelling of pine plantations will enable managers to continue indefinitely with the initiative taken by this study.

However, it means that this study should be ongoing and that vegetation succession should be regularly monitored, to build up a more accurate account of the successional processes occurring on the Eastern Shores.

2.4 EFFECTS OF PINE PLANTATIONS

Worldwide, it has been found that pine litter decomposes to yield acid leachate which lowers the pH of the soil (Barbour *et al.*, 1987; Killham, 1994). As a result, fewer base cations are held on exchange sites and more cations are released by acid weathering. Thus, cation exchange capacity is reduced (Barbour *et al.*, 1987) and soils that have been subject to afforestation are markedly less fertile (in terms of major cations) and are significantly more acidic than soils of grasslands adjacent to the afforested areas. Grassland soils, in general, are less acid, have higher base saturation and less surface organic matter accumulation than most adjacent forest soils (Barbour *et al.*, 1987; Miles, 1985; Ugolini and Edmonds, 1983). Phosphorus concentrations on the Eastern Shores of Lake St Lucia were, however, found by Blackmore (1993) to be similar under grasslands and areas under 34-35 year-old pine plantations.

Nakamura (1996) found that pine litter exerts a strong influence on germination, establishment and succession of individual plants. Litter alters the micro-environment and may affect ecosystem structure and dynamics. He found that the presence of litter plays an important role in promoting successional stages in the early stages of plant succession.

Soil pH influences the extent to which plant roots exude carbon, with carbon flow generally decreasing with increasing soil acidity (Killham, 1994). If less carbon is exuded by plant roots in acid soil, then less substrate will be supplied to the rhizosphere microbial population, which relies on carbon exuded from plant roots for its maintenance (Killham, 1994).

Soil animals generally have fairly narrow pH requirements, although variation is considerable from one soil to another. Earthworms (*Lumbricus* spp.) are generally highly sensitive to soil acidity and the range of pH tolerance of earthworms is such that species distribution is often highly indicative of soil pH (Killham, 1994).

In acid soils (below pH 5), such as under coniferous forests and moorlands, where acidity precludes the presence of earthworms, they are usually replaced by Enchytraeid worms which have considerable acid tolerance. The absence of earthworms in acid soils contributes to the

absence of large mole (*Chrysochloridae*) populations, earthworms being their primary prey. Amongst the major groups of soil microbes, sulphur-oxidising bacteria can tolerate pH as low as 1, whilst of the other microbes, fungi are best able to tolerate acidity. In general, microbial activity decreases at high and low pH (Killham, 1994).

Toxicity of certain metals, such as aluminium and manganese (which are more soluble at lower pH), could be a direct effect of pH. Rates of weathering, availability of nutrients such as nitrogen, phosphorus and sulphur, and the leachability of nutrients such as potassium are all influenced by soil pH. The availability of nutrients with low solubilities, such as phosphorus, is dramatically influenced by pH changes. High pH (alkalinity) reduces manganese and iron availability (solubility) to the root system and reduces phosphorus availability because of the formation of calcium phosphates. At both high and low pH, iron and aluminium phosphates are formed (Killham, 1994). Calcium phosphates are less soluble as the pH increases, and iron and aluminium phosphates are less soluble as the pH decreases (Barbour *et al.*, 1987; Killham, 1994). Low pH increases availability of aluminium and manganese. Phosphorus availability is reduced at high and low pH because of the formation of iron and aluminium phosphates (Duchaufour, 1982).

The presence of pine plantations sometimes causes podzolisation of soil. The term podzol refers to ash soil where the A0 horizon is brown or black mor or raw humus, the A2 horizon is ashy and without structure and the B horizon is strongly coloured by the accumulation of amorphous organic and mineral compounds (particularly iron and aluminium) (Soil Classification Working Group, 1991). Mor refers to raw humus, or a type of forest humus layer of unincorporated organic material, usually matted or compacted or both.

Podzols are generally distributed in very cold, wet, Boreal forests (coniferous forests in the north of the northern hemisphere, where the mean temperature for more than six months of the year is below 0 ° C) that favour the formation of mor, but they also occur in the temperate zone, particularly where there is a humid Atlantic climate, although they are less widespread, occurring only at particular sites and under particular vegetation. They occur very occasionally in tropical regions such as Amazonia and Zaire, where the formation is dependent on very particular site conditions, such as sandy parent materials, extreme rainfall and leaching and a

thick E-horizons (1-2m). They are often found in coarse river sands. In these conditions they are known as *giant* podzols because of the thick E-horizon (Duchaufour, 1982).

Podzolisation can occur in cold climates where litter decomposition is slow. In the Atlantic climate, podzolisation is closely related to the type of parent material. Podzols that are best developed and most differentiated occur on coarse-textured quartzose material, at least on the surface and on very gentle slopes, and those in weatherable minerals are poorly developed (Duchaufour, 1982).

Acidifying vegetation such as pine forests often causes podzolisation and it is only under acidifying vegetation that the podzol profile is fully developed (Duchaufour, 1982).

The Soil Classification Working Group (1991) define a Podzolic B Horizon as an horizon which:

- i) underlies an orthic E horizon;
- ii) does not qualify as a diagnostic placic pan;
- iii) occurs continuously or as mottles or tongues (cutans on ped faces are excluded);
- iv) has, in its uppermost part or at the points of accumulation in the horizon, more pyrophosphate extractable Fe + Al than the overlying horizon and at least three of:
 - more than 0.5 % pyrophosphate extractable C,
 - more acid oxalate extractable fulvic acid than the overlying horizon,
 - more than 0.3 % pyrophosphate extractable Fe + Al,
 - a $\frac{(Fe+Al)_p}{(Fe+Al)_d}$ ratio of 0.3 or more.

(Where p = pyrophosphate extractable and d = dithionite extractable Fe or Al);

- v) has, at the points of accumulation, a darker colour than an overlying E horizon or the horizon which directly underlies the podzol B;
- vi) when moist, has either loose to slightly firm or hard and brittle (cemented ortstein) consistence; it is non-plastic.

In this study, although the importance of plant-microbe relationships in ecosystem structure

and function is widely recognised (Archer and Pyke, 1991), no work was conducted on plant-microbe relationships. Since the absence of microbes (e.g. mycorrhiza) can severely limit seedling establishment, plant growth and plant survival, the success of revegetation efforts may be significantly influenced by the extent to which linkages between plants and the soil organisms are subsequently restored (Perry *et al.*, 1989). Mutualistic or free-living rhizosphere microbes can influence soil fertility (N₂ fixation) and structure (e.g. aggregate stability) and, thus, soil capacity to store and deliver resources. The absence of microbes (mycorrhiza) can severely limit seedling establishment, plant growth and plant survival. As a result, the success of revegetation efforts may be significantly influenced by the extent to which microbial activity in soils has been affected and by the extent to which the linkages between plants and soil organisms are restored (Perry *et al.*, 1989; Parker and Chatel, 1982; Miller, 1987; Allen, 1988).

Soil pH influences the success of infection of several species of vesicular-arbuscular (VA) mycorrhiza and symbiotic nitrogen-fixing bacteria (*Rhizobium* spp.) and influences their saprophytic growth with host plants (Archer and Pyke, 1991; Porter *et al.*, 1987a,b; Rice *et al.*, 1977).

Sturgess and Atkinson (1993) examined vegetation and soil changes following clearfelling of pine plantations on a number of different British sand dunes. Although the climate is different to that of the Eastern Shores, it is interesting to quote their work by way of comparison. Some, though not all of these factors would be relevant to the Eastern Shores. A comment on the anticipated applicability to the Eastern Shores is given in brackets after each.

The reasons listed by them for the removal of the pine trees were:

- i) pine trees eliminate most of the flora and fauna (not applicable);
- ii) plantations create shelter, which encourages scrub growth, causing disappearance of grassland plants and animals outside the plantation (partially true);
- iii) the lowering of the water table causes drying of dune slacks, resulting in loss of rare plants and development of scrub (possible);
- iv) pine seedlings are common around mature plantations and their control is a constant drain on resources (probably not);

- v) the removal of pine-woods could provide scope for increasing the amount of mobile and semi-fixed dune habitat (probably not);
- vi) the cost of managing a woodland on an exposed coastal site may be greater than the value of the timber (not applicable).

However, the pine plantations are often kept because they stabilise the dunes and prevent erosion; they are popular for recreation, and felling would cause disturbance which would be unpopular with the public. This point has already been expressed by some members of the public visiting the Eastern Shores; some contain rare and/or protected species; felled areas would not necessarily develop typical dune flora and fauna; plantations under 100 years have not yet developed diverse fauna and flora; the value of the timber is not high and felling may be more expensive than leaving the pines; and the pulse of nutrients following clearfelling would leach into the water table and possibly cause eutrophication in dune slacks. They would, thus, experience problems with disposal of poor-quality timber, brush, stumps and needle litter. It would be expected that with the high rainfall and higher temperatures on the Eastern Shores, nutrient cycling, successional processes and leaching would be far higher than in Britain.

Sturgess and Atkinson (1993) observed the following:

- i) A common response to clearfelling of the pines was the rapid establishment of ruderal flora associated with vigorous growth and high initial concentrations of available nutrients. The needle litter modified the soil by retaining nutrients and soil moisture and inhibiting germination from the existing seed bank. Removal of the litter accelerated the change to a "near-natural" sand dune community.
- ii) Soil changes varied in different areas of Britain. Some soils were apparently unchanged after 32 years under pines and others showed reduced pH and evidence of podzolisation, but all changes seemed to be in the top 5 cm. They found very little incorporation of organic matter into the soil of plantations, and a low diversity of seeds. Most of the seeds that they found were wind-dispersed.
- iii) Organic horizons had lower pH and higher concentrations of total and ammonium nitrogen. The sand below the needle layer seemed to vary in its response to afforestation. Acidification was thought to be inversely related to the calcium

- carbonate content of the sand and the age of the dunes prior to planting.
- iv) Acidification is usually associated with increased weathering and the surface horizons showed a higher proportion of quartz and feldspar than the soils of unplanted dunes, as the more unstable minerals, such as calcite, are the first to break down. Particle size analysis showed a higher proportion of grains less than 125 μm in the woodland Ea horizon than in the unplanted dune soil, which appears to be another result of weathering.
 - v) Although soil pH, nitrogen and phosphorus levels changed markedly after afforestation, burning and disturbance have instant and dramatic effects. Burning increases the amount of the highly soluble nitrate ion. Because interception of rainfall by the canopy and transpiration cease after clearfelling, increase in the amount of water percolating through the sand increased leaching.
 - vi) In young plantations, the majority of the litter consisted of a layer of recently fallen needles which decompose quickly. Older plantations had thicker F and H horizons which formed a compact layer and could, thus, reduce infiltration of rainfall and suppress germination from the buried seed bank. They found, in these areas, that removal of the litter accelerates the change to a near-natural dune habitat.
 - vii) The influence of adjacent vegetation was evident on the composition of establishing communities at some sites. Cleared land tended to take on the floristic character of the nearest vegetation and the plant species composition was strongly correlated with the age of plantations and the time of felling.
 - viii) Woodland plant species, and not necessarily dune specialists, established under the pines, many of which were brought in by birds. Stumps were found to remain intact for 20 years or more, but sometimes after seven to eight years they were sufficiently decomposed to be broken off and removed.

Apart from the universally accepted effects that pine plantations are known to have on soils, Blackmore (1993) noted that once clearfelling of the pine plantations occurs on the Eastern Shores of Lake St Lucia, the result is a notable increase in the availability of soil nutrients. Burning of the felled areas, however, decreases nutrient concentrations (Sturgess and Atkinson, 1993). According to Blackmore (1993), the major impacts of clearfelling on an area include: (i) the removal of indigenous vegetation established under the plantation canopy; (ii)

physical damage to the soil surface through roads, ploughing and rotovating; and (iii) an alteration in the soil chemical characteristics. Burning results in volatilization and loss of nutrients from the system (Sturgess and Atkinson, 1993), thus enhancing potential eutrophication of neighbouring wetlands. Burning of trimmings increases the soil repellency and increases the erodibility of the clearfelled area (Hendricks, 1979; Scott and van Wyk, 1990).

Felling not only removes large quantities of nutrients from the system through the removal of logs, but also results in the accumulation of large volumes of organic material (e.g. bark and needle litter, branches, resin exudate, sawdust and root material). Blackmore (1993) suggests that the accumulated organic matter does not balance the nutrient deficit created by logging but that it may play an important role in the initial rehabilitation of the deforested areas both aesthetically and floristically. The decay of the litter contributes to maintenance of soil organic matter and makes nutrients available for growth of pioneer species, which will contribute to the accumulation of organic matter and make the soil more hospitable for later successional species.

Hill and Wallace (1989) found that soil under pines was more acid than adjacent vegetation (0.20 units), but that the difference was only detectable in the top 5 cm. The pH values showed a clear relationship with age and pre-planting stability. Other effects of pines recorded by them were lowering of the water table and stabilization of the dunes. They quote a large-scale lysimeter experiment undertaken by Minderman and Leeftang (1968) in the Netherlands, in which they found that pines can, in fact, reduce that rate of leaching because they intercept much of the incident precipitation. They also found that changes in vegetation were greatest under trees and attributed this to shading, drought, competition for nutrients and the effects of needle litter. Thus, plantations modified duneland by increasing plant diversity, many species of which are directly dependent on trees for establishment (i.e. the forest environment).

In summary, the direct effects of soil pH on plant growth are very limited but the indirect effects are numerous and significant. The most important effect of soil pH is its control of nutrient availability.

2.5 FOREST REHABILITATION

In order to understand some of the processes occurring in succession on the Eastern Shores of Lake St Lucia and to give this study practical relevance, some background information on forest rehabilitation is given.

Throughout the world, destruction of indigenous forests is occurring at a rapid rate, often for the purposes of slash-and-burn agriculture in Africa or cattle ranching in Latin America. Slash-and-burn agriculture is the predominant farming method on roughly 30 % of the exploitable soils of the world and supports over 250 million people (Hauck, 1974). This converted land in both ecosystems is generally agriculturally unproductive, biologically impoverished and far more flammable than the forests that were replaced (Chapman and Chapman, 1996). There is, thus, a need to reclaim such forests and a need for research into forest rehabilitation. In other words, there is a need to understand forest succession so that it can be positively managed.

It is important that an understanding of the processes occurring in secondary forests are understood, as areas of secondary forests are increasing worldwide at the expense of primary forest (Brown and Lugo, 1990). Therefore, secondary forests will have to be managed and used in the future. Secondary forests are an important component of the shifting cultivation cycle and considerable pressure will be removed from primary forests if secondary forests can be managed sustainably to satisfy some of the human needs that lead, in the first place, to conversion of primary forests. Some of the values of secondary forests include provision of fruits, medicinal plants, construction materials, timber, animal browse, wood low in resins and waxes and rapid biomass production.

Proper management of valuable characteristics of secondary forests depends on how well they are understood (Brown and Lugo, 1990). Yet scientific understanding of tropical secondary forests is poor at best. Some of the assets of secondary forests are: high nett primary productivity (twice that of primary forests); fostering of future valuable species in the understorey; frequent provision of conditions to help improve soil and water quality or which conserve genetic material, nutrients, moisture and/or soil organic matter.

An understanding of plant autecology and plant-environment relationships is crucial to the success of restoration efforts. Biotic interactions, both plant-plant and plant-animal, will operate against a backdrop of edaphic and climatic constraints to further regulate and determine patterns of distribution, abundance and persistence over time (Archer and Pyke, 1991).

Tropical secondary forests appear to accumulate woody plant species at a relatively rapid rate but the mechanisms involved are complex and no clear pattern emerges (Brown and Lugo, 1990). The structure of the secondary forest is usually simple compared to the mature forest. Biomass accumulates rapidly and the recovery of organic matter in soil under the secondary forest is relatively fast. Nutrients are returned quickly by litter fall and decomposition for uptake by roots.

Although forest succession in the lowland tropics can be rapid, in many areas succession can be extremely slow, or not proceed at all. Factors that could exacerbate the situation are: dry climates, poor soil fertility, inhibition by extensive herbaceous growth and fire set by neighbouring agriculturists (Ewel, 1980; Uhl and Buschbacher, 1985; Lugo, 1988; Uhl *et al.*, 1981, 1988b, c; Janzen, 1988; Brown and Lugo, 1990; Nepstad *et al.*, 1991).

When planning for tropical forest restoration, there must be a clear assessment of what kind of forest one is dealing with and what kind of degradation has occurred, or is occurring (Hamilton, 1990). The desired restoration state must then be defined as some previous datum, e.g. the time before the arrival of the white man, or before the arrival of the Nguni people, in the case of St Lucia. There are, of course, cultural and philosophical, as well as biological dimensions to this.

Pickett *et al.* (1987) maintained that there are three basic causes of succession; site availability, differential species availability and differential species performance. These three components contributing to natural succession can be modified for application in resource management situations. To manage succession, three components are required; designed disturbance, controlled colonisation and controlled species performance. Designed disturbance refers to activities initiated to create or eliminate site availability; controlled colonisation refers to

methods used to decrease or enhance availability for specific plants species; and controlled species performance refers to methods used to decrease or enhance growth and reproduction of specific plant species.

Lugo (1992) suggested that exotic tree plantations should be considered as a means of rehabilitation of forest ecosystems. This would be a form of controlled colonisation (Pickett *et al.*, 1987). To be effective, however, it must be demonstrated that indigenous tree species can become established under the plantations and that the plantation harvest will not destroy the potential for the establishment of indigenous trees. Obviously there must also be certainty that the exotic species will not become invasive aliens. For example, the Nepal/Australian Forestry Project is currently using *Pinus roxburgii* as a nursery crop for more desirable native broad-leaved trees in the middle hills of Nepal (Hamilton, 1990).

In ultramafic soils in Tuscan, Italy, understory species density and pine canopy cover were positively correlated (Chiarucci and de Dominicis, 1985; de Dominicis and Chiarucci, 1996). In other words, pines allowed a larger number of species to grow on ultramafic soil. Additional soil resources provided by the pine canopy to endemic plant communities initially allowed the α -diversity to increase, but also led to the disappearance of specialised endemics, whereby biodiversity on larger areas is reduced. Therefore, a negative result of the presence of the pines was a loss of some endemics.

In industrial areas of West Germany, establishment of vegetation cover on derelict land is mostly done by reforestation (Jochimsen, 1996). However, the planting of young trees does not lead to development of a 'normal' plant community because a closed herbaceous layer is absent and many trees die (Jochimsen, 1996). The focus there is on fertilisation, seeding with a mixture of recognised ruderal or pioneer species and tree planting. Climate would obviously play a role, as would the sterile or polluted nature of the mine spoil on which the revegetation is taking place.

Chapman and Chapman (1996) evaluated the value of pine (*Pinus caribea* and *P. patula*) and cypress (*Cupressus lusitanica*) plantations as a means of allowing indigenous trees to become established on derelict land in the Kibale National Park of Western Uganda. The trees were

were planted between 1963 and 1965 in grassland areas that were the result of past human clearing and that were maintained by fires which inhibited natural colonisation by woody species. This is a similar situation to that on the Eastern Shores of Lake St Lucia, though it is not clear from their paper what soil conditions exist at Kibale.

Chapman and Chapman (1996) stated that areas that were not converted to plantations in the 1960's are still grassland, although some areas protected from fire have become forested. All of the areas under plantations showed high levels of natural regeneration. Wind-dispersed seeds made up a small proportion (3.2 %) of the seeds falling to the ground, relative to other tropical forests, and other seeds recorded mostly relied on animal dispersal. It is unlikely that the indigenous trees in the plantations came from a seedbank within the soil, since the planted areas had been grassland for many years, and had been regularly burnt. A number of frugivorous animals routinely used the exotic plantations, which confirmed that regeneration relied mainly on animal dispersal.

In that study, the reasons for the high levels of natural regeneration included the exclusion of fire and the presence of frugivorous animals which imported seeds. The simple exclusion of fire without the use of conifer plantations could assist in forest rehabilitation but the process may then be slower and it would remove the desirable economic incentive of plantations. Economic factors and economic analysis are usually crucial components of range revegetation decisions (Workman and Tanaka, 1991). Miles (1985) reported that where there was negligible grazing and no burning, scrub and woodland eventually recolonise but the rate depends on the extent of the seed rain.

The only negative factor in Kibale reported by Struhsaker *et al.* (1989) was a dieback of three species of rainforest trees which were down-slope from the conifers. The cause of the dieback in Uganda was not established, but it could possibly be due to the decrease in pH associated with conifers, leaching of acids down-slope, aluminium toxicity or pathogenic agents associated with conifers. They, thus, suggested that conifer plantations not be planted near natural forests in the tropics. This would obviously not serve the purpose of using plantations to aid in the regeneration of natural forest, since frugivorous animals, the essential component in seed dispersal, would not visit isolated plantations.

Connel and Slatyer (1977) wrote that certain mechanisms, particularly the effects of grazing animals, were often ignored in successional studies. However, plant ecologists knew something of the effects of grazing, that species were dispersed by grazing and seed-eating animals, and that succession could be modified or controlled by animals (Dyksterhuis, 1948; Ellison, 1960; Penfold, 1964; Smith, 1940). Pickett and Kolasa (1989) stated that the role of animals in succession is receiving more attention and this should improve the systematization of the theory.

Dispersal of plant propagules is of central importance in succession and restoration. This is particularly the case when dealing with large areas where re-seeding is not economically feasible. Archer and Pyke (1991) suggest that a strategy to deal with this would be to concentrate resources so that plant establishment is facilitated on smaller patches arranged in a pattern across the landscape. These patches then serve as nuclei for seed production and dispersal. To achieve this, groups of trees and shrubs have been transported with their soil onto mined land using tree-spades and front-end loaders (McGinnies and Wilson, 1982). Advantages are transport of soil microbes, introduction of species capable of rapid seed establishment, and establishment of large plants capable of coping with herbivory and competition. The major disadvantage is cost.

Archer and Pyke (1991) argued that more use should be made of animals as dispersers of seeds to aid in revegetation and rehabilitation. They cautioned, however, that if this technique is to be used, then plant species which are able to tolerate grazing should be used. Livestock dosed with desirable seeds can disperse them with their dung across the landscape, thereby creating patches of desirable plants. The seeds could even be inoculated with mycorrhiza, nitrogen-fixing bacteria or actinomycetes to enhance establishment, productivity and nutrient quality of rangeland species while increasing rates of succession. Lieberman *et al.* (1979) found that germination of seeds removed from baboon dung was significantly improved over that of fresh seeds in most species tested (75 %). Hartshoorn (1980) found that tropical forest pioneer trees are widely dispersed by birds and bats. Howe (1980) found that conspicuous features of tropical forests are plants with fleshy fruits adapted for attraction of vertebrate dispersers (birds and mammals) that utilise fruit as a major source of food during all, or part of the year. Uhl *et al.* (1981, 1988b) found that common woody species invading after cutting and burning in

the upper Rio Negro Basin of the Amazon had bat or bird dispersed seeds and that many of the forbs and grasses had wind-dispersed seeds.

Work done by Hooper and Bullington (1972), Uhl *et al.* (1981), McDonnell and Stiles (1983) and McClanahan and Wolfe (1993) found high concentrations of bird-dispersed seed growing under man-made structures or under trees and near decaying logs. They, therefore, concluded that introduction of man-made structures increased the rate of woody plant species invasion. These structures often have clumps of vegetation which are different to the surrounding vegetation, indicating that the structures serve as recruitment foci. McDonnell and Stiles (1983) found that the height of the structure was more important than the type of structure. Where animals are important agents of dispersal, Archer and Pyke (1991) suggested that provision for suitable cover and food should be made in reclamation plans.

Although there are many advantages, the disadvantages of using animals as dispersion agents include granivory, dispersal of undesirable species and excessive herbivory of desirable species (Archer and Pyke, 1991). The most effective agent in seed dispersal transports large numbers of seeds and deposits them in a germinable form in a micro-habitat favourable for establishment. Therefore, simply transporting large numbers is not enough and transporting few propagules is not necessarily ineffective if the few are able to establish effectively (Archer and Pyke, 1991).

One factor that often controls the presence of plant species on a site is propagule availability (Houle, 1996; Uhl *et al.*, 1988b). Seed availability was shown to be of significance in several primary seres, often slowing down the rate of succession (McClanahan, 1986). Seed availability depends in part on local production, the dispersal ability and the survival of seeds (Houle, 1996).

Plant ecologists have historically focused on post-germination processes such as competition, herbivory, longevity and disturbance frequency determinants of plant community structure. Reproduction and dispersal are often assumed to be sufficient for regeneration, but many temperate forest species do not develop persistent seedbanks and, therefore, seedbanks have limited value in reforesting disturbed sites. In fragmented landscapes, the role of birds as

dispersers is extremely important (McClanahan and Wolfe, 1993; Uhl *et al.*, 1988b).

The time necessary for plants to colonise slash-and-burn successional sites and the species composition of those sites is influenced by the dispersal strategies of the surrounding flora (Uhl *et al.*, 1981).

Uhl *et al.* (1981) found succession after burning of a cut forest to be different from succession following clearfelling. This occurs as a result of damage to meristematic tissue of sprouted shoots. The density of viable seeds in the soil is also reduced by burning. In slash-and-burn disturbances, the first woody plant colonizers originate from seeds already in the soil. Uhl *et al.* (1982b) concluded, in a study on abandoned slash-and-burn farm sites, that primary forest must be close to the farm clearing for forest trees to colonise.

The probability exists that juveniles of some forest trees not only tolerate the environment of a pioneer forest canopy, but require it. In the tropics, species of late successional and mature forests do not colonise abandoned forest clearings until there is a well-established pioneer vegetation dominated by fast-growing pioneer trees (Finegan, 1984). Daubenmire (1968) also postulated that the presence of pioneer woody species often increases the rate of colonisation of a site by other woody species whose seeds are dispersed by animals and birds, since the pioneers render the site more attractive to dispersal vectors. The behaviour of the vectors is probably decisive.

Based on the findings of Chapman and Chapman (1996), it is clear that conifer plantations could have a role to play in the regeneration of tropical forests but, clearly, more research is needed. As a tool, the exotic plantations aid natural forest succession by a number of means. Chapman and Chapman (1996) recorded exclusion of fire, proximity of natural forests and presence of frugivores as the major factors but others are probable, such as provision of a favourable habitat and micro-climate for establishment of forest species, *viz*, shade (Uhl *et al.*, 1982), increased humidity, lowered soil surface temperature (Uhl *et al.*, 1982a), increased organic matter and shelter for the frugivores. Exotic plantations have the added attraction of income which can be derived from their eventual felling but depending on the methods used, this felling has the potential to damage the newly-established, indigenous understorey. It would

be more desirable though to identify fast-growing indigenous species with a commercial value which could be utilised for the same purpose.

However, before ecologists adopt the use of exotic plantations as the sure way of re-establishing forests, Cairns (1986a&b) notes that it is important to assess the reliability of extrapolations from one system to another. In the case of Kibale (Chapman and Chapman, 1996), Nepal (Hamilton, 1990), indigenous trees do re-establish under the pine canopy, but in other areas the soils could be unsuitable or the indigenous trees sensitive to the effects that the pines might have on soils and the trees themselves. Luken (1990) recorded that data are often contradictory and that one must accept the fact that the response of a particular system to management may not be predictable. This lends weight to the argument that site-specific research should take place before large-scale management programmes are implemented.

Exotic plantations could have other negative effects such as lowering of the water table, an important factor when the potential exists for essential hydrological regimes of landscapes to be compromised.

In summary, the above description of forest rehabilitation is applicable to the Eastern Shores because:

- i) In many of the plantations on the Eastern Shores, there is a well-developed indigenous plant understorey, which is immediately obvious, even to the casual observer.
- ii) Pine plantations have been successfully used as a means of restoring indigenous forests in the tropics (Hamilton, 1990; Chapman and Chapman, 1996).
- iii) Chapman and Chapman (1996) recorded that the pine plantations in Kibale attracted frugivorous animals which would import indigenous seeds into the plantations. The same could occur on the Eastern Shores.
- iv) Apart from attracting forest animals, the mere provision of perches in the form of pine trees could increase importation of bird-disseminated seeds (McDonnell and Stiles, 1983).
- v) The juveniles of some late-successional forest trees require the environment of a pioneer forest canopy in order to grow successfully (Finegan, 1984). Pine plantations thus have the potential to accelerate succession.

thus have the potential to accelerate succession.

- vi) Since the cost of restoring ecosystems is often prohibitive, any technique that is both successful and has attached economic incentives should be considered worthy of investigation.

3 STUDY AREA

3.1 LOCATION

The study area is situated in the Mfabeni Section (formerly the Eastern Shores State Forest) of the Greater St Lucia Wetland Park (Figure 1.1, p. 4). The section lies between Lake St Lucia in the west and the Indian Ocean in the east, St Lucia village in the south and Cape Vidal in the north, between coordinates 28°6' S and 28° 21' S; 32° 25' E and 32° 33' E. It forms part of the most southerly portion of the broad, flat Mozambique Coastal Plain.

3.2 CLIMATE

The high, vegetated coastal dunes on the Eastern Shores of Lake St Lucia rise steeply from the sea to almost 200 m in places. They are said to be the highest afforested dunes in the world (Anon, 1975) and are the highest ascending parabolic dunes in South Africa (Davies, Lynn and Partners, 1992). Being so high, these dunes deflect warm, moist onshore winds upwards, causing water condensation and increasing the local annual rainfall above that of surrounding areas. For example, Cape Vidal has a mean annual rainfall of 1 200 mm while Lister's Point, only 15 km to the west, has 700 mm. Rainfall has been recorded in the area since the early 1920's. About 40 % of the rain falls during the winter months, from June to August (Brooks *et al.*, 1982). The typical rain patterns include spring rains in September, followed by no rain until December, with the wettest months being January to March. Most rains are associated with cold fronts moving up from the southern oceans.

The dunes also act as a sand catchment, redirecting some of the rain water eastward to the sea and the rest westwards, first towards the low-lying wetlands and then into the Lake, providing up to 10 % of the fresh water input to the Lake (Kriel, 1966; Hutchinson, 1976; Taylor, 1995) and in extreme droughts are the sole source of fresh water for the Lake (Taylor, 1995). Approximately 21 % of the groundwater seepage from the dunes is towards the lake/swamp system. This has varied from 18 % under drought conditions (1983) to 22 % during extreme cyclonic events (1984) (Kelbe and Rawlins, 1992). Prevailing winds are mainly north-east and south-west, and it is generally the latter which brings the rain. The relative humidity is high,

generally exceeding 90 %. In January, temperatures range from 22-30 ° C, with a mean of 25 ° C. In July, they range from 12-23 ° C, with a mean of 18 ° C.

3.3 TOPOGRAPHY

As a result of complex, simultaneous dune building and erosion processes, the landscape between the dunes and Lake St Lucia is undulating, resulting in low-lying plains, consisting of a matrix of grassy ridges interspersed with a diversity of wetlands, and the water table is exposed in the troughs to form pans and vleis (Blackmore and Goodman, 1994), i.e. well-drained dunes and moist slacks (Conlong and Breen, 1982). The drainage lines may develop into swamp forests (MacDevette and Gordon, 1991; Taylor, 1995), and the dune systems, therefore, consist of a wide range of small landscape units.

These landscape units, together with the range of exposures to salt sea spray dictated by the topographical position in relation to the prevailing winds and the orientation of the shoreline, generate a wide range of micro-habitats which are reflected in the vegetation. This vegetation is a complex arrangement of coastal lowland forest, estuarine and lake systems, lowland wetlands, hygrophilous grassland and vegetated barrier dunes (Blackmore and Goodman, 1994).

3.4 GEOLOGY AND SOILS

Geological formations largely determine the topographical features and soil characteristics of an area and they are, therefore, important to keep in mind. The geomorphology of the study area is largely related to a large dune cordon parallel to the coastline, developed by bidirectional parabolic dunes (Davies, Lynn and Partners, 1992).

The following description of geology and soils has been adapted from Maud (1991) and Davies, Lynn and Partners (1992). The dune systems of the KwaZulu-Natal north coast are developed on a buried platform of gently seaward-sloping sedimentary rocks, mainly siltstones of marine origin. These generally fossiliferous marine rocks range in age from early Cretaceous to Palaeocene and comprise the Makatini, Mzinene and St Lucia Formations in

upward succession. Deposited on top of the Cretaceous and Palaeocene rocks are lower marine shelly coquina and upper aeolian calcarenite of the Uloa Formation of the late Miocene age. In places, these Tertiary rocks crop out from beneath a younger covering to give the clayey, red sand of the Berea formation.

Overlying the Tertiary sedimentary rocks is a thin veneer of unconsolidated sediments of Middle and Late Pleistocene age. These include the Port Durnford and Muzi Formations. Aeolian reworking of the surfaces of the Tertiary Uloa and Pleistocene Port Durnford and Muzi Formations has given rise to a number of sandy dune cordons on the Zululand coastal plain. Maud (1991) reported that in the wetter portions of the region, the surface of the less permeable Port Durnford and Muzi Formations are characterised by perched water table conditions, but Davies, Lynn and Partners (1992) found no elevated impermeable hardpan horizon within the dune cordon which would create significant perched water table conditions.

The soils of the Zululand coastal plain are characteristically relatively deep and sandy, clayey materials being relatively rare. The main source of the sand was probably the Tugela, Mlatuse and Umfolozi rivers.

The primary coastal sand is mainly of granitic origin, the rivers having significant portions of their catchments located in deeply-dissected, granitic areas. The sand, thus, contains significant amounts of weatherable minerals, as well as heavy minerals that are of economic interest. The most important weatherable mineral present is microcline feldspar, which weathers to give the clay minerals present in the older soil materials.

Concurrent weathering of the ferromagnesium minerals present, primarily hornblende, releases the iron that gives the older, and generally more clayey soils, their characteristically reddish-brown colour. The originally calcareous coastal sands rapidly lost their calcium carbonate by rainwater leaching after deposition, some of the lime being deposited at lower levels to cement the cores of the dunes in places. Aeolian reworking of the weathered sands on a number of occasions removed their clay content, and partially or wholly the ferruginous coating of the resistant quartz grains. The resulting sands which can overlie older reddish-brown, clayey sands are thus paler, greyish-brown in colour and comprise only uncoated quartz

grains with a few resistant heavy minerals.

Soils of the seaward facing slopes are young (Fernwood form), and those on the landward side are older (Clovelly form) (Davies, Lynn and Partners, 1992).

In the youngest coastal dunes, buried soil profiles with organic enrichment of their former topsoils are frequently present. In inter-dune areas and stream valley bottoms near the coast, where shallow water table conditions exist, accumulations of organic matter in the form of peat occurs in places.

The sandy soils of the region, with the exception of older, clay-enriched dunes, are generally of low to very low natural fertility because of their high permeability and consequent rapid leaching of nutrients. High rainfall further aggravates this condition. As a result, most of the nutrients are retained in plant biomass which slowly accumulates over time. Clearing of indigenous vegetation could result in loss of the nutrient store and necessitate a new process of nutrient accumulation (Taylor, 1995).

3.5 HYDROLOGY

The plains of the Eastern Shores have a shallow water table (usually within 0-3 m of the surface) (Rawlins, 1991; Lindley and Scott, 1987). This allows a two-way interaction between the saturated and unsaturated soil moisture zones whereby ground-water is directly recharged by percolating precipitation and discharged by evaporation and transpiration. Capillary processes may raise water from the ground-water to replenish evapotranspired soil moisture, depending on the particle size distribution of the soil (Lindley and Scott, 1987).

According to Tinley (1969, 1971), extensive, shallow water tables of sand plains with subsurface, indurated "pan" horizons are important in determining vegetation patterns. Lateral flow is low due to a small gravitational gradient in such systems. He states that abstraction by vegetation with roots tapping the ground water affects the rate of outflow markedly. The ratio of vertical to lateral movement would, therefore, increase if grassland were replaced by plantations of trees. Exotic timber plantations could be the principal reason for the reduction

of perennial fresh water seepage around the Lake (Tinley, 1971). Lindley and Scott (1987) maintained that the pine plantations on the Eastern Shores will increase evapotranspiration rates compared to grass cover. This is likely to reduce soil moisture beneath the plantations and cause a lowering of the water table in underlying and adjacent saturation zones. It must be stressed that there is an incomplete knowledge of the ground water hydrology of the Eastern Shores (Lindley and Scott, 1987).

It has been established that where water is not a limiting factor, such as on low-lying plains with a shallow water table, fast-growing pine trees consume more water than the indigenous, slower growing vegetation (Bosch and Hewlett, 1982). Studies on the coastal plain by Rawlins (1991) have suggested that pine (*Pinus elliotii* & *P. caribea*) plantations transpire at a rate up to 450 mm yr⁻¹ higher than the surrounding grasslands (an increase of 40 %). However, they believe that to extrapolate these findings to other types of indigenous vegetation would be invalid. The effects of exotic pine plantations on the hydrology of the Eastern Shores is also likely to be more apparent during dry periods (Rawlins, 1991; Rawlins and Kelbe, 1992). There is no indication that he directly measured transpiration under natural forest.

Terrestrial ecosystems could also have been modified by lower ground water levels as a result of increased transpiration losses caused by afforestation (Taylor, 1982a & c; Lindley and Scott, 1987).

3.6 FAUNA AND FLORA

Due to the geomorphological history of the KwaZulu-Natal coastline, the Zululand coastal dunes represent the only expansive area where large coastal dune cordons occur in KwaZulu-Natal.

The area has a wide diversity of plant and animal species, partly as a result of the merging tropical and temperate biomes. Many tropical faunal and floral species which extend down the coastal plain from equatorial East Africa, have their southern-most range limits in the St Lucia area. Similarly, many of the temperate species which extend northwards from the southwestern Cape, occur about as far north as St Lucia (Bainbridge, 1991). The climate and

development history of the dune system cause the Zululand dunes to have the highest woody plant species richness in South Africa (16.4 % of all known Natal species) and to have a number of local endemics (Lubke, Avis and Phillipson, 1992). The area is considered very important for the conservation of a substantial number of woody plant species (Gordon and MacDevette, 1989). The long linear dune cordons play a vital role in the dispersal and migration of species as the dunes act as an important corridor for the movement of species (Gordon and MacDevette, 1989). Increased fragmentation of the forest into isolated patches may prevent effective migration of species along the coast (Lubke, Avis and Phillipson, 1992).

The dune vegetation has developed over a period of approximately 10 000 years, with man being a major influence (slash-and-burn agriculture, selective cutting and grazing) for around 1300 years, and modern man (mechanical implements and pine plantations) for about 100 years. The present-day vegetation largely reflects these influences and the exclusion of man-induced disturbance in the dunes will lead to a decrease in species richness of the dunes (Gordon and MacDevette, 1989). Complete information is not available for many plant species occurring in the area. This reflects the paucity of botanical research undertaken in the region. In general, more information is available for tree and other woody species than for herbaceous species (Lubke, Avis and Phillipson, 1992).

Natural disturbance is an essential process for the maintenance of species diversity and vegetation on the dune cordon. Aggressive invaders such as *Chromolaena odorata* (L.) pose a threat to the dune vegetation as they can colonize gaps which are continually being left by the disturbance process and, thereby, prohibit the development of indigenous vegetation (Gordon and MacDevette, 1989).

Dune plant species are able to survive and reproduce at low concentrations of essential nutrients. A key role in nutrition of coastal dune species is played out by mycorrhizal fungi, one major benefit believed to be improvement of phosphorus nutrition (Maun, 1994).

The climax vegetation community of the dunes is tall coastal forest but this climax cannot be attained on the harsh, seaward slopes of the dunes which, as a result, have fewer species than the climax forest and the individuals present are stunted. The climax forest may be up to 20 m

tall with a thickly wooded understorey (Taylor, 1995). Weisser (1978) distinguished between coastal dune medium and coastal dune high forests. He recorded that in coastal dune medium forests, the species composition may vary considerably depending on the site.

Coastal dune high forests are found in dune valleys between high dune ridges and are characterised by a mosaic structure given by the presence of emergent, tall trees (20-30 m) and areas densely covered with climbers. Weisser (1978) considers this type of forest to be in a “decompositional phase” owing to, what he terms, an “over-maturity” of the forest. When old trees die and fall, climbers soon invade the area with a blanket of lush vegetation. Whether, or how quickly the trees can reconquer the spaces invaded by climbers is unknown. If the forest is able to reinstate itself with a species composition similar to the original, a cyclical climax would exist in which a forest stage and a climber stage would alternate. As the invasion of the climbers occurs at different times and in small areas (where openings occurred through the falling of large trees) a mosaic landscape is constantly provided, formed by high forest and areas densely covered with climbers. An obvious characteristic of the coastal thicket is the limited cover, or total lack of a herbaceous field layer under the dense canopy (Lubke, Avis and Phillipson, 1992).

Weisser (1978) reported changes in the extent of grasslands on the dunes between Richards Bay and the Umfolozi River between 1937 and 1974, since the Department of Forestry took control of the area. He found that they had diminished considerably, from occupying 32 % of the area in 1937 to 4.8 % in 1974. There is no reason to consider that the Eastern Shores area should be any different. Weisser believes that the grassland will disappear if direct, or indirect human interference ceases, to be replaced either by secondary dune forest or *Acacia karroo* woodland. The secondary grasslands do add to the diversity of fauna and flora, and Weisser (1978) judged that it would, therefore, be desirable to preserve some of these grasslands through burning.

The dunes of Mount Tabor (inland from the northern end of Mission Rocks) and Ochre Hill (Figure 1.1, p. 4) are covered with dry grassland. Between approximately the 4th Century AD and arrival of Europeans in the early 1800's, a specialised iron-smelting industry existed on the Eastern Shores. Since smelting of iron required large quantities of charcoal, it is thought

that the present-day grassy dunes were cleared of their forests by the iron workers and maintained by frequent burning. Up until the mid-1950's (Hall and Vogel, 1978; Hall, 1984; Weisser, 1978), the effects of the land-use methods of the local black people (shifting cultivation and cattle grazing, with applied burns to improve grazing) resulted in a mosaic of grasslands, shrub lands and forest (Von Maltitz *et al.*, 1989, 1996) covering the dune systems. The last of the subsistence farmers were removed by the Department of Forestry in the 1970's (Von Maltitz *et al.*, 1996). Within the grassland area are abundant woody plants which resist the effects of fire by means of large, underground storage roots and bulbs. Present management practices perpetuate the *status quo* through regular burning. In grassy areas which have been protected from fire, pioneer woody plants quickly invade (Taylor, 1995).

In general, burning has largely occurred at the whim of the manager (Conlong, 1986), but in recent years the policy has been to block-burn in alternate years (A.C. Blackmore, 1997, *pers. comm.*) In reality, as a result of forestry activities, burning has taken place every 3-5 years.

In the low-lying areas the vegetation is determined by the height of the water table. Where the water is close to the surface, woody plants cannot survive, and hygrophilous grasslands occur (Taylor, 1995).

The influence of large herbivores was dramatically reduced by the large-scale destruction of elephants, with the arrival of the European sport hunters in the early part of the 19th Century. The last elephant was shot in the 1920's in the Dukuduku Forest, west of St Lucia. At the time, black rhino were still in the False Bay area (Wearne, 1970) and are now found in the Tewate Wilderness Area on the Eastern Shores. The reintroduction of elephants into the area has been decided on by the Natal Parks Board, but has been delayed due land claim negotiations.

Acacia karroo woodland and secondary scrub correspond to different successional stages that follow secondary grassland when human interference ceases or is greatly reduced. Secondary dune scrub occurs in the north and *A. karroo* woodland in the south, with the Mbonambi Mission Station (between Richards Bay and St Lucia village) as the rough dividing line. *A. karroo* grows rapidly and is able to colonize bare sand when conditions are favourable

(protection from wind and sun with little, or no salt spray, and favourable rains) (Weisser, 1978). Weisser postulated that *A. karroo* woodland and secondary scrub would probably, by way of a long successional process, evolve towards a similar kind of dune forest.

In areas near Richards Bay where the exotic conifer *Cassuarina equisetifolia* has been planted to stabilise the dunes, it has been found to exclude all other growth and was, therefore, experimentally thinned in some places by the Department of Forestry (Weisser, 1978). *C. equisetifolia* is also considered an invasive alien in the area (Lubke, Avis and Phillipson, 1992).

3.7 PINE PLANTATIONS

Having a fairly reliable supply of perennial fresh water, the Eastern Shores has a history of occupation by Zulu and/or Tembe-Thonga people (Wearne, 1965, 1970; Hall and Vogel, 1978; Crass, 1982; Taylor, 1982b) before becoming State land and being set aside for a combination of forestry and Nature conservation (Conlong and Breen, 1982).

Of the 15 000 ha of the Mfabeni Section, the Department of Forestry (now known as SAFCOL - the South African Forestry Corporation Limited) established 4 726 ha (30 %) as pine plantations (91 % *Pinus elliotii* and 9 % *P. caribea*) within the study area (Blackmore and Goodman, 1994). These very productive plantations were an important source of pulpwood (Thompson, 1991). The Department had the policy of leaving patches of natural forest untouched and confining planting mainly to secondary and disturbed sites (Weisser, 1978).

All of the pine plantations, currently aged between five and 32 years, are to be progressively felled at a rate of 250 ha/yr, to be completed by the year 2011 (Blackmore, 1993). Afforested compartments are to be felled once the average age of the trees exceeds 25 years. Both drought or fires may, however, bring forward the felling date provided that the average minimum basal diameter of the trees within the affected compartment exceeds 100 cm. In general, the afforestation has been limited to low-lying hygrophilous grasslands and high-lying secondary grasslands (Brooks *et al.*, 1982). Most first-rotation plantations were felled after approximately 30 years.

4 METHODS

4.1 STUDY DESIGN

The basic tenet of this study was a space-for-time substitution, derived from sampling vegetation in sample plots placed within undisturbed vegetation, and pine plantations or clearfelled areas of different ages.

Prior to data collection, a preliminary survey was undertaken to determine the extent of variation of key environmental and management determinants. The purpose was to determine the optimal plot size for sampling; how the different growth forms would be measured; whether the sampling would differ for grassland and forest; and how many soil samples would be needed in relation to the edaphic variability of the site.

This preliminary survey revealed a number of problems which would impact on the sampling procedure. These were:

- i) There were no clearfelled plots older than six years, although preliminary information indicated that clearfelling went back ten years.
- ii) Within that six year period there was not a consistent spread of different ages of clearfelled plots.
- iii) Clearfelled plots were spread over four different plantation areas, all of which had different altitudes, adjacent vegetation, water tables and micro-habitats (due to exposure to winds and salt spray).

Since successional processes are affected by environmental factors, and since the soil is usually the one major environmental determinant that is affected by afforestation with pine trees, soil analysis served as the basis for site evaluation.

The approaches used to test each hypothesis generated in the introduction, were as follows:

H1: The nature of adjacent undisturbed vegetation determines the initial floristic composition, and the direction of succession after clearfelling.

Determined and compared quantitatively and qualitatively, woody and herbaceous species composition for matching pairs of sites.

H2: The number of rotations of pine plantations affects the soil characteristics and the initial floristic composition (i.e. type of seeds persisting and indigenous species established under the pine canopy).

Compared chemical analysis results of soils for first and second rotation pine plantations and compared species richness.

H3: Pine plantations create a favourable micro-habitat for the establishment of a dune forest understorey

Recorded the indigenous plant species growing within the plantations and compared the species composition and diversity to undisturbed dune forest.

H4: Soil under pine plantations, relative to the soil under adjacent indigenous sites, has lower pH and reduced fertility (in terms of major cations) and reduced extractable phosphorus.

Compared soil pH and soil fertility at each of the paired sites using the paired t-test and analysis of variance (ANOVA).

H5: Soil pH, fertility and extractable phosphorus continue to decline with increased time under pines.

Displayed graphically, using regression analysis, soil characteristics under pine plantations with increasing age of the plantations.

H6: Pine-induced soil acidity changes texture through increased weathering of particles.

Compared soil particle size as in H3.

H7: Pine-induced acidity causes aluminium and iron toxicity.

Determined aluminium and iron concentrations within plantations.

H8: The presence of pine plantations causes podzolisation of the soil.

Judged whether or not podzolisation occurred by referring to the conditions outlined for podzolisation in Soil Classification Working Group (1991).

4.2 DATA COLLECTION

There are four pine plantations (A - D) on the Eastern Shores. Plantation A (Figure 4.1) is in the north-east, plantation B (Figure 4.2) in the north-west, plantation C (Figure 4.2) in the south-east and plantation D (Figure 4.2) in the south-west. Plantations are divided into numbered blocks, A1-A26, B1-B34, C1-C22 and D1-D27. Unfortunately, the clearfelling history in each area was not the same, so it was possible that north-south and east-west differences could confound results.

To ensure maximum efficiency and accuracy of sampling within the plantation blocks, stratified systematic, unaligned sampling was used (Greig-Smith, 1983). Once a plantation block had been chosen, two random numbers were generated using a calculator to obtain coordinates for a block, measured from the first corner encountered. The soil sample would be taken at that point and the vegetation sampling performed in the area that included that point.

As far as possible, sample plots were chosen so that pine plantations and clearfelled areas could be compared in a pairwise manner with adjacent vegetation. Thus, for example, a pine plantation opposite forest refers to a pine plantation with the nearest indigenous vegetation being forest. These plots were placed parallel to contours to minimise altitudinal effects and exclude obvious pedological variations. The sampling of pairwise sites was performed in order to make direct comparisons between the effects of various management regimes on the soils of the Eastern Shores.

The number of sites were chosen as detailed in Table 4.1.



Figure 4.1

MAP OF STUDY AREA - NORTHERN SECTION - PLANTATIONS A & B

1km

Lake St Lucia

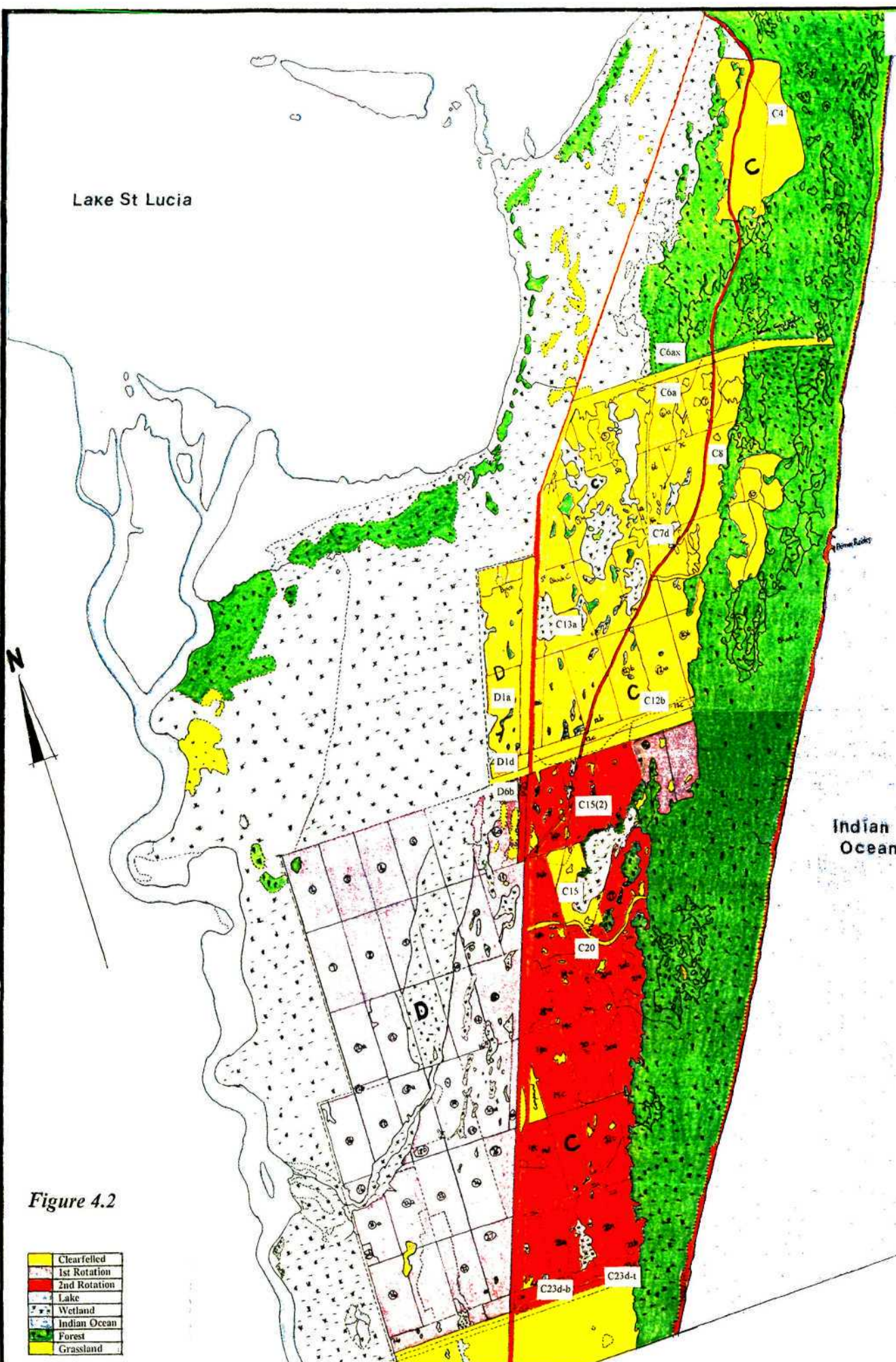
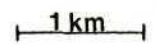
Indian Ocean



Figure 4.2

	Clearfelled
	1st Rotation
	2nd Rotation
	Lake
	Wetland
	Indian Ocean
	Forest
	Grassland

MAP OF STUDY AREA - SOUTHERN SECTION - PLANTATIONS C & D



Where particular combinations of management units are under-represented in the sampling, it is a result of their being either under-represented or not existing in the area (Table 4.1).

Table 4.1 Summary of sample plots (Details in Appendix 1).

DESCRIPTION	No. of Sites
1st Rotation pine - Opposite grassland	0
1st Rotation pine - Opposite grassland with scattered trees	6
1st Rotation pine - Opposite forest	1
1st Rotation pine - Within plantation which was opposite grassland	4
2nd Rotation pine - Opposite grassland	0
2nd Rotation pine - Opposite grassland with scattered trees	1
2nd Rotation pine - Opposite forest	6
2nd Rotation pine - Within plantation which was opposite forest	2
Clearfelled 0 yrs - Opposite grassland	1
Clearfelled 2 yrs - Opposite grassland with scattered trees	3
Clearfelled 6 yrs - Opposite grassland with scattered trees	1
Clearfelled 4 yrs - Opposite grassland and forest	1
Clearfelled 5 yrs - Opposite forest	3
Clearfelled 5 yrs - Within pine plantation which was opposite forest	7
Grassland	2
Grass/Trees	7
Indigenous forest	5
TOTAL SAMPLE SITES	50

Both indigenous and alien vegetation were sampled. Floristic composition and structure of the woody component was assessed by measurement of the height and basal diameter of individual trees within the sample plot. Herbaceous species were recorded according to cover, using the van der Maarel cover scale (Jongman *et al.*, 1995). Density, species richness and diversity were calculated using these data.

The minimal area for the sites was determined by means of a species-area curve (Figure 4.3). The species-area curve was compiled using nested quadrats (Barbour *et al.*, 1987). As each larger quadrat was located, a list was kept of additional species encountered (Appendix 2). The point on the curve where the slope most rapidly approaches the horizontal is called the minimal area (Barbour *et al.*, 1987). The minimal area was determined using a four year old clearfelled site, C4, which had been felled after one 28 year rotation of pine trees. The minimal area for this plot was found to be 500 m² for woody and herbaceous species combined, and 125 m² each for woody and herbaceous (Figure 4.3), i.e. the inflection point for accumulated species of the species-area curve. For the sake of consistency, especially as regards newly clearfelled areas, it was decided to multiply the area by four and use a convenient size of 40 x 50 m, or 2000 m² throughout.

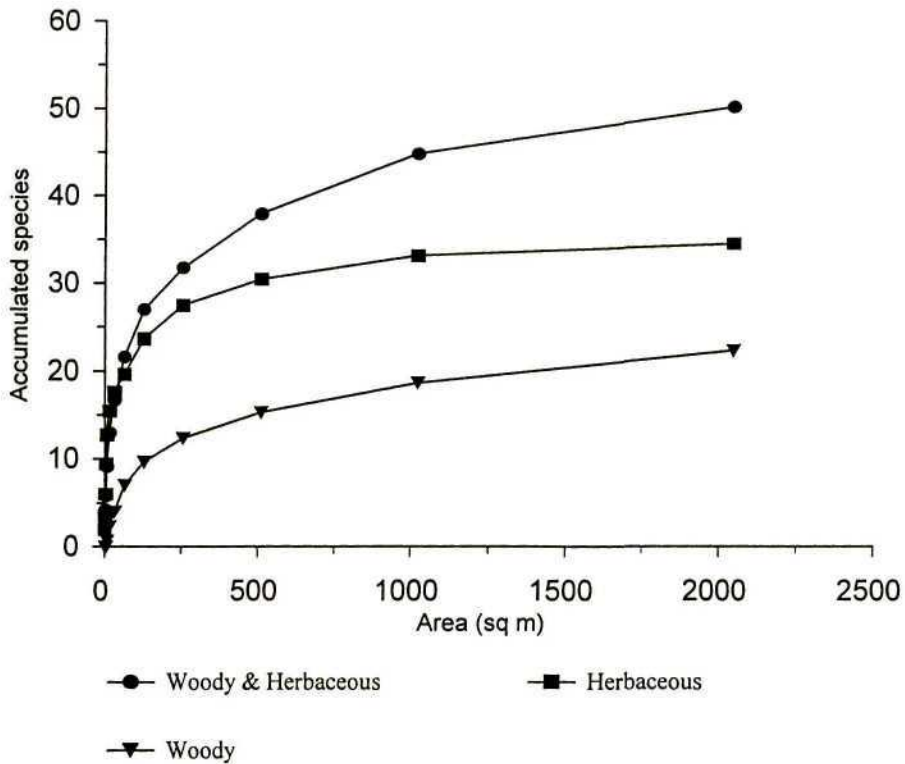


Figure 4.3 Minimal area for woody and herbaceous species - site C4 - Eastern Shores of Lake St Lucia.

A rectangular shape was chosen to minimise edge effects and because most plant distributions are clumped, making rectangular plots efficient and representative for sampling patches of different species (Greig-Smith, 1983). The plot was demarcated with rope, which was marked at regular intervals. A 50 m rope was divided to give five points, 12.5 m apart. At right angles from each of the five points, a 40 m rope, marked at intervals of 13.33 m, was spread. This gave a total of 20 points at which to systematically place a 0.5 m x 0.5 m quadrat for the recording of herbaceous species.

Auger samples were taken down the soil profile for each site to a maximum depth of 1.26 m using a bucket auger with a 14 cm long barrel. After sampling, the auger holes were filled in immediately. Soil samples were, for the most part, taken from 0-14 cm, 14-28 cm, 28-42 cm and 112-126 cm down the profile, unless visual examination revealed obvious colour changes, then all of the buckets were taken.

SOIL ANALYSIS

Exploratory analysis involved an initial set of soil samples to determine trends and to decide on what further analyses to perform on all fifty site samples. The initial analyses involved 16 paired sites (8 pairs) and three levels down the profile, ie. 0-14 cm, 28-42 cm, and 112-126 cm. The method for each of the analyses listed below are described in Appendix 3 and a summary of the results is given in Appendices 4-6.

- i) Particle Size.
- ii) pH - In water and KCl*.
- iii) Organic carbon*.
- iv) Exchangeable bases*.
- v) Exchangeable acidity.
- vi) Phosphorus*.
- vii) Extractable iron and aluminium.

After the exploratory analyses, all fifty topsoil samples were analysed using only the above methods marked with asterisks (Chapter 5).

4.3 EXPLORATORY ANALYSIS

Once the initial soil analyses had been performed, a series of exploratory statistical analyses were undertaken. These involved determining whether trends observed over sites under various management regimes were consistent down the soil profile, to what extent soil chemical and physical variables changed down the profile, and the degree of correlation between the various soil variables themselves, and soil variables and management regimes. All non-significant relationships were noted as such and the significant ones explored in greater detail.

The woody data were summarised and transformed in the following ways:

- i) The heights of individual trees for each species were summed to derive “cumulative tree height” (Appendix 10). This gives a combined synthetic index of both tree density and tree height and, ultimately, an indication of biomass for comparative purposes. These data were then log transformed.
- ii) From tree circumferences, individual basal area per tree was calculated, as well as total basal area for each species and each site. These data were then log transformed (Appendix 11).

Before proceeding with multivariate analysis of woody vegetation data, it was necessary to decide which index of woody species status would be used for the ordinations. It was necessary to determine whether the chosen index was correlated with other important indices before using it to make broad statements about the state of woody vegetation at a site, or to make comparisons between sites. Table 4.2 gives correlations between the important indices.

Table 4.2 Correlations between woody species indices
(Significance: * = 0.05, ** = 0.01, *** = 0.001 at 48df)
Product moment correlation coefficient (Fowler and Cohen, 1990)

	Mean Basal Area	Mean Height	Tree Density (0.1 ha)	Cumulative Basal Area
Cumulative Height	0.16*	0.62***	0.73***	0.93***
Cumulative Basal Area	0.36**	0.74***	0.63***	
Tree Density (0.1 ha)	0.02	0.36**		
Mean Height	0.76***			

Cumulative height was chosen because it was well correlated with cumulative basal area, tree density and mean height, as well as giving a combined index of tree density and the height of the woody component at each site. Since neither mean height nor mean basal area give an indication of tree density, they were not used.

4.4 MULTIVARIATE ANALYSIS

The computer program CANOCO (Ter Braak, 1988) was used for all multivariate analyses of soil and vegetation data. Ordination was used to arrange sites along multi-dimensional axes on the basis of data on species composition or soil chemistry. The resultant diagrams show an arrangement of points along the axes such that points close together correspond to sites that are similar in species composition, and points far apart correspond to sites that are dissimilar in species composition. The arrangement can reveal an underlying structure in the data that is related to an unknown (or known) environmental gradient.

The two primary ordination techniques used in this study were principal components analysis (PCA) and correspondence analysis (CA), both of which detect different types of underlying structure. Principal components analysis relates to a linear response model in which the abundance of any species (or soil chemical characteristic) either increases or decreases with the value of each of the latent environmental variables. Correspondence analysis is related to a unimodal response model in which any species occurs in a limited range of values for each of the latent variables. For this study, PCA was used for soil data analysis and CA for vegetation data analysis, since they exhibited the appropriate response models for the respective analyses. Principal components analysis and correspondence analysis both provide simultaneously an ordination for the sites and an ordination for the species. The two ordinations may be plotted in the same diagram to yield 'joint plots' of site and species points, but the interpretation of the species points is different between PCA and CA (Jongman *et al.*, 1995).

Correspondence analysis cannot be applied to data that contain negative values. Therefore, the vegetation data were not centred or standardized. Jongman *et al.* (1995) recommended that if the abundance data of each species have a highly skewed distribution with many small

values and a few extremely large values, they be transformed by taking logarithms. In this study, this was done for woody species basal diameters and cumulative height. Cumulative height was eventually chosen for detailed analysis, for reasons explained in Section 4.3. The soil data were centred and standardized before applying PCA.

The scores obtained from PCA for soil properties and sites can be used to prepare a biplot. The biplot serves the same function as a joint plot in CA, but the rules to interpret a biplot are different. The prefix 'bi' refers to the joint representation of sites and variable, and not to the dimensions of the plot. For each variable, PCA fits a straight line in one dimension to the (centred) abundances of the variables. The direction of the arrow in the biplot indicates the direction of steepest ascent of the plane, i.e. the direction in which the abundance of the corresponding variables increases most, and the length of the arrow equals the rate of change in that direction.

Arrows that point in the same direction indicate positively correlated variables (or soil chemical characteristics) and arrows pointing in the opposite direction indicate negatively correlated variables.

Both CA and PCA are forms of indirect gradient analysis. In other words, ordination is followed by environmental gradient interpretation. If ordination of the data is readily interpretable with a particular set of environmental conditions, these conditions are sufficient to explain the main variation in the variable composition. However, if the conditions cannot explain the main variation, they may still explain the remaining variation which might be displayed on an ordination axis not extracted and, which may be substantial.

Canonical ordination is used to overcome this limitation. Canonical ordination techniques are designed to detect patterns of variation in the variable data that can be explained best by the observed environmental variables. Thus, canonical ordination combines aspects of regular ordination with aspects of regression. In other words, it expresses both the pattern of variation in species composition and the main relations between the species and each of the environmental conditions (Jongman *et al.*, 1995).

Redundancy analysis (RDA) is a canonical form of PCA which selects the linear combination of environmental variables that gives the smallest residual sum of squares. PCA also minimizes the total residual sum of squares, but it does so without looking at the environmental variables. The RDA ordination diagram can be interpreted as a biplot. The species (soil chemical variables in this case) points and site points jointly approximate the species abundance data as in PCA, and the species and environmental arrows jointly approximate the covariances between species and environmental variables. If species are represented by arrows as well, the cosine of the angle between the the arrows of the species and the environmental variable is an approximation of the correlation coefficient between the species and the environmental variable.

All pine plantation and clearfelled data were ordinated using canonical correspondence analysis (CCA) in order to check that the main relations were accounted for in the CA ordination.

The environmental variables used in each ordination were pH, sum of bases (\approx cation exchange capacity), phosphorus, organic carbon, years under pine, years succession and total cumulative height of woody component. Rotation 1 and rotation 2 were included as nominal variables.

Principal components analysis and redundancy analysis were used for soil variables, whilst correspondence analysis and canonical correspondence analysis were used for woody and herbaceous data analysis. In both CA and CCA, symmetric scaling of sample and species scores was used.

4.5 STATISTICAL ANALYSIS

Statistical analyses of soil and vegetation data was included using calculations of correlation coefficients, linear, multiple and non-linear regression analysis, paired t-tests, analysis of variance (ANOVA), linear contrasts and determination of diversity indices and evenness. To determine the relationships between management history, vegetation type and soils, principal components analysis, calculation of correlation coefficients and regression analysis were used.

Linear regression is the procedure of fitting the best line to a scattergram so that the sum of the vertical distances (deviations) of all points from the line is minimised. The method of fitting the line is known as the method of least squares (Fowler and Cohen, 1990). In multiple regression, the response variable is expressed as a function of two or more explanatory variables (response-surface analysis) (Jongman *et al.*, 1995). The t-test is used for comparing the means of two small samples (Fowler and Cohen, 1990). Analysis of variance (ANOVA) is a statistical technique that allows comparisons to be made between any number of sample means. Linear contrasts are a form of ANOVA in which groups of vegetation types were compared with other groups. The determination of diversity, the distribution of observations among categories, was performed using the Shannon-Weaver Diversity Index (Zar, 1996). Evenness (homogeneity or relative diversity) was calculated as the Shannon-Weaver Diversity Index divided by the maximum possible diversity for that data (Zar, 1996).

Linear regression analyses were performed using the spreadsheet software package, Corel Quattro Pro 6.0 for Windows 3.1. Multiple regression and non-linear regression analyses were performed using the GENSTAT (Genstat 5, 1988) and STATISTICA 5.1 (Statsoft, Inc, 1996) statistical software packages. The one-way ANOVA and linear contrasts were performed using STATISTICA.

5 RESULTS

5.1 SOILS

Data from the soil analyses are to be found in Appendices 4-6.

Logistical constraints dictated that not all four soil samples collected down the profile, for fifty sites could be analysed, as this would have amounted to 200 samples. Therefore, a selection of paired sites was chosen. Initial soil analyses of 16 sites (8 pairs) and three levels (0-14 cm, 18-42 cm & 112-126 cm) down the profile was performed (Table 5.1 & Appendix 4.1). These analyses revealed factors that enabled refinement of the soil analysis process, to concentrate only on those factors of major importance to the study. Once these factors had been determined, further analysis took place.

Table 5.1 Paired sites selected for preliminary soil analysis

SITE #	DESCRIPTION	SITE #	DESCRIPTION
B9	1st Rotation Pine - 34 yrs	B9X	Grassland
B19	1st Rotation Pine - 12 yrs	B19X	Grassland with trees
A1	2nd Rotation Pine - 7 yrs	A1X	Indigenous forest
B12	Clearfelled after 35 yrs - 1yr	B12X	Grassland
B13	Clearfelled after 36 yrs - 1yr	B14	1st Rotation Pine - 32 yrs
C15	Clearfelled after 36 yrs - 4yrs	C20	2nd Rotation Pine - 10 yrs
A4	Clearfelled after 35 yrs - 1 yr	A5	2nd Rotation Pine - 8 yrs
A25	Clearfelled after 28 yrs - 1 yr	A26(2)	2nd Rotation Pine - 7 yrs

The means for each soil variable (pH, CEC, C, P) at each level in the soil profile are presented in Table 5.2 and Figure 5.1(a-d). The degree of correlation between each level for soil variables over 16 sites is also given in Table 5.2. It can be seen that there is a rapid change in soil chemistry down the profile, and that there is a degree of correlation down the profile.

Table 5.2 Comparison between soil chemical variables at different depths in the soil profile. (Significance * < 0.1, ** < 0.05, *** < 0.01)

DEPTH	ORGANIC CARBON %	pH (KCl)	EXCH. PHOSPH. mg/kg	CEC (cmolc/kg)
1-14 cm	0.425	4.337	6.082	0.702
14-28 cm	0.212	4.544	3.810	0.504
112-126 cm	0.082	4.751	2.460	0.377

CORRELATIONS				
Level 1 vs 2	0.32	0.47*	0.54**	0.56**
Level 2 vs 3	0.29	0.71***	0.33	0.67***
Level 1 vs 3	-0.11	0.08	0.32	0.16

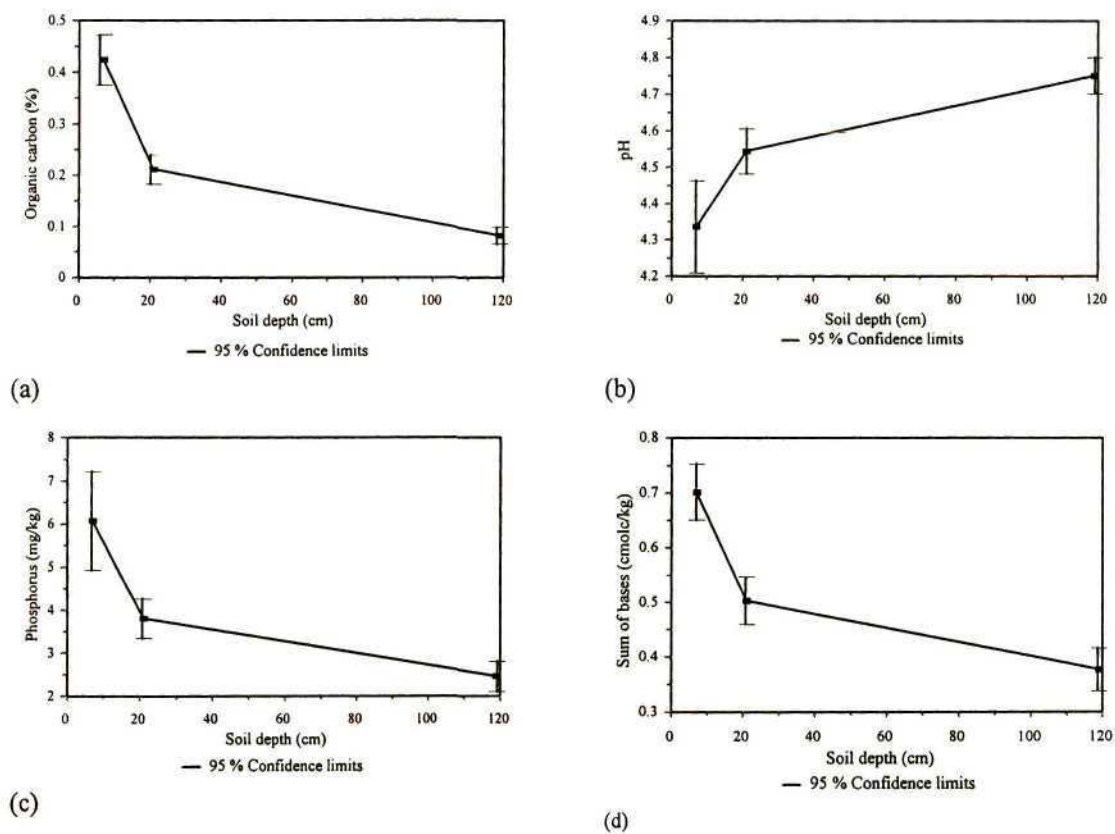


Figure 5.1 Changes in selected chemical factors down the soil profile (a) Organic carbon; (b) pH; (c) Phosphorus; (d) Sum of bases.

Due to the rapid change in soil chemical variables which would result in comparing extremely low values, and since there was a degree of correlation down the profile, in addition to financial and time constraints, only the topsoil samples were analysed for all 50 sites (Appendix 4.2).

Soil samples analysed for the 16 sites (8 pairs) and three levels (48 samples) showed a mean particle size distribution of 98.25 % sand, 0.86 % silt and 0.89 % clay for all levels, with a mean difference between observed and calculated sand content of 0.5 %. The pipette method of particle size analysis is the most accurate method available, but with the extremely low silt and clay percentages, a large experimental error resulted which made it difficult to come to any meaningful conclusions about changes in particle sizes due to weathering. Sieving and weighing out of the various sand fractions (Appendix 5) after clay and silt percentages have been determined resulted in unavoidable loss of some of the finer soil fragments which got stuck in the sieve.

The t-test on paired sites to determine whether soils under pines showed any marked difference in soil texture to those under undisturbed vegetation revealed that no measurable differences in particle sizes existed (Table 5.3). Possibly the pines have not been established long enough for affects to be noticed. For all practical purposes, no increased weathering has taken place as a result of the presence of pine plantations. No further particle size analysis was undertaken.

Table 5.3 Results of t-test for differences in means of particle sizes between pine plantations and adjacent, undisturbed vegetation (n = 4).

Depth	Clay	Silt	Sand
1-14 cm	2.37	0.56	-1.57
28-42 cm	0.27	1.62	-1.03
112-126 cm	0.08	-0.11	-0.00

	Sand		
	Coarse	Medium	Fine
1-14 cm	0.30	-0.15	0.10
28-42 cm	0.31	1.26	-1.15
112-126 cm	1.75	1.62	-2.19

Critical value: $t = 3.182$ ($\alpha = 0.05$ and $n = 4$). If the value of t is less than the critical value, then the difference is insignificant.

Comparing results for the 16 sites and 3 levels, exchangeable acidity, pH in water and pH in 1 M potassium chloride, were found to be strongly correlated (Table 5.4). Determination of pH in KCl is known to be more reliable than that in water because KCl is a more reliable buffer (Rowell, 1994). When measuring pH in water, the readout on the pH-meter tends to drift continually and it is difficult to decide which reading to record, whereas, when using KCl, the pH-meter stabilises quickly. This factor means that the correlation coefficient between the two is lower than would be expected (0.68). Yet the correlation coefficient between pH in KCl and pH in H₂O, later determined for all 50 sites, is 0.80. Determination of exchangeable acidity is a lot more labourious than determination of pH and, given the statistical significance of the strong correlation between the results from this and the two pH measurements, it was decided to use pH in KCl as the standard measure of acidity for all remaining samples.

Table 5.4 Correlation between pH in different solutions, and exchangeable acidity.

pH (KCl) and pH (H ₂ O)	0.68
pH (KCl) and exchangeable acidity	-0.73
pH (H ₂ O) and exchangeable acidity	-0.79
<i>(P = 0.01, n = 48)</i>	

Organic carbon did not show any clear trends in the initial analysis, but the analysis was continued for all topsoil samples. For organic carbon, only the topsoil in this preliminary analysis contained appreciable organic carbon. As expected, for sandy soils with rapid recycling of organic matter, there was a rapid drop in organic carbon down the profile, from a mean of 0.42 % for topsoil, to 0.08 % at 112cm (Appendix 4.1).

Cation exchange capacity is usually calculated as the sum of exchangeable bases (Ca, Mg, Na, K) plus exchangeable acidity. The calculated exchangeable acidity was extremely low in the initial analyses, therefore, the sum of bases was used as an approximation of cation exchange capacity. After the initial analyses of the 16 samples down the profile, all 50 topsoil samples were analysed for exchangeable cations.

Since phosphorus is another measure of soil fertility which is important to the study, it was decided to continue with this analysis for all 50 topsoil samples before coming to any conclusions.

No clear trends were established for all three methods of determination of extractable iron and aluminium in the initial analysis (Appendix 3 & 6) and, comparing paired sites, there was no evidence of iron or aluminium toxicity or podzolization as a result of the pine plantations, so no further exchangeable iron and aluminium analyses were performed.

5.1.1 Effects of different vegetation types on soil chemistry

To explore relationships between soil chemistry (pH, organic carbon, phosphorus, calcium, magnesium, sodium, potassium and sum of bases) and environmental variables and management regimes (adjacent vegetation type, cumulative height of woody component, first or second rotation pine, time under pines, and time since clearfelling), Principal Components Analysis and Redundancy Analysis (RDA) were applied for the topsoil of all 50 sites. Symmetric scaling was used for ordination scores.

The PCA output in Figures 5.2 (a-c) and 5.3 and Table 5.5 indicate the following:

After the first PCA run there was one outlier, C23d-b. This was a low-lying, first rotation, pine plantation that had exceptionally high organic carbon, to the extent that the soil was black, unlike other samples. This site was excluded for a second PCA run and for the RDA.

Axis 1 accounts for 46 % of the variance (Figure 5.2a). This axis describes a gradient of exchangeable bases and pH, which are related to the growth of the woody component, i.e. increasing woody understorey in pine plantations would increase pH. The axis also describes the gradient from grassland to forest. The variable "YRSPINE" (years under pines) is completely orthogonal to pH and exchangeable bases. Therefore, time under plantations has no direct effect on soil pH and cation exchange capacity. Axis 2 (18.5 % of the variance) represents a gradient in phosphorus and organic carbon levels, which are both related to time under pine plantations. The nett result is that cation exchange capacity is related to increased indigenous woody cover. The third axes describes 14.5 % of the variance and the fourth,

8.7%. They are, thus, not important since the soil chemical-environment correlations are only reasonably high for the first axis, and lower for the other three. The first two axes combined describe 65.2 % of the variance, therefore, they are the most important. However, it is interesting to note that on the third axis, organic carbon is negatively correlated with pH. This is probably because most of the sites had very little organic carbon, and those that had litter accumulation were pine plantations, which has acidic litter.

The RDA output indicates that, on the first axis (12.7 % of the variance), pH and cation exchange capacity are, once again, related to the cumulative height of the woody component. Axis 2 (3.9 % of the variance) describes a gradient in Phosphorus and organic carbon, which are both related to time under pines. The difference in percentage variance accounted for in the PCA and RDA output indicate that not all of the important environmental variables were taken into account. Nevertheless, there is a strong soil chemical variable-environmental correlation (0.525) for Axis 1 of the RDA, indicating the importance of the woody component in determining soil chemical characteristics.

Table 5.5 Summary of: (a) Principal Components Analysis (PCA) and (b) Redundancy Analysis (RDA) for the Eastern Shores of Lake St Lucia soils.

(a)	Axis order				Total variance
	1	2	3	4	
Eigenvalues	0.467	0.185	0.145	0.087	1.000
Soil chemical-environment correlations	0.519	0.399	0.278	0.355	
Cumulative percentage variance					
of soil chemical data	46.7	65.3	79.8	88.5	
of soil chemical-environment relation	65.8	81.2	87.1	92.8	
Sum of all unconstrained eigenvalues					1.000
Sum of all canonical eigenvalues					0.191
(b)	1	2	3	4	Total variance
Eigenvalues	0.127	0.040	0.014	0.006	1.000
Soil chemical-environment correlations	0.525	0.491	0.395	0.282	
Cumulative percentage variance					
of soil chemical data	12.7	16.7	18.1	18.6	
of soil chemical-environment relation	66.6	87.4	94.4	97.5	
Sum of all unconstrained eigenvalues					1.000
Sum of all canonical eigenvalues					0.191

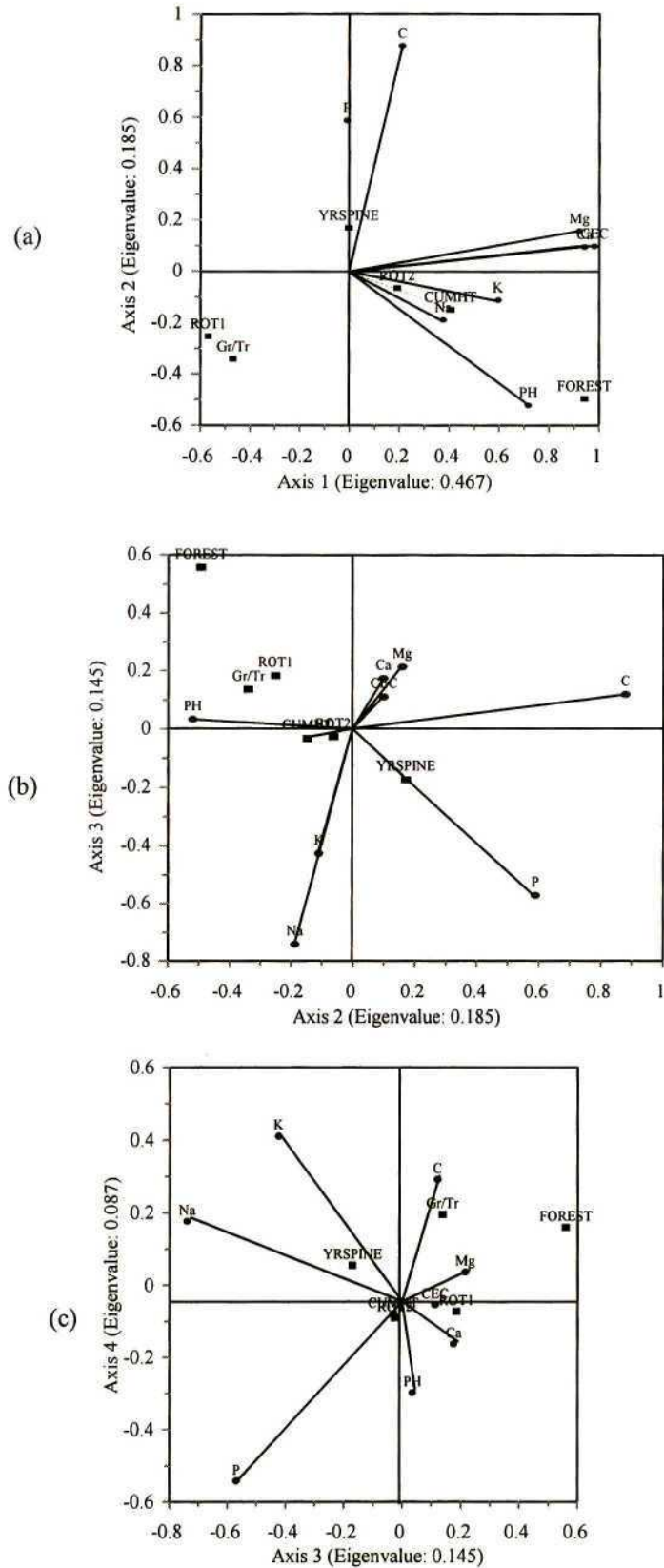


Figure 5.2 PCA plot of soil chemical variables passively related to a set of vegetation and management variables. (a) Axes 1 & 2; (b) Axes 2 & 3; (c) Axes 3 & 4. Soil chemical variables: Ca = Calcium; C = Organic carbon; CEC = Sum of bases; K = Potassium; Mg = Magnesium; Na = Sodium; pH = pH measured in KCl; P = Phosphorus. Vegetation and management variables: CUMHT = Cumulative height of woody component; Gr/Tr; FOREST, ROT1 & ROT2 = Nominal variables indicating whether rotation 1 or 2; YRSPINE = Time under pines. Eigenvalues: Axis 1 = 0.467; Axis 2 = 0.185; Axis 3 = 0.145; Axis 4 = 0.087.

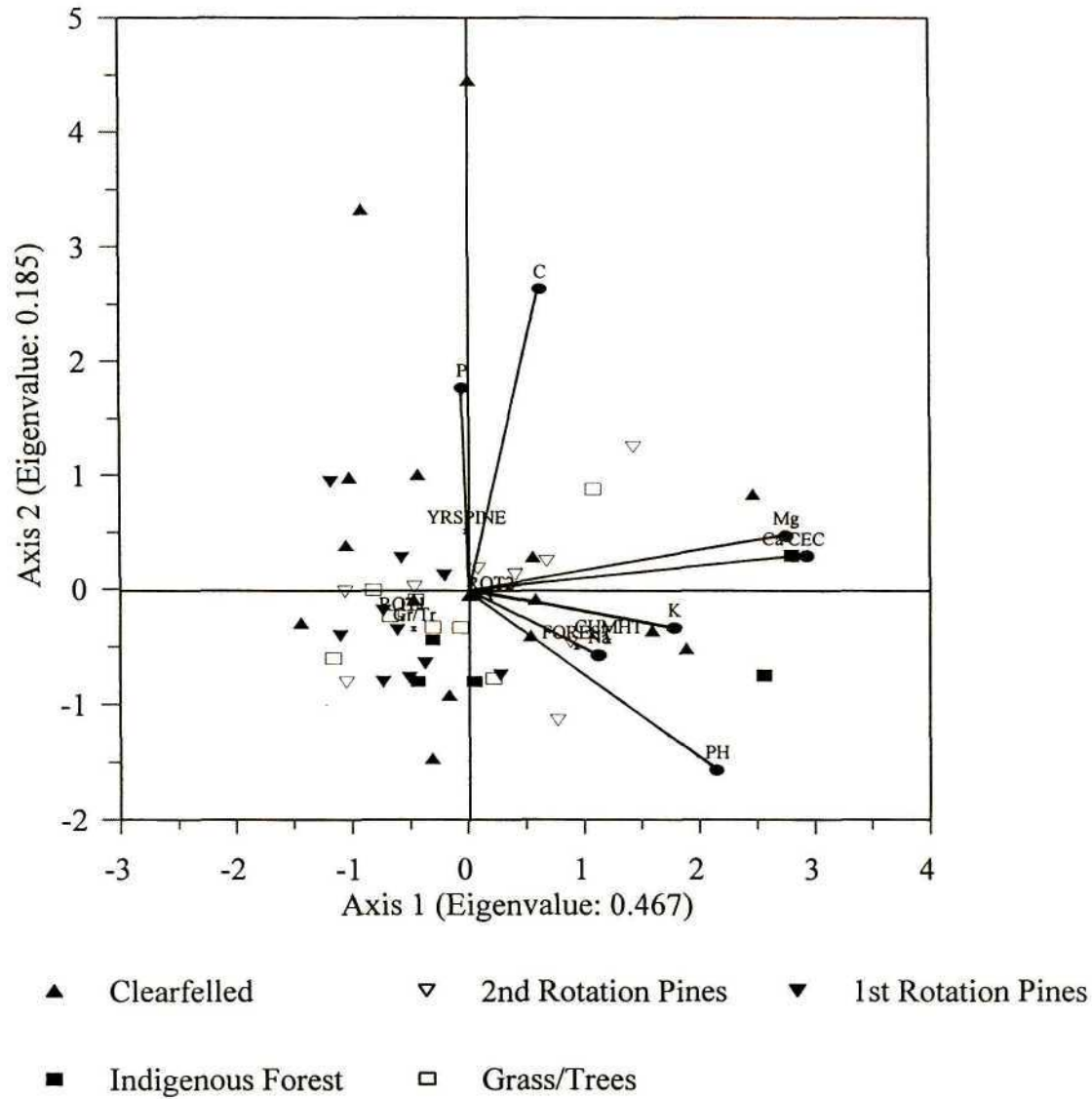
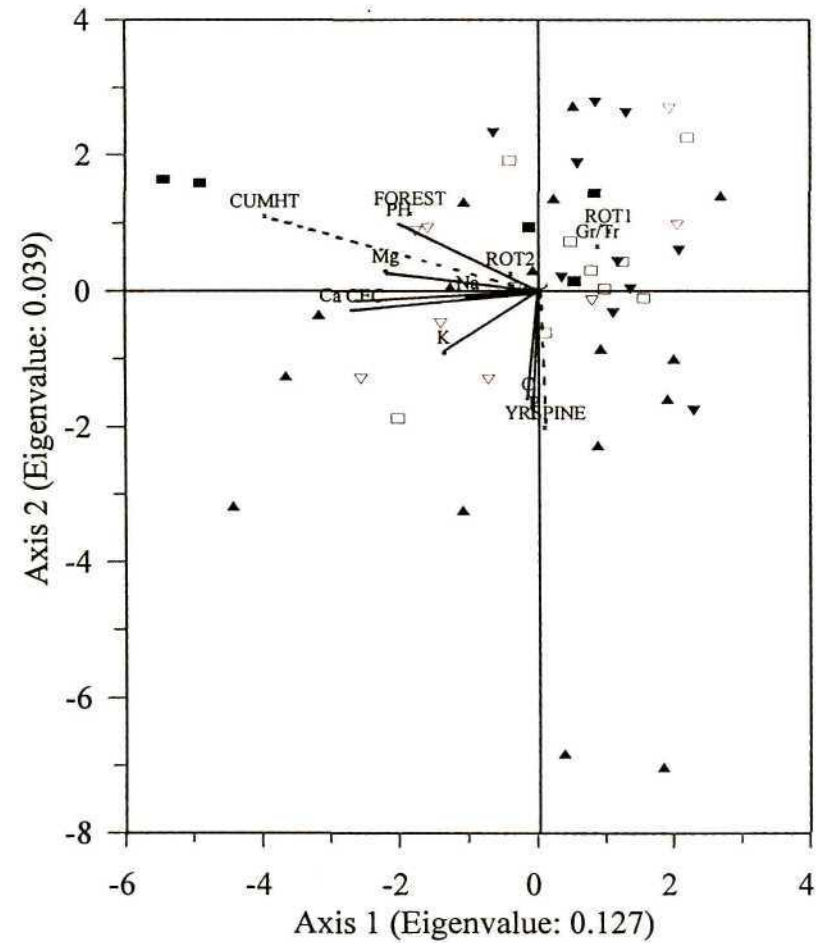


Figure 5.3 PCA Biplot for four soil chemical variables, passively related to five management/vegetation variables and fifty sites (Eigenvalues: Axis 1 = 0.467, axis 2 = 0.185). Chemical variables: Ca = Calcium; C = Organic carbon; CEC = Sum of bases; K = Potassium; P = Phosphorus; pH = pH measured in KCl. Management/vegetation variables: Gr/Tr, FOREST; ROT1 & ROT2 = Nominal variables indicating whether rotation 1 or rotation 2; YRSPINE = Time under pines.



- ▲ Clearfelled ▽ 2nd Rotation Pines ▼ 1st Rotation Pines
- Indigenous Forest □ Grass/Trees

Figure 5.4 RDA Biplot for four soil chemical variables, related to five management/vegetation variables and fifty sites (Eigenvalues: Axis 1 = 0.127, Axis 2 = 0.039). Chemical variables: Ca = Calcium; C = Organic carbon; CEC = Sum of bases; K = Potassium; P = Phosphorus; pH = pH measured in KCl. Management/vegetation variables: Gr/Tr; FOREST; ROT1 & ROT2 = Nominal variables indicating whether rotation 1 or rotation 2; YRSPINE = Time under pines.

Table 5.6 illustrates further the relationship between the various soil chemical variables, with pH and sum of bases generally showing a strong relationship to cumulative height of the indigenous understorey. The high correlations displayed between organic carbon vs sum of bases and carbon vs phosphorus in pine plantations is due almost entirely to site C23d-b, a first rotation pine plantation in a dune slack in the south, which had an exceptionally high organic carbon content relative to the rest of the sites.

Table 5.6 Correlation coefficients between soil and vegetation variables under various management regimes. Significance: * = 0.05, ** = 0.01, *** = 0.001.

Indigenous vegetation (n= 14)

	Cumulative Height	CEC	Phosphorus	Carbon
pH	0.48	***0.84	-0.18	*0.55
Carbon	-0.18	*0.56	0.10	
Phosphorus	-0.48	-0.25		
CEC	0.39			

All pines (n= 20)

	Cumulative Height	CEC	Phosphorus	Carbon
pH	**0.56	0.43	0.05	-0.24
Carbon	0.04	*0.43	***0.75	
Phosphorus	0.10	0.39		
CEC	**0.56			

1st Rotation pines (n=11)

	Cumulative Height	CEC	Phosphorus	Carbon
pH	*0.72	0.29	-0.22	-0.33
Carbon	0.09	*0.68	***0.88	
Phosphorus	0.17	0.55		
CEC	*0.63			

2nd Rotation pines (n= 9)

	Cumulative Height	CEC	Phosphorus	Carbon
pH	0.35	0.39	-0.12	-0.14
Carbon	0.40	0.23	-0.23	
Phosphorus	0.41	0.31		
CEC	0.25			

Clearfelled sites (n=16)

	Cumulative Height	CEC	Phosphorus	Carbon
pH	*0.57	*0.60	-0.39	*-0.55
Carbon	-0.21	0.16	0.31	
Phosphorus	-0.11	0.01		
CEC	0.39			

No significant relationship was found between age of pine plantations or successional age of clearfelled areas and any of the soil variables.

The effects of each vegetation or plantation type on soil chemistry was tested using one-way analysis of variance and linear contrasts (Figure 5.5, p. 90; Tables 5.7, 5.8 & 5.9). Although small differences are noticeable in the different means for each vegetation type, according to Tables 5.8 and 5.9, none are statistically significant, indicating that generalisations about the effects of different vegetation types on the soils should be made with caution.

By using the results of soil analysis for paired, adjacent sites and comparing the means using the paired t-test it was possible to determine whether pine plantations have had a direct effect on the following soil variables: (i) pH; (ii) sum of bases (CEC \approx sum of bases); (iii) individual bases (Ca, Mg, Na, K); (iv) organic carbon; and (v) phosphorus (Table 5.10). This indicates that statistically significant differences are only evident when pairwise comparisons are made between adjacent plots of a sufficient number. Thus, simply grouping sites into different vegetation types does not take into account all of the other environmental variables that would impact on soil chemistry, especially in this context where soil fertility is low and where any differences in soil chemistry are small.

Table 5.7 Comparison between means of soil chemical characteristics under different vegetation types (pH), organic carbon (c), phosphorus (P) and sum of bases (CEC).

<i>Groups</i>	<i>n</i>	<i>pH</i>	<i>C</i> %	<i>P</i> mg/kg	<i>CEC</i> cmol _e /kg
Grass	2	4.5(0.15)	0.7(0.30)	11.1(0.38)	1.7(0.64)
Grass/Trees	7	4.2(0.13)	0.4(0.04)	7.6(1.46)	1.0(0.12)
Forest	5	4.7(0.23)	0.4(0.14)	5.9(1.30)	2.2(0.67)
1st Rot	11	4.1(0.10)	0.7(0.43)	9.8(2.15)	1.1(0.15)
2nd Rot	9	4.4(0.17)	0.5(0.13)	8.7(1.35)	1.6(0.22)
Clearfelled	16	4.3(0.15)	0.7(0.18)	11.2(1.46)	1.5(0.20)

Table 5.8 One-way ANOVA for soil chemical characteristics across six vegetation types (Grass; grass/trees; forest; 1st rot; 2nd rot; & clearfelled).

	<i>SS</i>	<i>df</i>	<i>Mean sq.</i>	<i>F</i>	<i>p-level</i>
pH	1.389	5	0.278	1.173	0.338
Carbon	0.945	5	0.189	0.281	0.921
Phosphorus	146.794	5	29.359	1.015	0.420
Sum of bases	0.748	5	1.150	1.959	0.104

Table 5.9 Linear contrasts of soil chemical variables for groups of vegetation types.

pH	SS	Mean Sq.	F	p-level
1st vs 2nd Rot	0.391	0.391	1.652	0.205
Pine vs clear	0.001	0.001	0.005	0.942
Pine vs undisturbed	0.175	0.175	0.737	0.395
Clear vs undisturbed	0.316	0.316	1.335	0.254
Organic C	SS	Mean Sq.	F	p-level
1st vs 2nd Rot	0.028	0.028	0.042	0.838
Pine vs clear	0.028	0.028	0.042	0.840
Pine vs undisturbed	0.065	0.065	0.097	0.757
Clear vs undisturbed	0.241	0.241	0.359	0.552
Phosphorus	SS	Mean Sq.	F	p-level
1st vs 2nd Rot	6.350	6.350	0.220	0.642
Pine vs clear	32.135	32.135	1.111	0.298
Pine vs undisturbed	5.242	5.243	0.181	0.672
Clear vs undisturbed	57.270	57.270	1.981	0.166
Sum of bases	SS	Mean Sq.	F	p-level
1st vs 2nd Rot	1.108	1.108	1.888	0.176
Pine vs clear	0.277	0.277	0.472	0.496
Pine vs undisturbed	0.279	0.279	0.475	0.494
Clear vs undisturbed	0.076	0.076	0.129	0.721

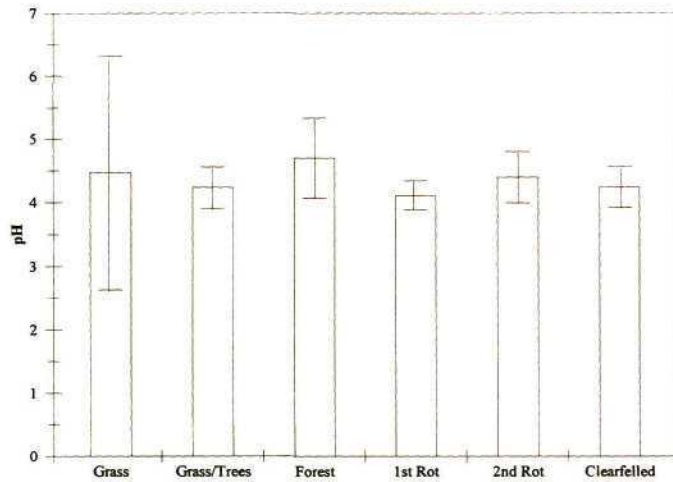
A graphical representation of the analysis of variance (Figure 5.5 a-d) indicates the following:

- a) pH
 - i) pH in indigenous forest is different to grass/trees, first rotation pines and clearfelled areas, but not *vice versa*.
 - ii) pH in grassland is different to first rotation pines, but not *vice versa*.
 - iii) Second rotation pines are different to first rotation, but not *vice versa*.
- b) Organic carbon
 - i) First rotation pines, clearfelled sites and grassland are different to grass/trees, but not *vice versa*.
- c) Phosphorus
 - i) Indigenous forest is different to clearfelled and *vice versa*, being lower in the

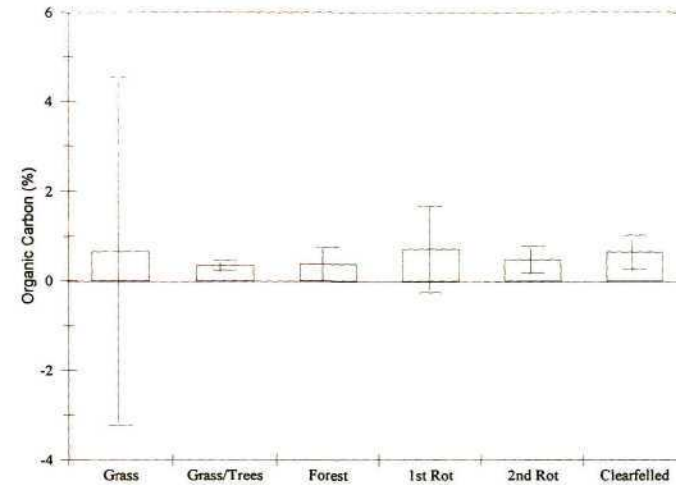
forest. This corresponds to the pattern shown in the second axis of the PCA (Figures 5.2a, 5.3 & 5.4).

- ii) Indigenous forest is different to grassland and *vice versa*, being lower in the forest. This corresponds to the pattern shown in the second axis of the PCA (Figures 5.2a, 5.3 & 5.4).
 - iii) Grass/trees is different to clearfelled and *vice versa*, being lower in the grass/trees.
- d) Sum of bases
- i) Grassland is different to grass/trees and to first rotation, but not *vice versa*.
 - ii) Indigenous forest is different to grass/trees, first rotation pines, second rotation pines and clearfelled, but not *vice versa*.
 - iii) First rotation pine is different to second rotation and clearfelled and *vice versa*. This corresponds to the first axis of the PCA (Figures 5.2 & 5.3) and RDA (Figure 5.4). First rotation pine plantations have less development of indigenous understorey than second rotation, for reasons explored later, and pH and sum of bases are related to the development of the woody component.
 - iv) Clearfelled areas are different to grass/trees, but not *vice versa*.

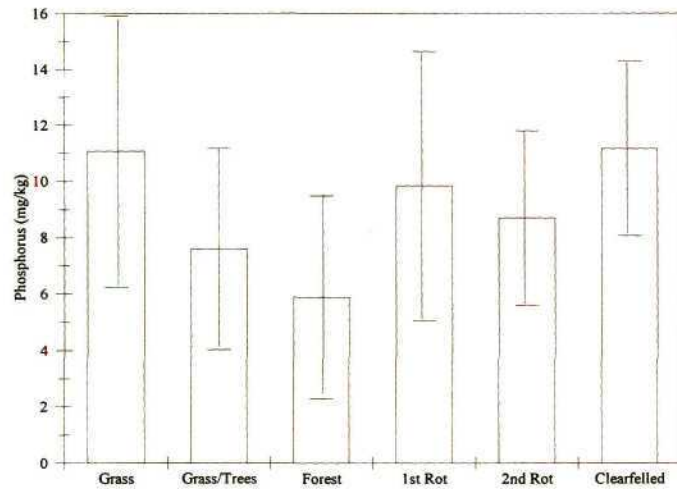
In all cases, grassland seems to be particularly variable, possibly suggesting considerable environmental variation within this vegetation type.



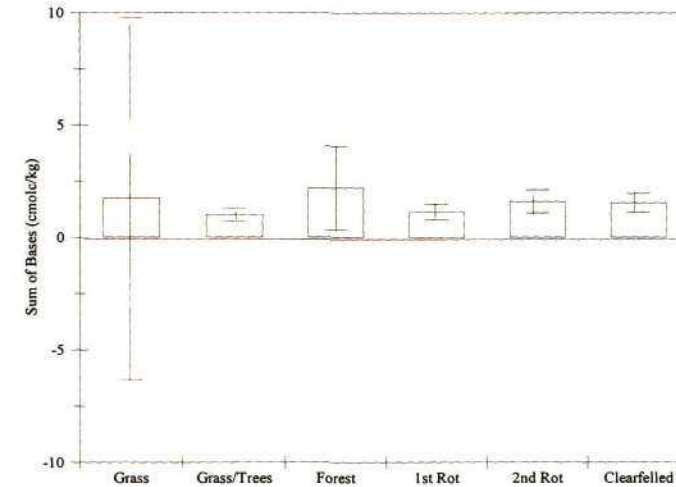
(a)



(b)



(c)



(d)

Figure 5.5 Bar chart showing 95 % confidence intervals about the means for different vegetation types and one-way analysis of variance for: (a) pH ($F=7.060$); (b) Organic carbon ($F = 2.24$); (c) Phosphorus ($F = 7.839$); and (d) sum of bases ($F = 4.481$). $F\text{-crit.} = 2.316$.

Table 5.10 Pairwise comparisons between soil chemical variables under various vegetation types.

Soil variable	Mean		t-value
	All Pines	All Undist.	
pH	4.09	4.39	3.166*
Organic Carbon (%)	0.37	0.38	0.473
Phosphorus (mg/kg)	7.19	7.30	0.280
Calcium (cmol _c /kg)	0.60	0.93	2.141
Magnesium (cmol _c /kg)	0.33	0.45	2.370*
Sodium (cmol _c /kg)	0.21	0.20	0.650
Potassium (cmol _c /kg)	0.03	0.06	2.150
Sum of bases (cmol _c /kg)	1.08	1.45	2.252*

Critical value = 2.201 (n = 12, α = 0.05)

Soil variable	Mean		t-value
	1st Rotation	Grass/trees	
pH	4.15	4.41	1.734
Organic Carbon (%)	0.17	0.51	2.896*
Phosphorus (mg/kg)	8.06	8.74	1.216
Calcium (cmol _c /kg)	0.46	0.81	1.964
Magnesium (cmol _c /kg)	0.22	0.35	1.494
Sodium (cmol _c /kg)	0.21	0.22	1.039
Potassium (cmol _c /kg)	0.03	0.07	3.911*
Sum of bases (cmol _c /kg)	0.92	1.45	2.069

Critical value = 2.776; n = 5

Soil variable	Mean		t-value
	1st Rotation	Clear	
pH	3.91	3.70	0.756
Organic Carbon (%)	0.52	0.46	0.276
Phosphorus (mg/kg)	7.13	12.37	3.828
Calcium (cmol _c /kg)	0.37	0.37	0.022
Magnesium (cmol _c /kg)	0.28	0.15	1.459
Sodium (cmol _c /kg)	0.19	0.19	0.198
Potassium (cmol _c /kg)	0.01	0.02	0.745
Sum of bases (cmol _c /kg)	0.85	0.74	0.635

Critical value = 4.303; n = 3

Soil variable	Mean		t-value
	2nd Rotation	Forest	
pH	4.19	4.57	2.048
Organic Carbon (%)	0.54	0.36	0.669
Phosphorus (mg/kg)	7.05	5.24	1.423
Calcium (cmol _e /kg)	0.78	1.10	1.126
Magnesium (cmol _e /kg)	0.47	0.57	1.402
Sodium (cmol _e /kg)	0.21	0.20	0.780
Potassium (cmol _e /kg)	0.05	0.06	0.811
Sum of bases (cmol _e /kg)	1.50	1.93	1.241

Critical value = 2.571; n = 6

Soil variable	Mean		t-value
	2nd Rotation	Clear	
pH	4.71	4.81	0.516
Organic Carbon (%)	0.62	0.56	0.900
Phosphorus (mg/kg)	10.65	13.02	1.418
Calcium (cmol _e /kg)	1.14	1.40	0.972
Magnesium (cmol _e /kg)	0.60	0.71	1.291
Sodium (cmol _e /kg)	0.24	0.28	1.006
Potassium (cmol _e /kg)	0.04	0.16	2.877
Sum of bases (cmol _e /kg)	2.02	2.55	1.467

Critical value = 3.182; n = 4

Soil variable	Mean		t-value
	Clear	Grass/trees	
pH	3.74	4.21	2.017
Organic Carbon (%)	0.70	0.30	0.947
Phosphorus (mg/kg)	13.34	9.88	0.499
Calcium (cmol _e /kg)	0.40	0.49	0.514
Magnesium (cmol _e /kg)	0.17	0.23	0.977
Sodium (cmol _e /kg)	0.19	0.17	0.523
Potassium (cmol _e /kg)	0.02	0.04	1.551
Sum of bases (cmol _e /kg)	0.79	0.92	0.525

Critical value = 4.303; n = 3

On the basis of the data contained in Tables 5.7, 5.8, 5.9 and 5.10 and Figure 5.5 it is concluded that:

- i) No general comparisons can be made between the effects of different vegetation types on soils of the Eastern Shores, unless direct pairwise comparisons are made.
- ii) Differences that do exist are so small that small sample sizes do not show statistically significant differences in soil chemistry.

- iii) Soils under pines are more acidic than those under indigenous vegetation.
- iv) Soils under pines have a lower cation exchange capacity (sum of bases) to those under indigenous vegetation, although this is entirely a product of a significant difference in magnesium.
- v) Soils under pines have less organic carbon and potassium than soil under grassland, but they are not significantly different to those under indigenous forest.
- vi) Soils under pines did not show a significant difference in extractable phosphorus to those under indigenous vegetation. This is consistent with Blackmore's (1993) findings.
- vii) In general, because of the absence of finer particles in the soil and the low organic carbon, the soil of the Eastern Shores has low fertility which results in high percentage error in laboratory chemical analysis and difficulty in coming to statistically valid conclusions.
- viii) Pine plantations on the Eastern Shores of Lake St Lucia have had minimal effects on soil chemistry and fertility.

5.1.2 Effects of indigenous understorey on soils under pines.

(a) pH

The PCA output (Figures 5.2a-d, 5.3 & 5.4) and calculation of correlation coefficients indicates that pH tends to increase within pine plantations as cumulative indigenous tree height increases. Regression analysis gives a clearer picture (Figures 5.6 & 5.7).

From Figures 5.6 and 5.7, it is clear that growth of the indigenous understorey serves to reduce acidity in pine plantations and clearfelled areas. There was no significant relationship between the soil pH and the cumulative height of the woody component in undisturbed vegetation. This is to be expected since soil under grassland is known to have a higher pH than under pine forest (Barbour *et al.*, 1987; Miles, 1985; Ugolini and Edmonds, 1983), thus, the soil in the undisturbed areas without trees has never been acidified.

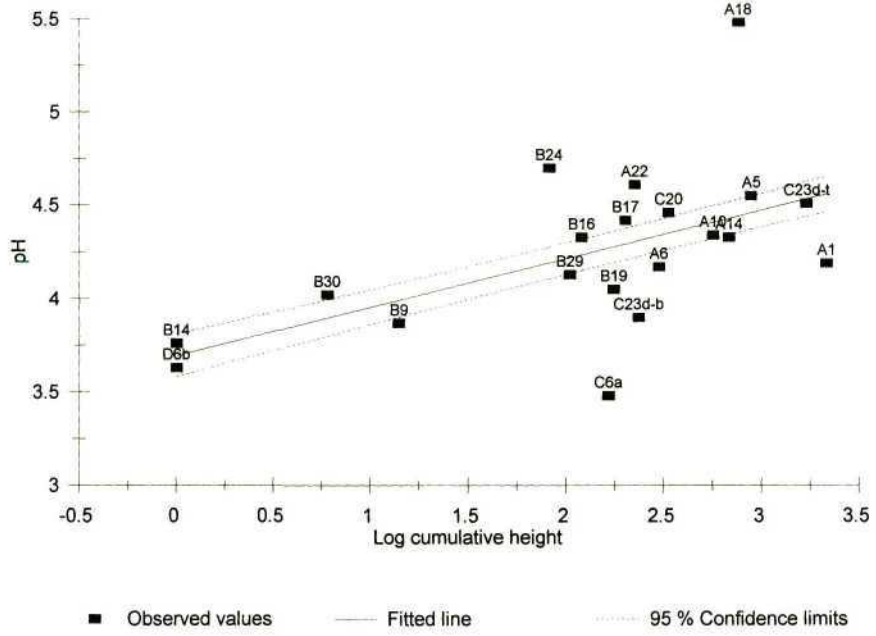


Figure 5.6 pH vs cumulative height of indigenous understorey in the 1st and 2nd rotation pine plantations. $r^2 = 0.312$; $P = 0.01$

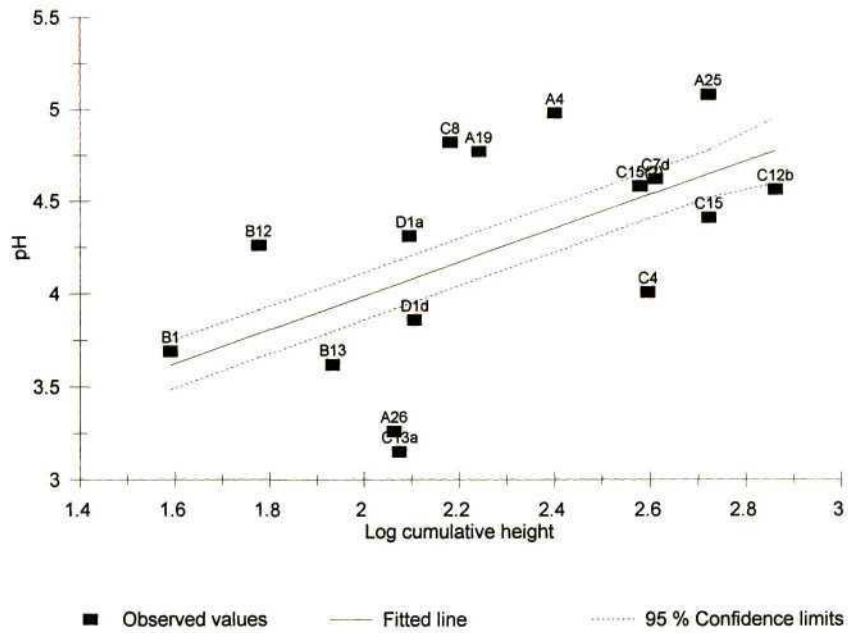


Figure 5.7 pH vs cumulative height of woody component in clearfelled areas. $r^2 = 0.322$; $P = 0.02$

(b) Sum of bases (\approx CEC)

The PCA output (Figures 5.2, 5.3 & 5.4) and Regression analysis (Figures 5.8 & 5.9) show that there is an increase in sum of bases in both pine plantations and clearfelled areas with increase in indigenous woody biomass. Regression analysis was also performed for undisturbed vegetation sites and it was found that there was no significant relationship between cumulative height of the woody component and sum of bases. A possible explanation is that the herbaceous component plays a greater role in maintaining soil fertility in the undisturbed vegetation than it would under pine plantations and in clearfelled areas.

(c) Organic carbon

No relationship was found to exist between organic carbon and cumulative height of indigenous trees, yet most, if not all, of the base cations must reside in the organic matter and there is a relationship between base cations and extent of establishment of indigenous understorey. Possibly the explanation is that under pines without a well-established indigenous understorey there is a lot of pine litter which gives a relatively high organic carbon content but acidifies the soil, thus reducing cation exchange capacity.

(d) Phosphorus

No significant relationship was found between phosphorus and establishment of the indigenous understorey.

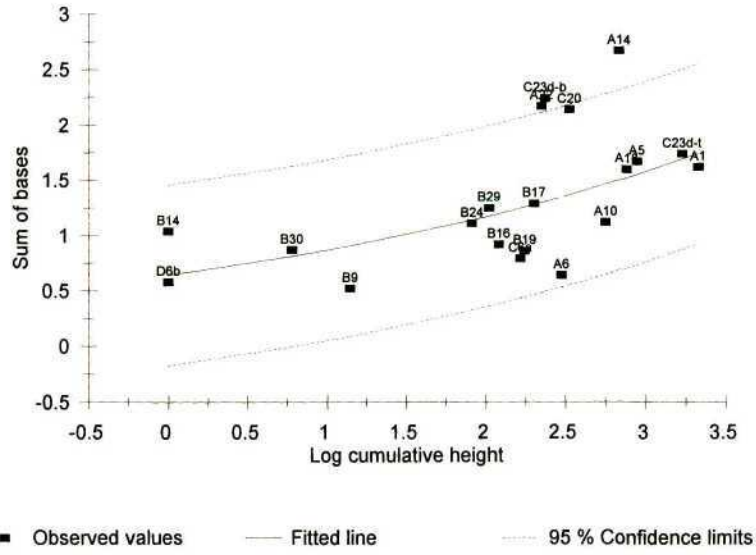


Figure 5.8 Sum of bases vs log cumulative height of indigenous understorey in first and second rotation pine plantations. $r^2 = 0.362, P < 0.01$

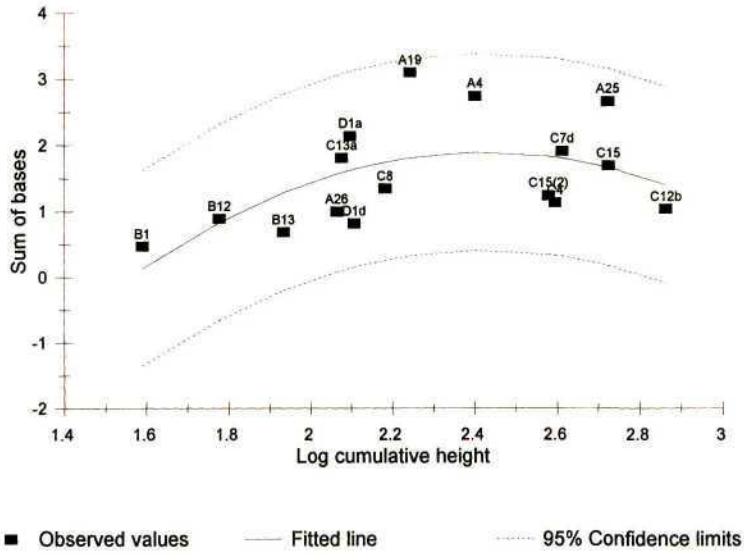


Figure 5.9 Sum of bases vs log cumulative height of indigenous understorey in clearfelled areas. $r^2 = 0.231, P < 0.01$

5.1.3 Effects of organic carbon on soil chemistry

(a) Sum of bases

No significant relationship was found between organic carbon and sum of bases for clearfelled areas.

There is not a sufficiently representative spread of clearfelled areas of different ages to track the dynamics of soil fertility immediately pre and post-clearfelling, and through successional time. One would expect a pulse of nutrients as pine litter breaks down, a lowered level of nutrients when litter is completely broken down and then a rise as the successional process continues (Blackmore, 1993; Sturgess and Atkinson, 1993).

(b) Phosphorus

No relationship between organic carbon and phosphorus was found in any of the three classes of vegetation - undisturbed, pine plantations, or clearfelled areas.

(c) pH

No relationship between organic carbon and pH was found in any of the three classes of vegetation - undisturbed, pine plantations, or clearfelled areas.

5.1.4 Effects of pH on soil chemistry

It is clear from Figures 5.10, 5.11 and 5.12 that a direct relationship exists between increase in soil acidity (lower pH) and reduction in cation exchange capacity (\approx sum of bases).

In summary: The paired t-tests on all pine plantations relative to adjacent undisturbed vegetation confirm that pine plantations acidify the soil and reduce cation exchange capacity (\approx sum of bases) relative to all adjacent undisturbed vegetation types. However, when first and second rotation pines are compared independently to adjacent vegetation, grassland for first

rotation pines and forest for second rotation pines, the differences, although still evident, are not statistically significant. This apparent discrepancy is probably due to the small sample size when the pine plantation data is separated into first and second rotation.

There is no evidence that age of plantations has any direct effect on soil chemistry (Figure 5.13), but there is evidence that the soil chemistry in both pine plantations and clearfelled areas is influenced by the extent of establishment of indigenous woody species.

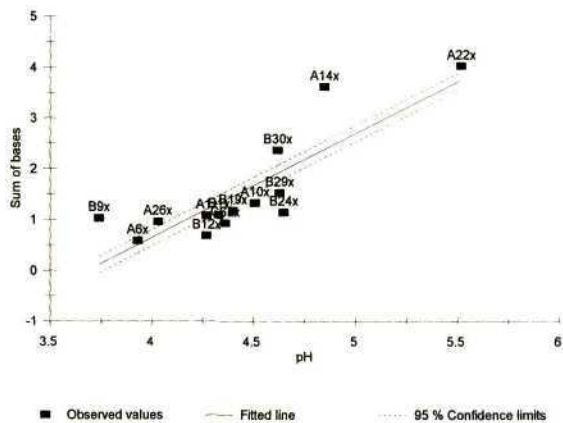


Figure 5.10 Sum of bases vs pH for undisturbed vegetation.
 $r^2 = 0.705$ $P = 0.0001$.

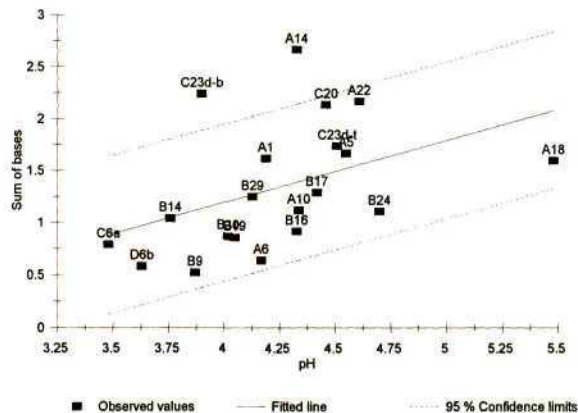


Figure 5.11 Sum of bases vs pH for all pine plantations.
 $r^2 = 0.185$ $P = 0.58$.

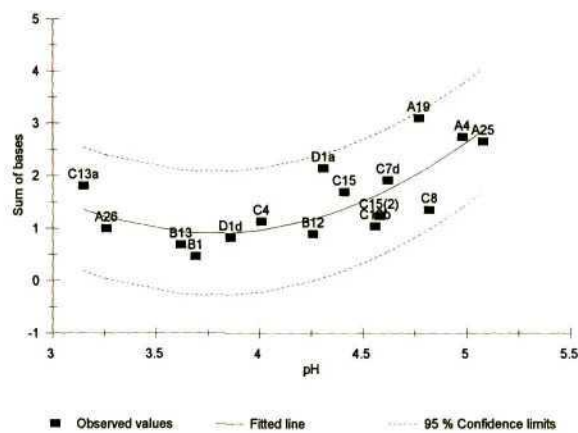


Figure 5.12 Sum of bases vs pH for clearfelled areas
 $r^2 = 0.517$ $P < 0.05$.

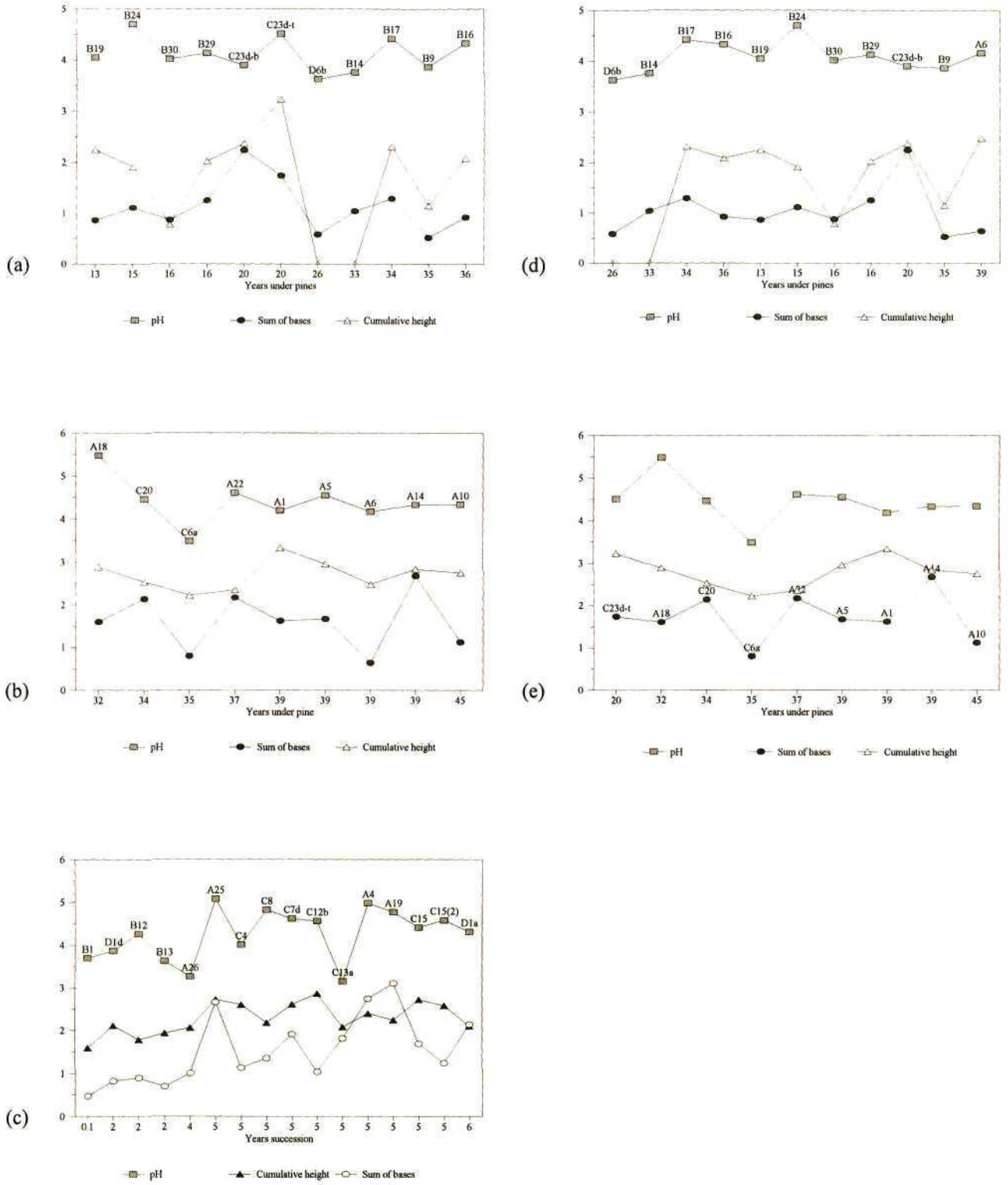


Figure 5.13 Time track of changes in pH, sum of bases and cumulative height of indigenous understorey under different vegetation types: (a) All first rotation; (b) All second rotation; (c) All clearfelled; (d) Pine (first & second) adjacent to grassland; (e) Pine (first & second) adjacent to forest.

5.2 WOODY DATA ANALYSIS

Within the 50 sites sampled, a total of 143 different woody species were identified (Appendices 8 & 9). Most (>85 %) of these species have fleshy fruits which is an indication that they are animal dispersed (Appendix 8).

Initial ordinations, both Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA), were performed using CANOCO (Ter Braak, 1987,1988) for all 50 sites. These ordinations were related to environmental variables: organic carbon (C), sum of bases (CEC), extractable phosphorus (P), pH (measured in KCl), years under pines (YRSPINE), and nominal variables, GRASS, SCRUB (Grass/Trees), FOREST, ROT1, ROT2, CLEAR which represent vegetation type (Figures 5.14 & 5.15). For all ordinations of woody data, any species with a single occurrence was deleted, and the CANOCO selection for down-weighting of rare species was selected. Scaling was symmetrical, and the Monte Carlo re-randomization procedure was conducted for each CCA run. The purpose of this procedure is as a direct test of whether the included environmental variables have a significant effect on compositional variation. The ordination statistics for all ordinations are given in Table 5.11 and the results of the Monte Carlo Test in Table 5.12. The eigenvalues for each axis are equal to the maximised dispersion of the species scores on the ordination axis, and is thus a measure of the importance of the axis. Values over 0.5 often denote a good separation of the species along the axis, lower values could be attributable to noise in the data.

In the CA output (Figure 5.14), the first axes (Eigenvalue: 0.235) describes a gradient from second rotation pines and sites with high woody abundance and diversity to first rotation pines and sites with low woody diversity and abundance. This axis includes a gradient in pH and cation exchange capacity, with second rotation pines having higher pH and cation exchange capacity sites than first rotation pines. The clearfelled site on the extreme right of axis 1 represents site B1, a recently cleared site opposite grassland which had very few woody species and the forest site on the extreme left represents site A14x, a site with dense woody vegetation. The second axis (Eigenvalue: 0.200) describes a similar gradient from forest to grassland with scattered trees. First rotation sites are grouped closer to sites with grassland and scattered trees and second rotation sites are grouped closer to forest in the ordination diagram.

This reflects the situation in the field, as most of the second rotation sites are located adjacent to forest and most of the first rotation sites adjacent to grassland or grassland with scattered trees. Thus, the pine plantations are reflecting the woody diversity of the sites adjacent to them and are grouped close to their adjacent sites in the ordination diagram. Increasing cation exchange capacity (\approx sum of bases) is correlated with an increase in woody diversity and abundance on axis 2. This was also shown in the soils results.

In the CCA plot (Figure 5.15), axis 1 (Eigenvalue: 0.155) shows a clear separation between undisturbed vegetation and sites that have been planted to pines, whereas axis 2 (Eigenvalue: 0.135) describes a gradient in woody diversity and abundance. For both axes pH and cation exchange capacity increase with increasing woody cover and in the direction of undisturbed vegetation.

The first four axes of the CA for all sites accounted for 1.5 times the species variance accounted for by the CCA (Table 5.11), whilst the variance of the species-environment relation accounted for by the CCA was 56 % greater than that accounted for by the CA. The overall ordination of the CCA was significant ($P < 0.05$: Table 5.12), therefore, the environmental variables chosen explained a significant proportion of the community variation. For all axes in the CCA, there is a very high (> 0.8) species-environment correlation (Table 5.11). The differences between the first and second axis eigenvalues in the CA were 15 %, and between the second and third, 10 %, after which differences between subsequent axes were minimal. The differences between the first and second axis eigenvalues in the CCA were 12 %, between the second and third, 13 %, and between the third and fourth, 15 %. Therefore, the pattern of floristic variation along the gradient from undisturbed sites to sites influenced by pines is the primary gradient and the gradient of increasing woody component of adjacent vegetation is the secondary gradient. The species most strongly associated with the gradients of change are listed in Table 5.13 and the most important species related to environmental variables are displayed in Figure 5.16.

The low eigenvalues indicate noise in the data from undisturbed sites, which means that it is difficult to clearly separate sites out when applying ordination to all 50 sites. Patterns become clearer when separate ordinations are applied to pine plantations and clearfelled sites.

Table 5.11 Summary of correspondence (CA) and canonical correspondence (CCA) analyses for the vegetation of the Eastern Shores of Lake St Lucia: woody component: axes 1-4 for a) CA - all 50 sites, b) CCA - all 50 sites, c) CA - all pine plantations, d) CCA - all pine plantations, e) CA - all clearfelled sites, f) CCA - all clearfelled sites, g) CA - clearfelled sites minus outliers B1, B12, B13, h) CCA - CA - clearfelled sites minus outliers B1, B12, B13. Rare species were down-weighted.

		Axis order			
		1	2	3	4
a)	CA - all 50 sites, axis 1-4				
	Eigenvalue	0.235	0.200	0.180	0.172
	Species-environment correlation	0.574	0.622	0.787	0.580
	Cumulative percent variance of:				
	Species data	8.0	14.8	20.9	26.7
	Species environment	9.4	18.9	32.4	39.5
b)	CCA - all 50 sites, axis 1-4				
	Eigenvalue	0.155	0.135	0.117	0.099
	Species-environment correlation	0.929	0.875	0.921	0.840
	Cumulative percent variance of:				
	Species data	5.2	9.8	13.8	17.2
	Species environment	18.8	35.3	49.6	61.6
c)	CA - all pine plantations, axis 1-4 (n = 20)				
	Eigenvalue	0.360	0.283	0.268	0.227
	Species-environment correlation	0.872	0.776	0.736	0.579
	Cumulative percent variance of:				
	Species data	12.6	22.6	32.0	39.9
	Species environment	20.8	33.8	44.8	50.6
d)	CCA - all pine plantations, axis 1-4 (n = 20)				
	Eigenvalue	0.313	0.246	0.214	0.165
	Species-environment correlation	0.963	0.976	0.963	0.968
	Cumulative percent variance of:				
	Species data	11.0	19.6	27.1	32.9
	Species environment	23.8	42.5	58.8	71.3

		Axis order			
		1	2	3	4
e)	CA - all clearfelled sites, axis 1-4 (n = 16)				
	Eigenvalue	0.434	0.286	0.256	0.211
	Species-environment correlation	0.767	0.754	0.581	0.670
	Cumulative percent variance of:				
	Species data	18.1	30.0	40.7	49.5
	Species environment	22.2	36.4	43.9	52.1
f)	CCA - all clearfelled sites, axis 1-4 (n = 16)				
	Eigenvalue	0.337	0.219	0.179	0.148
	Species-environment correlation	0.937	0.946	0.978	0.932
	Cumulative percent variance of:				
	Species data	14.1	23.2	32.7	36.8
	Species environment	29.3	48.4	64.0	76.9
g)	CA - clearfelled sites minus outliers, axis 1-4 (n = 13)				
	Eigenvalue	0.298	0.220	0.212	0.190
	Species-environment correlation	0.770	0.737	0.840	0.889
	Cumulative percent variance of:				
	Species data	16.6	28.8	40.6	51.1
	Species environment	17.2	28.8	43.3	57.9
h)	CCA - clearfelled sites minus outliers, axis 1-4 (n = 13)				
	Eigenvalue	0.244	0.201	0.166	0.154
	Species-environment correlation	0.966	0.994	0.977	0.949
	Cumulative percent variance of:				
	Species data	13.5	24.7	33.9	42.5
	Species environment	23.7	43.1	59.3	74.2

Table 5.12 Monte Carlo Test (No. permutations = 99) Woody species CCA.

		50 Sites	Pine	All Clearfelled	Clear minus outliers
1st axis	Eigenvalue	0.15	0.31	0.34	0.24
	F-Ratio	1.77	1.24	1.31	0.78
	P-Value	0.08	0.78	0.72	1.00
Overall test:	Trace	0.82	1.32	1.15	1.03
	F-Ratio	1.37	1.23	1.05	0.96
	P-Value	0.01	0.14	0.40	0.57

Table 5.13 Fit per species as fraction of variance of species (species most strongly associated with gradients of change) for all sites (20 % cutoff). Plots of species distribution in Figures 5.16a & b. Species reference number according to species list in Appendix 8.

Ref.	CA	Axis 1	Ref.	CCA	Axis 1
58	<i>Eugenia woodii</i>	53.81%	52	<i>Euclea natalansis</i>	40.15%
18	<i>Canthium ciliatum</i>	40.34%	18	<i>Canthium ciliatum</i>	35.75%
134	<i>Tricalysia lanceolata</i>	39.51%	134	<i>Tricalysia lanceolata</i>	35.35%
76	<i>Monanthes affra</i>	39.01%	76	<i>Monanthes affra</i>	31.34%
44	<i>Drypetes natalensis</i>	39.01%	127	<i>Tacezea apiculata</i>	31.34%
127	<i>Tacezea apiculata</i>	39.01%	8	<i>Anisochaetes mikanioides</i>	31.34%
8	<i>Anisochaetes mikanioides</i>	39.01%	44	<i>Drypetes natalensis</i>	31.34%
142	<i>Xylothea kraussiana</i>	36.19%	59	<i>Ficus burtt-davyii</i>	30.26%
66	<i>Grewia occidentalis</i>	35.15%	111	<i>Sapium intergerrimum</i>	23.88%
60	<i>Ficus natalensis</i>	34.71%	22	<i>Carissa bispinosa</i>	22.60%
59	<i>Ficus burtt-davyii</i>	29.15%			
80	<i>Ochna arborea</i>	28.87%			
1	<i>Acacia karroo</i>	27.84%			
30	<i>Clerodendrum glabrum</i>	22.74%			
22	<i>Carissa bispinosa</i>	20.77%			

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
35	<i>Dichrostachys cinerea</i>	41.22%		Nothing over 20 %	
83	<i>Ozoroa engleri</i>	37.82%			
113	<i>Sclerocarya birrea</i>	33.53%			
11	<i>Apodytes dimidiata</i>	27.10%			
19	<i>Canthium inerme</i>	26.63%			
107	<i>Rhus nebulosa</i>	25.15%			
119	<i>Strelitzia nicolai</i>	20.03%			

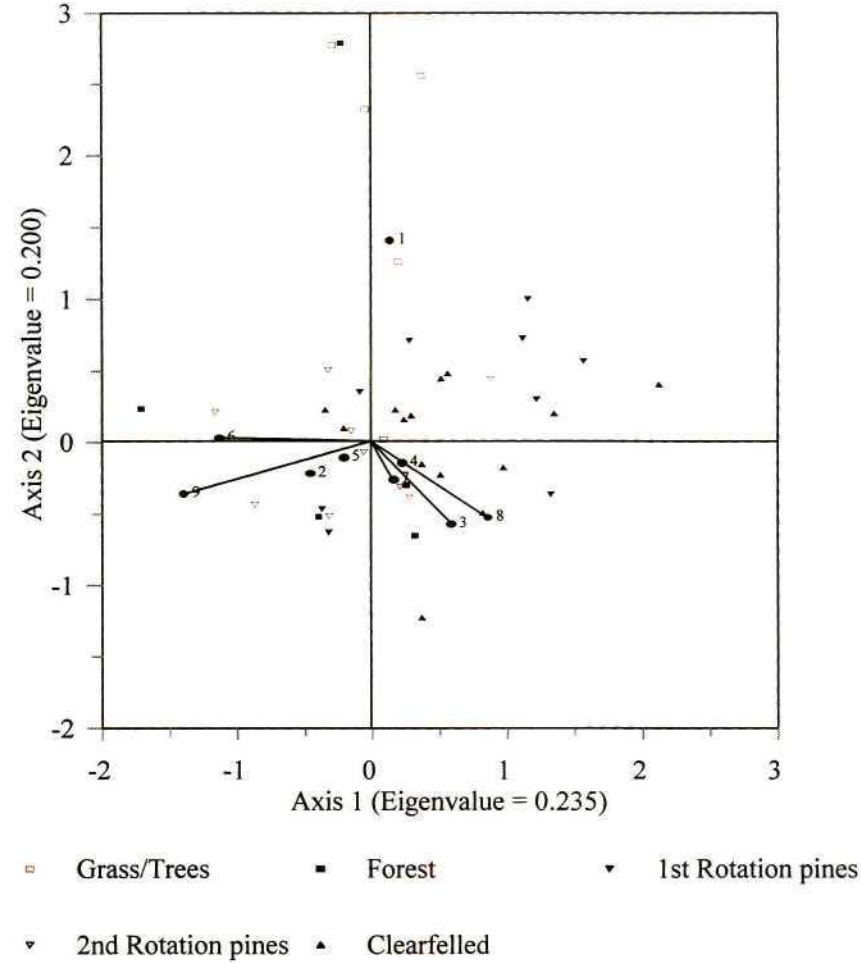


Figure 5.14 Joint plot of sites and environmental variables for the first two axes of correspondence analysis for all sites. Refer to Table 5.11 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: 7 = Organic carbon; 9 = Sum of bases; 8 = Phosphorus; 6 = pH measured in KCl; 3 = Years under pines; 1 (Grass/Trees), 2 (Forest), 4 (1st Rotation pines), 5 (2nd Rotation pines) = Centroids for vegetation type.

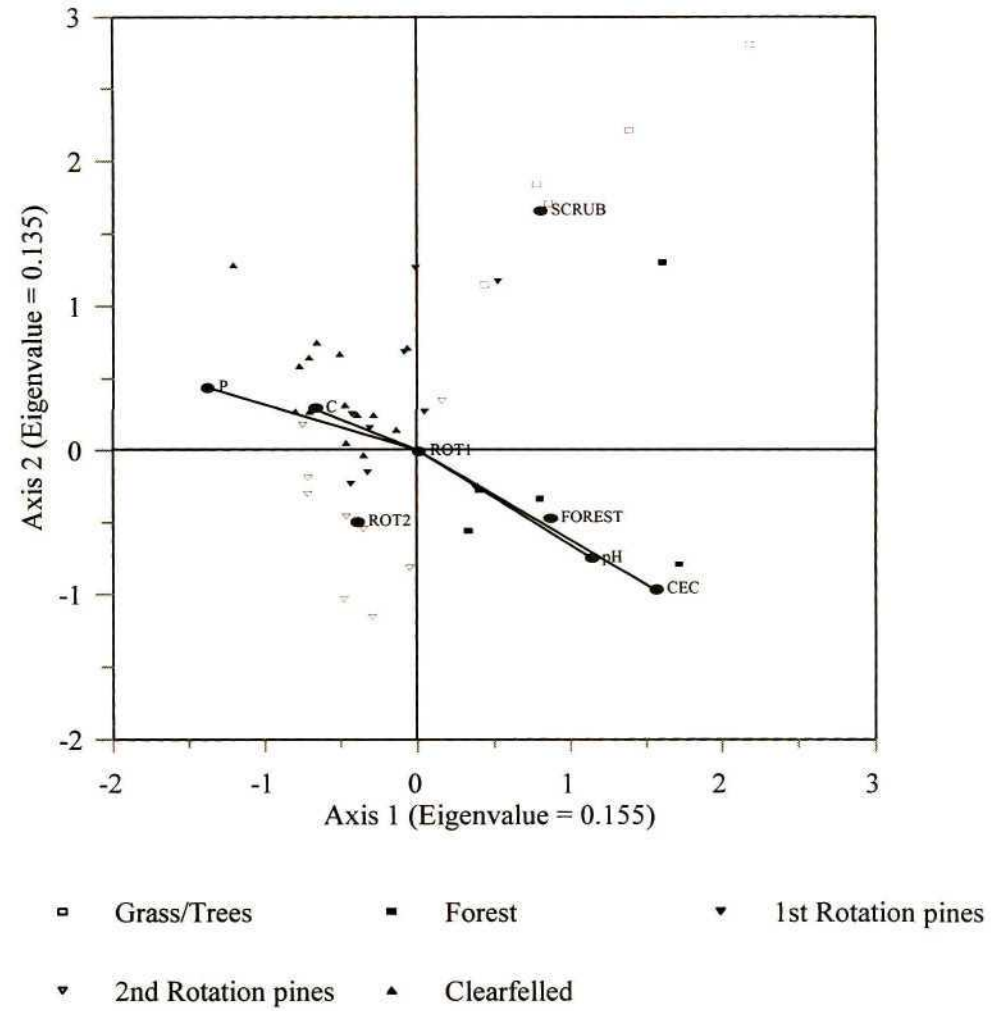
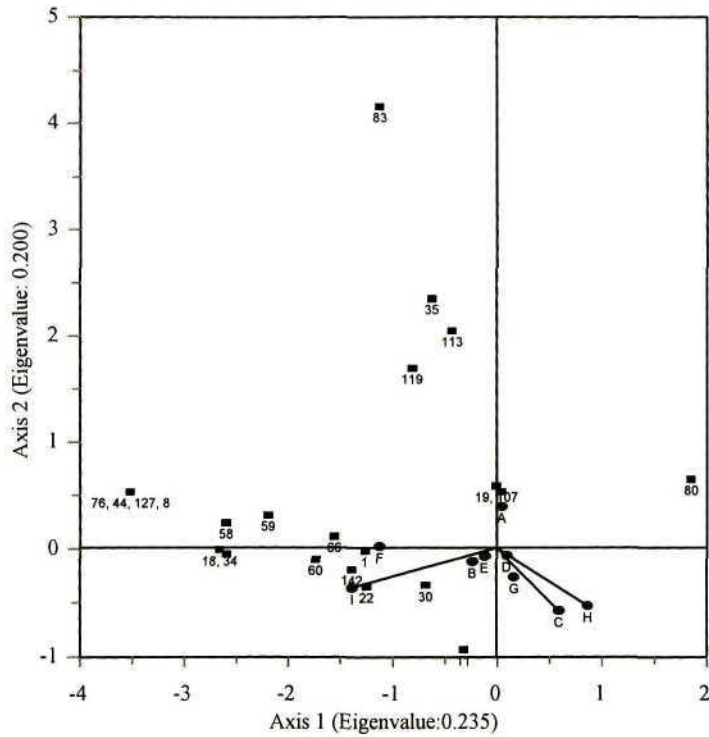
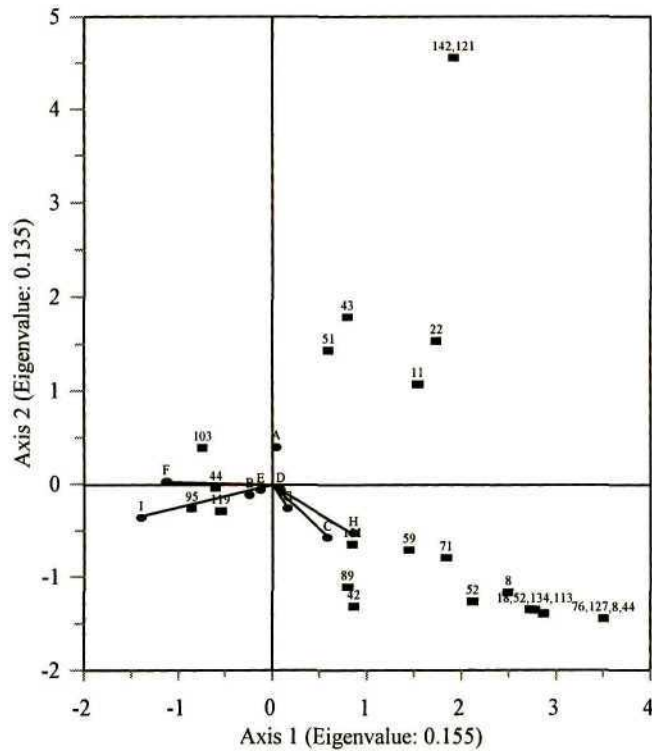


Figure 5.15 Joint plot of sites and environmental variables for the first two axes of canonical correspondence analysis for all sites. Refer to Table 5.11 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: C = Organic carbon; CEC = Sum of bases; P = Phosphorus; pH = pH measured in KCl; YRSPINE = Years under pines; SCRUB, FOREST, ROT1, ROT2 = Centroids for vegetation type.



(a)



(b)

Figure 5.16 Species plot for woody species most strongly associated with environmental gradients for all sites, (a) Correspondence analysis - 20 % cutoff as in Table 5.13; (b) Canonical correspondence analysis - 15 % cutoff for species fit. Species numbered according to Appendix 8. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: G = Organic carbon; I = Sum of bases(CEC); H = Phosphorus; F = pH measured in KCl; C (YRSPINE) = Years under pines; A (SCRUB), B (FOREST), D(ROT1), E(ROT2) = Centroids for vegetation type.

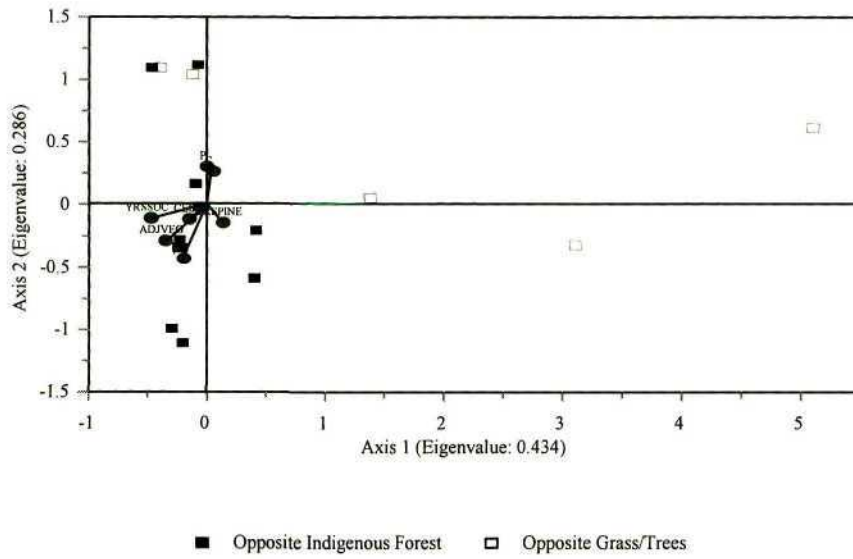
To refine the process further, CA and CCA ordination of pine plantations and clearfelled sites were performed separately. Soil variables remained the same, but vegetation variables for the pine ordination were changed to years under pines (YRSPINE), extent of woody component in adjacent vegetation (ADJVEG), and the nominal variables, (ROT1) and (ROT2). For the clearfelled ordination these were: years under pines (YRSPINE), extent of woody component in adjacent vegetation (ADJVEG) and time since clearfelling (YRSSUC).

After the first iteration for clearfelled areas, sites B12 and B13 were seen to be outliers, and after a second iteration, B1 was another outlier (Figures 5.17a & 5.18a). These three sites were then excluded from further ordination (Figures 5.17b & 5.18b). All three sites were in the extreme north-west plantations and had no nearby indigenous forest influence. B1 was felled only a week before sampling and, in fact, part of the block was still in the process of being felled during sampling. Both B12 and B13 were felled as a result of drought damage to the pine trees, and there were still many dead pine trees standing on the site (Figure 5.30: p. 127). Most of these dead trees were rotting and from time to time one would simply collapse. Thus, there was a lot of rotting wood scattered over the sites. With removal of these outliers, only two clearfelled sites adjacent to grassland remained. This is an unavoidable consequence of the fact that most clearfelled sites in the study area were adjacent to forest.

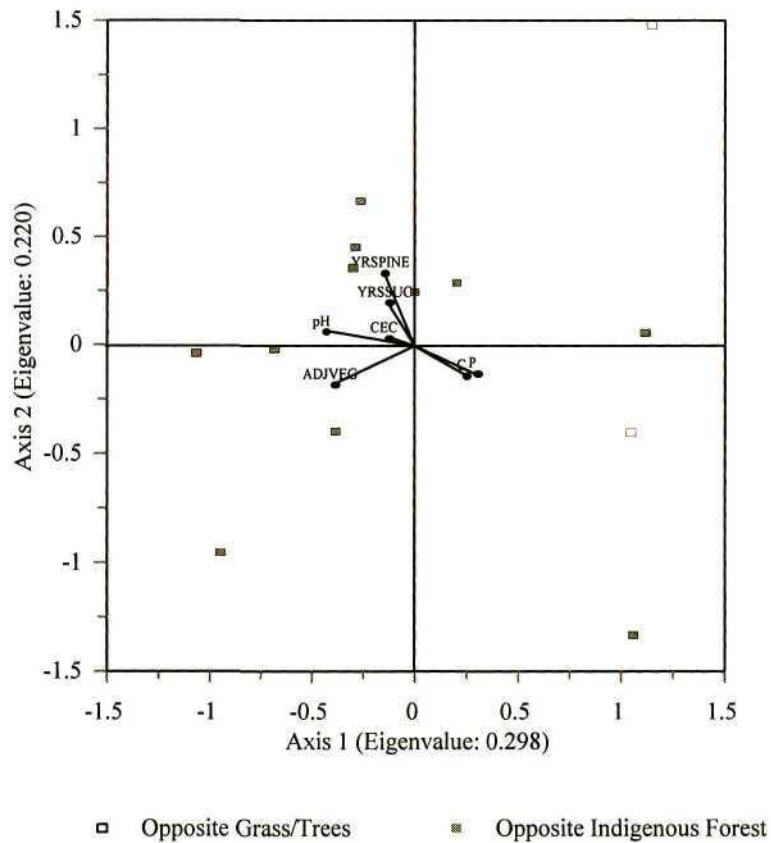
The CA and CCA ordination diagram for the clearfelled sites before (Figures 5.17a & 5.18a) and after (Figures 5.17b & 5.18b) the outliers are removed, display a gradient on the first axis (Eigenvalues: 0.434 & 0.298, with and without outliers) from sites opposite forest to those opposite grassland. This gradient describes a gradient in pH and cation exchange capacity (\approx sum of bases) in one direction and carbon and phosphorus in the other. One would expect organic carbon, cation exchange capacity and pH to be positively correlated, but in these clearfelled sites most of the organic carbon consists of acidic pine litter in the process of breaking down. The second axis (Eigenvalues: 0.286 & 0.220, with and without outliers) describes a gradient in time under pines and time since clearfelling. Most clearfelled sites are five years old, so this could skew the result.

The first four axes for the CA for all clearfelled sites minus the outliers accounted for 1.2 times the species variance accounted for by the CCA (Table 5.11), whilst the variance of the

species-environment relation accounted for by the CCA was 28 % greater than that accounted for by the CA. For all axes, there is a very high (>0.7 for CA and > 0.9 for CCA) species-environment correlation (Table 5.11), but the overall ordination of the CCA minus outliers using the Monte Carlo test was not significant ($P = 0.17$: Table 5.12). This could indicate that the environmental variables do not explain a significant proportion of the community variation, or it could simply be the result of the small size of the clearfelled sample, or a result of the variability in clearfelled sites. Unfortunately, there was not a representative spread of different aged clearfelled sites to be able to pick up clear trends. Most clearfelled sites are adjacent to forest and most are five years old. But, as with the overall ordination, the adjacent vegetation seems to be a significant factor affecting both the community structure and chemical characteristics of the clearfelled sites. The differences between the first and second axis eigenvalues were 26 % for the CA and 17 % for the CCA, after which differences between subsequent axes were minimal. Therefore, the pattern of floristic variation along the gradient of increasing woody component of adjacent vegetation is the primary gradient with a few subsidiary gradients. The species most strongly associated with the gradients of change are listed in Table 5.14 and the most important species related to environmental variables are displayed in Figures 5.19a & b. These figures show the same gradients as described in the discussion above.

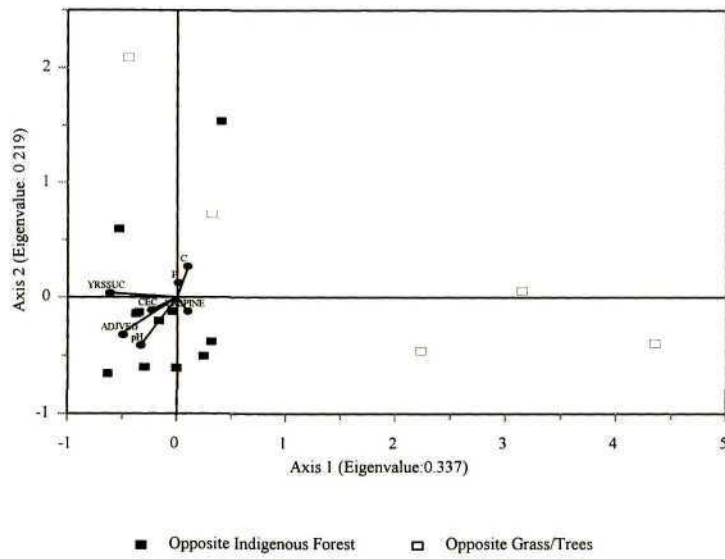


(a)

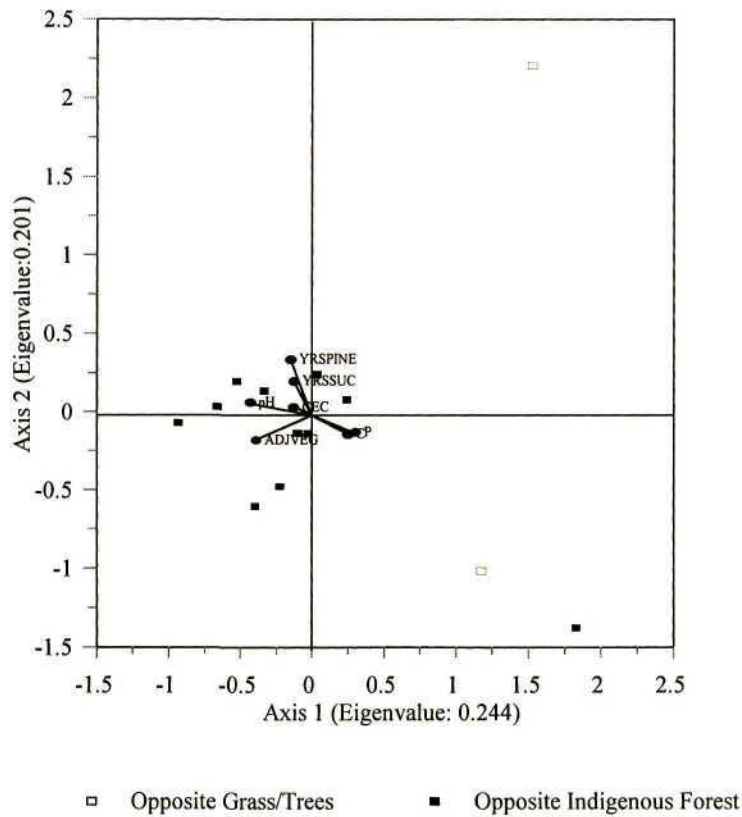


(b)

Figure 5.17 Joint plot of sites and environmental variables for the first axes of correspondence analysis, for (a) all clearfelled sites, (b) clearfelled sites minus outliers, B1, B12 & B13. Refer to Table 5.11 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: YRSPINE = Total years under pines; CEC = Sum of bases; pH = pH measured in KCl; C = Organic carbon; P = Extractable phosphorus; YRSSUC = Years since clearfelling; ADJVEG = Ordinal scale for amount of woody vegetation.



(a)



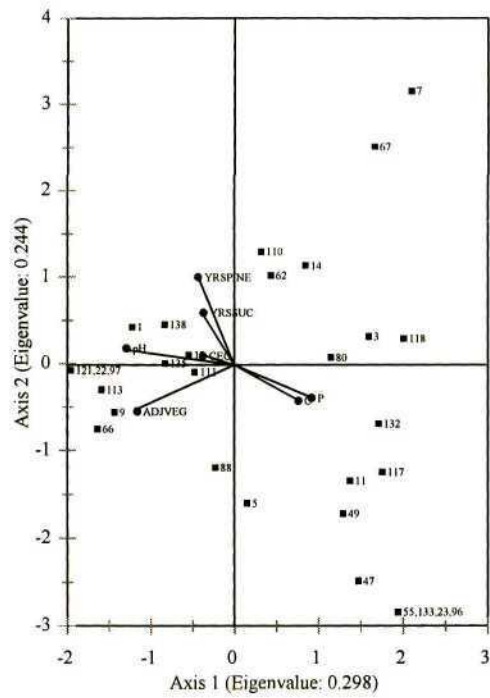
(b)

Figure 5.18 Joint plot of sites and environmental variables for the first axes of canonical correspondence analysis, for (a) all clearfelled sites, (b) clearfelled sites minus outliers, B1, B12 & B13. Refer to Table 5.11 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: , YRSPINE = Total years under pines; CEC = Sum of bases; pH = pH measured in KCl; C = Organic carbon; P = Extractable phosphorus; YRSPINE = Years since clearfelling; ADJVEG = Ordinal scale for degree of woody component in adjacent vegetation.

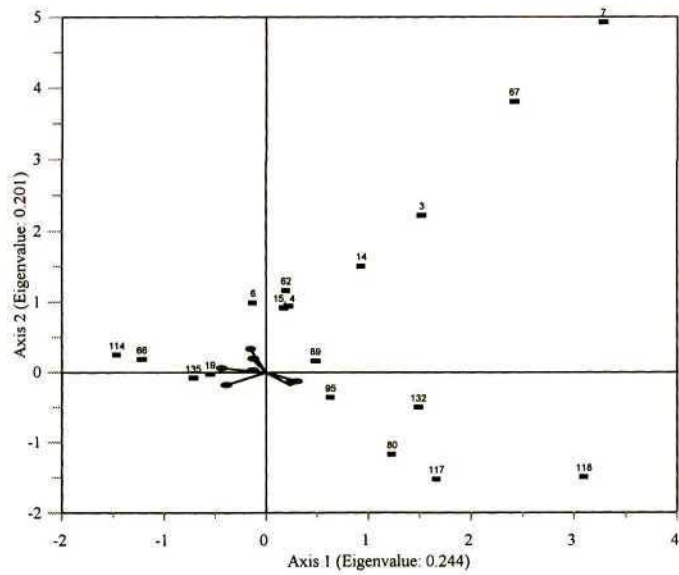
Table 5.14 Fit per species as fraction of variance of species (species most strongly associated with gradients of change) for all clearfelled sites minus outliers (20 % cutoff) for both CA and CCA. Plots of species distribution in Figures 5.19a & b.

Ref.	CA	Axis 1	Ref.	CCA	Axis 1
135	<i>Tricalysia sonderiana</i>	61.37%	118	<i>Solanum mauritianum</i>	65.12%
132	<i>Trema orientalis</i>	55.35%	135	<i>Tricalysia sonderiana</i>	40.22%
9	<i>Annona senegalensis</i>	50.16%	132	<i>Trema orientalis</i>	38.19%
66	<i>Grewia occidentalis</i>	47.99%	117	<i>Solanum aculeastrum</i>	35.89%
117	<i>Solanum aculeastrum</i>	43.72%	19	<i>Canthium inerme</i>	34.45%
111	<i>Sapium integerrimum</i>	41.74%	7	<i>Aloe thraskii</i>	30.50%
11	<i>Apodytes dimidiata</i>	41.30%	67	<i>Hibiscus tiliaceus</i>	29.80%
19	<i>Canthium inerme</i>	38.24%	80	<i>Ochna arborea</i>	27.85%
118	<i>Solanum mauritianum</i>	30.22%	95	<i>Psidium guajava</i>	26.64%
138	<i>Vangueria infausta</i>	29.23%	89	<i>Phoenix reclinata</i>	24.30%
3	<i>Acokanthera oppositifolia</i>	28.16%	66	<i>Grewia occidentalis</i>	23.84%
113	<i>Sclerocarya birrea</i>	27.03%	3	<i>Acokanthera oppositifolia</i>	23.22%
80	<i>Ochna arborea</i>	26.48%	114	<i>Scutia myrtina</i>	23.08%
1	<i>Acacia karroo</i>	25.84%			
121	<i>Strychnos madagascariensis</i>	24.86%			
22	<i>Carissa bispinosa</i>	24.86%			
97	<i>Pteleopsis myrtifolia</i>	24.86%			
55	<i>Eugenia erythrophylla</i>	22.21%			
133	<i>Tricalysia capensis</i>	22.21%			
23	<i>Carissa macrocarpa</i>	22.21%			
96	<i>Psychotria capensis</i>	22.21%			

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
5	<i>Albizia adianthifolia</i>	58.04%	62	<i>Garcinia livingstonei</i>	46.22%
47	<i>Erythrina lysistemon</i>	44.87%	14	<i>Bridelia cathartica</i>	43.40%
62	<i>Garcinia livingstonei</i>	37.32%	15	<i>Bridelia micrantha</i>	32.45%
88	<i>Peddiea africana</i>	35.50%	6	<i>Allophylus natalansis</i>	28.92%
67	<i>Hibiscus tiliaceus</i>	30.41%	4	<i>Adenia gummifera</i>	25.85%
49	<i>Erythroxylum emarginatum</i>	29.44%			
7	<i>Aloe thraskii</i>	26.81%			
110	<i>Salacia kraussii</i>	26.13%			
14	<i>Bridelia cathartica</i>	25.93%			



(a)



(b)

Figure 5.19 Species plot for species most strongly associated with environmental gradients in clearfelled sites (a) CA, and (b) CCA - 20% cutoff as in Table 5.14. Species numbered according to Appendix 8. Environmental variables: YRSPINE = Total years under pines; CEC = Sum of bases; pH = pH measured in KCl; C = Organic carbon; P = Extractable phosphorus; YRSSUC = Years since clearfelling; ADJVEG = Ordinal scale for degree of woody component in adjacent vegetation.

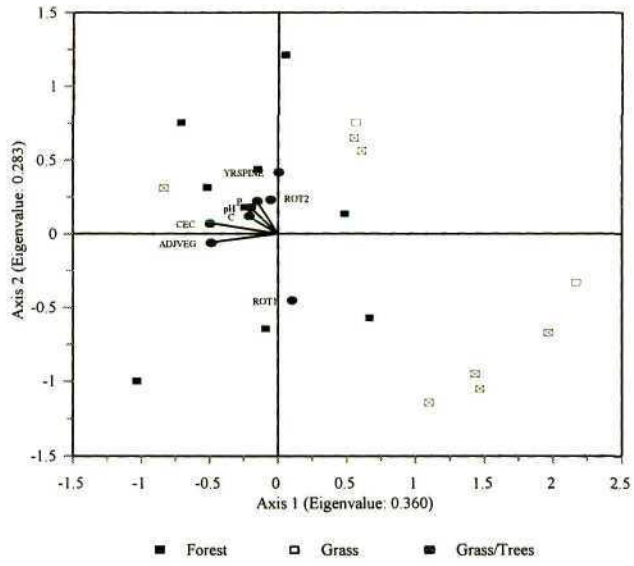
The results of the CA and CCA ordination for pine plantations are displayed in Figure 5.20a & b. On the first axis (Eigenvalue: 0.360 in CA; 0.313 in CCA) in both the CA and CCA output, there is a definite gradient from plantations adjacent to forest and those adjacent to grassland, i.e. a gradient in woody diversity and abundance, along with a gradient in pH and cation exchange capacity (\approx sum of bases). The second axis (Eigenvalue: 0.283 in CA; 0.246 in CCA) describes a gradient from first to second rotation pines and includes a gradient from grassland to forested adjacent sites. Most second rotation pines are located opposite forest, and most first rotation opposite grassland and this is reflected in ordination space.

The first four axes of the CA for all pine plantations accounted for 1.2 times the species variance accounted for by the CCA (Table 5.11), whilst the variance of the species-environment relation accounted for by the CCA was 41 % greater than that accounted for by the CA. For all axes, there is a very high (> 0.5 for CA and > 0.9 for CCA) species-environment correlation, indicating that the chosen environmental variables explain the community variation in pine plantations. As with the clearfelled sites the Monte Carlo test on the first run suggested that the overall CCA ordination was not significant, but running the test five times gave one significant result and four insignificant. Since both the clearfelled ($n = 13$) and pine plantation ($n = 20$) sample sizes are much smaller than the overall sample size ($n = 50$), and some of the sites have no trees, these erratic results are assumed to be a direct result of the sample size. Given the high species-environment correlations for all ordinations, we can thus conclude that a large proportion of the environmental variation has been captured in the choice of environmental variables for pine plantations.

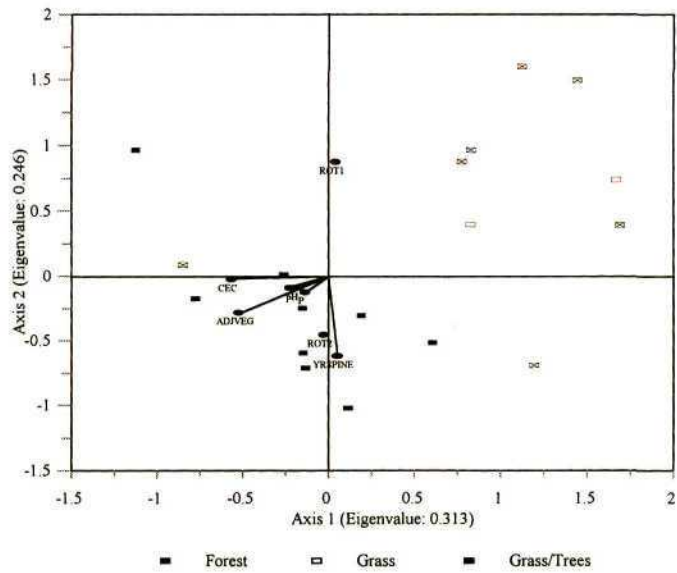
The differences between the first and second eigenvalues were 28 % for the CA and 21 % for the CCA, after which differences between subsequent axes are minimal. Therefore, the pattern of floristic variation along the gradient of increasing woody component of adjacent vegetation is the primary gradient with a few subsidiary gradients. The species most strongly associated with the gradients of change are listed in Table 5.15 and the most important species related to environmental variables are displayed in Figures 5.21a & b.

It is clear from all of the joint plots discussed above that the adjacent vegetation influences the character of both pine plantations and on clearfelled areas and, thus, on the direction of

succession. pH and cation exchange capacity increase in both the CCA and CA ordinations in the same direction as increasing woody influence, as does organic carbon in pine plantations but not in clearfelled sites.



(a)



(b)

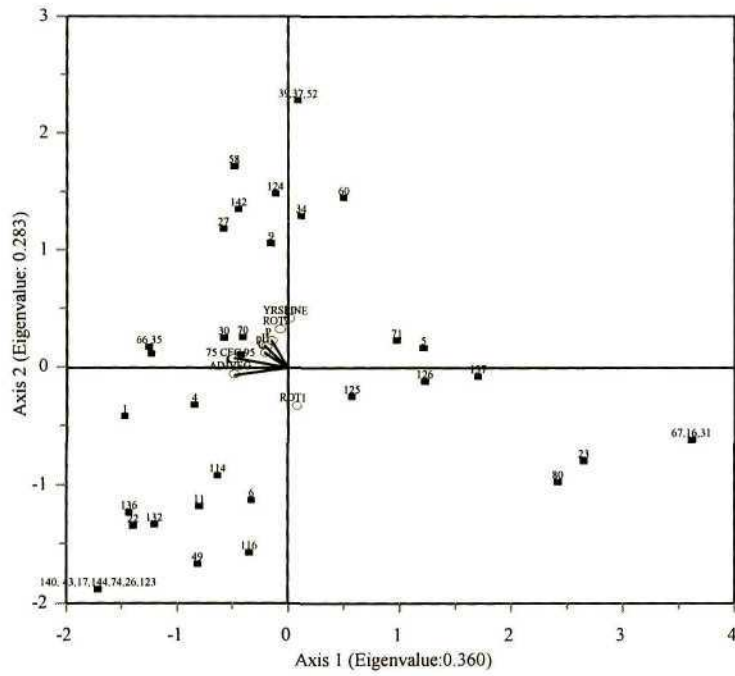
Figure 5.20 Joint plot of sites and environmental variables for the first axes of (a) correspondence analysis, and (b) canonical correspondence analysis for all pine plantations. Adjacent vegetation is indicated in the legend. Refer to Table 5.11 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: ADJVEG = Ordinal scale for degree of woody component in adjacent vegetation, C = Organic carbon; CEC = Sum of bases; pH = pH measured in KCl; P = Extractable phosphorus; YRSPINE = Total years under pines; YRSSUC = Years since clearfelling. ROT1 & ROT2 = centroids for first and second rotation pines.

Table 5.15 Fit per species as fraction of variance of species (species most strongly associated with gradients of change) for all pine plantations (20 % cutoff). Plots of species distribution in Figures 5.21a & b.

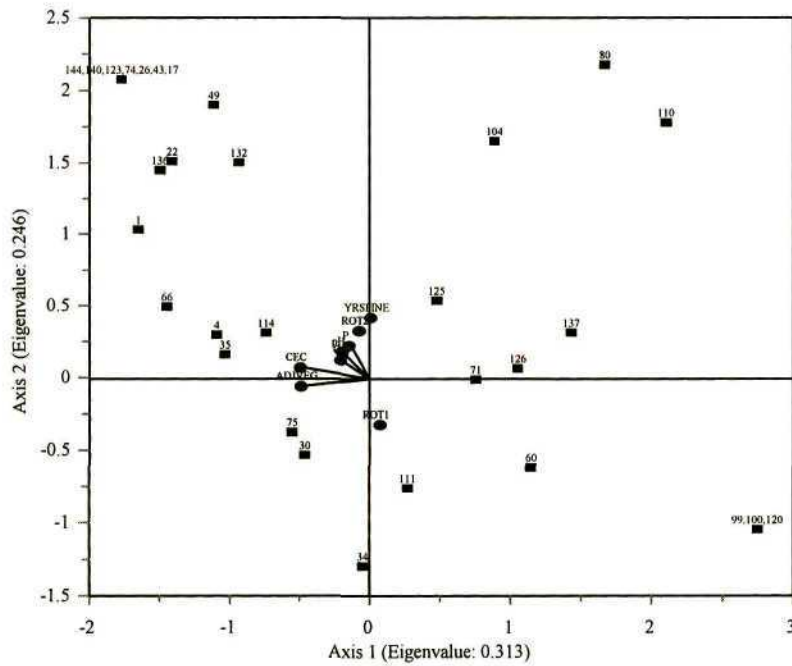
Ref.	CA	Axis 1	Ref.	CCA	Axis 1
71	<i>Landolphia kirkii</i>	42.14%	4	<i>Adenia gummifera</i>	47.29%
137	<i>Uvaria caffra</i>	41.30%	1	<i>Acacia karroo</i>	43.72%
126	<i>Syzigium cordatum</i>	39.29%	66	<i>Grewia occidentalis</i>	38.86%
1	<i>Acacia karroo</i>	37.39%	136	<i>Urera trinervis</i>	28.40%
80	<i>Ochna arborea</i>	33.04%	144	<i>Ziziphus mucronatha</i>	28.27%
30	<i>Clerodendrum glabrum</i>	32.32%	140	<i>Vepris reflexa</i>	28.27%
125	<i>Synaptolepis kirkii</i>	31.61%	123	<i>Strychnos spinosa</i>	28.27%
66	<i>Grewia occidentalis</i>	31.31%	74	<i>Maytenus undata</i>	28.27%
4	<i>Adenia gummifera</i>	30.59%	26	<i>Celtis africana</i>	28.27%
35	<i>Dichrostachys cinerea</i>	30.50%	43	<i>Dovyalis lucida</i>	28.27%
5	<i>Albizia adianthifolia</i>	30.03%	17	<i>C23d-t/11-Big tree *</i>	28.27%
140	<i>Vepris reflexa</i>	28.38%	137	<i>Uvaria caffra</i>	27.22%
43	<i>Dovyalis lucida</i>	28.38%	75	<i>Mimusops caffra</i>	26.90%
17	<i>C23d-t/11-Big tree *</i>	28.38%	126	<i>Syzigium cordatum</i>	26.88%
144	<i>Ziziphus mucronatha</i>	28.38%	22	<i>Carissa bispinosa</i>	26.48%
74	<i>Maytenus undata</i>	28.38%	114	<i>Scutia myrtina</i>	24.21%
26	<i>Celtis africana</i>	28.38%	71	<i>Landolphia kirkii</i>	23.59%
123	<i>Strychnos spinosa</i>	28.38%	60	<i>Ficus natalensis</i>	22.42%
22	<i>Carissa bispinosa</i>	27.89%	99	<i>Rauwolfia caffra</i>	21.69%
136	<i>Urera trinervis</i>	27.87%	100	<i>Rawsonia lucida</i>	21.69%
95	<i>Psidium guajava</i>	27.63%	120	<i>Strychnos gerrardii</i>	21.69%
23	<i>Carissa macrocarpa</i>	26.68%	110	<i>Salacia kraussii</i>	21.34%
75	<i>Mimusops caffra</i>	25.95%	125	<i>Synaptolepis kirkii</i>	20.18%
67	<i>Hibiscus tiliaceus</i>	23.65%	35	<i>Dichrostachys cinerea</i>	20.04%
16	<i>Burchellia bubalina</i>	23.65%			
31	<i>Commiphora woodii</i>	23.65%			
70	<i>Kraussia floribunda</i>	21.65%			
11	<i>Apodytes dimidiata</i>	21.04%			

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
116	<i>Sideroxylon inerme</i>	61.39%	111	<i>Sapium integerrimum</i>	44.45%
58	<i>Eugenia woodii</i>	38.82%	49	<i>Erythroxylum emarginatum</i>	36.19%
6	<i>Allophylus natalensis</i>	38.70%	104	<i>Rhus chirendensis</i>	28.39%
114	<i>Scutia myrtina</i>	35.36%	132	<i>Trema orientalis</i>	24.90%
60	<i>Ficus natalensis</i>	34.25%	34	<i>Dalbergia armata</i>	24.09%
142	<i>Xylothea kraussiana</i>	32.54%	80	<i>Ochna arborea</i>	22.17%
27	<i>Chromolaena odorata</i>	30.14%	30	<i>Clerodendrum glabrum</i>	22.01%
49	<i>Erythroxylum emarginatum</i>	29.78%			
34	<i>Dalbergia armata</i>	25.81%			
39	<i>Diospyros scabrida</i>	25.73%			
37	<i>Diospyros inhacaensis</i>	25.73%			
52	<i>Euclea natalensis</i>	25.73%			
9	<i>Annona senegalensis</i>	25.21%			
124	<i>Strychnos usambarensis</i>	23.85%			
132	<i>Trema orientalis</i>	21.04%			

* Note: The species named C23d-t/11-Big tree was only found in site C23d-t. It was found in extremely dense forest, the bark was unfamiliar and the tree was too tall to take a leaf specimen, or even to see the leaves clearly.



(a)



(b)

Figure 5.21 Species plots for species most strongly associated with environmental gradients in pine plantations (a) CA, and (b) CCA. - 20 % cutoff as in Table 5.15. Species numbered according to Appendix 8. Environmental variables: ADJVEG = Ordinal scale for degree of woody component in adjacent vegetation, C = Organic carbon; CEC = Sum of bases; pH = pH measured in KCl; P = Extractable phosphorus; YRSPINE = Total years under pines; YRSSUC = Years since clearfelling. ROT1 & ROT2 = centroids for first and second rotation pines.

5.2.1 Woody species richness

To further consider the effect of adjacent vegetation on pine plantations, the woody species richness, diversity, evenness and composition for each pair of adjacent sites was compared. The correlation coefficient was calculated for species richness across the matched sites. There was a high degree of correlation between woody species diversity (0.850) and richness (0.902) over paired sites (Table 5.16).

Table 5.16 Woody species richness in paired sites

PINE PLANTATIONS				UNDISTURBED VEGETATION			
Site No.	Richness	Diversity	Evenness	Site No.	Richness	Diversity	Evenness
B1 (1st)	8	1.68	0.10	B1x (grass)	0	0.00	0.00
B30 (1st)	2	0.69	1.00	B30x(grass)	0	0	0
B9 (1st)	2	0.45	0.65	B9x (gr/trees)	0	0	0
B24 (1st)	12	2.14	0.86	B2x (gr/trees)	8	1.47	0.71
B29 (1st)	12	1.51	0.61	B2x (gr/trees)	12	2.04	0.82
B19 (1st)	19	2.27	0.77	B1x (gr/trees)	18	2.07	0.72
A6 (2nd)	19	2.07	0.70	A6x (gr/trees)	19	1.93	0.66
C6a (2nd)	19	2.23	0.76	C6ax (forest)	6	1.54	0.86
A1 (2nd)	32	2.59	0.75	A1x (forest)	38	2.69	0.74
A10 (2nd)	29	2.68	0.80	A10x (forest)	44	2.96	0.78
A14 (2nd)	22	2.56	0.83	A14x (forest)	36	3.17	0.89
Mean	16	1.90	0.71		16.45	1.62	0.56

Comparisons between tree species richness in pine plantations and clearfelled areas opposite grassland, grassland with scattered trees and forest are displayed in Figures 5.22 and 5.23. It can be seen that the species richness within the sites in pine plantations and clearfelled areas is directly related to the vegetation adjacent to that site. Figure 5.24 illustrates an increase in tree species richness over successional time.

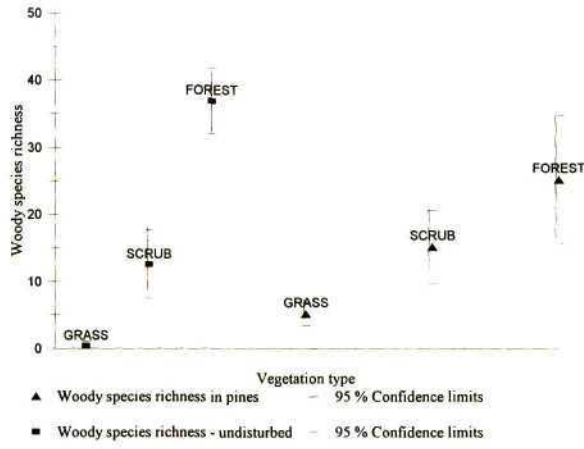


Figure 5.22 Woody species richness in pine plantations according to adjacent vegetation, compared to richness for undisturbed vegetation.

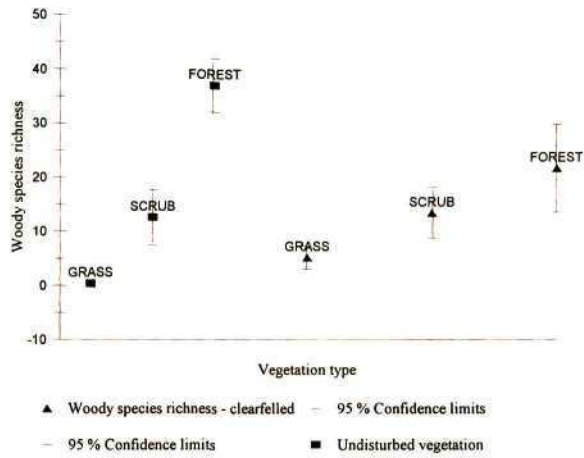


Figure 5.23 Woody species richness in clearfelled areas according to adjacent vegetation, compared to richness for undisturbed vegetation.

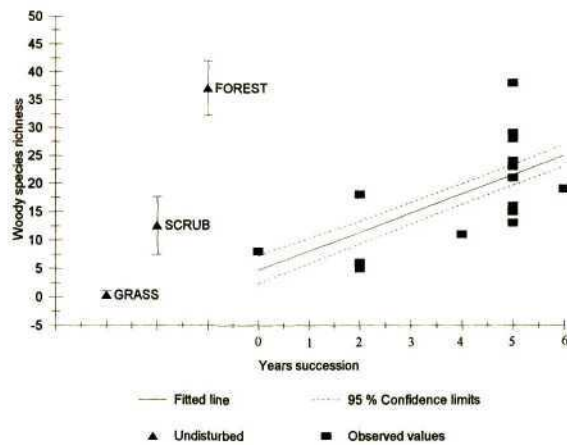


Figure 5.24 Woody species richness in clearfelled areas over successional time, compared to richness for undisturbed vegetation.

5.2.2 Woody successional trajectories

Within the 50 sites sampled, 143 woody species were recorded. An index of proportional abundance for each woody species was calculated, using average cumulative height for each species as a percentage of total cumulative height for all species in that vegetation type.

Woody species for each vegetation/management type are listed; those with the greatest average cumulative height being listed first, and the remainder in decreasing overall density. Any species with an average cumulative height of less than 1 % of the total cumulative height are not recorded here but are recorded in Appendices 9-11. The chronological spread of clearfelled areas available does not allow an accurate tracking of the successional trajectory over the six years of succession. Nevertheless, taking the species composition of grassland areas as one extreme, and established dune forest as another, a crude successional trajectory can be established.

Table 5.17 Woody species proportional abundance by vegetation type
(* denotes alien species).

Species	Grass/Trees	Pine opp. grass/trees	Pine opp. forest	Forest	Clearfelled
	%	%	%	%	%
<i>Syzigium cordatum</i>	25%	8%	1%	8%	2%
<i>Sapium integerrimum</i>	1%	2%	6%	3%	26%
<i>Rhus nebulosa</i>	8%	4%	14%	2%	9%
<i>Brachylaena discolor</i>	10%	10%	6%	4%	3%
<i>Psidium guajava</i> *	0%	11%	17%	1%	1%
<i>Kraussia floribunda</i>	5%	6%	4%	7%	4%
<i>Bridelia micrantha</i>	7%	6%	1%	2%	1%
<i>Albizia adianthifolia</i>	0%	3%	0%	7%	5%
<i>Canthium inerme</i>	5%	1%	4%	1%	5%
<i>Strelitzia nicolai</i>	9%	0%	0%	5%	0%
<i>Synaptolepis kirkii</i>	1%	6%	2%	2%	1%
<i>Apodytes dimidiata</i>	0%	0%	2%	9%	1%
<i>Tricalysia sonderiana</i>	2%	0%	3%	1%	4%
<i>Adenia gummifera</i>	0%	0%	4%	5%	1%
<i>Antidesma venosum</i>	1%	3%	1%	1%	3%
<i>Chromolaena odorata</i> *	0%	4%	2%	3%	0%
<i>Mimusops caffra</i>	1%	1%	2%	2%	2%
<i>Pteleopsis myrtifolia</i>	0%	6%	1%	1%	0%
<i>Bersama lucens</i>	7%	0%	0%	0%	0%
<i>Garcinia livingstonei</i>	2%	2%	0%	1%	2%
<i>Landolphia kirkii</i>	0%	4%	1%	0%	1%
<i>Annona senegalensis</i>	1%	3%	1%	0%	1%
<i>Ochna arborea</i>	1%	3%	0%	0%	1%
<i>Dalbergia armata</i>	0%	0%	3%	2%	0%

Species	Grass/Trees	Pine opp gr/tr	Pine opp forest	Forest	Clearfelled
	%	%	%	%	%
<i>Phoenix reclinata</i>	1%	0%	1%	0%	3%
<i>Ozoroa engleri</i>	5%	0%	0%	0%	0%
<i>Dichrostachys cinerea</i>	4%	0%	0%	0%	0%
<i>Sclerocarya birrea</i>	3%	0%	0%	1%	0%
<i>Salacia kraussii</i>	1%	1%	0%	0%	1%
<i>Allophylus natalansis</i>	0%	0%	1%	1%	1%
<i>Clerodendrum glabrum</i>	0%	0%	1%	1%	1%
<i>Ficus natalensis</i>	0%	1%	0%	2%	0%
<i>Catunaregum spinosa</i>	0%	0%	1%	1%	1%
<i>Monanthes affra</i>	0%	0%	0%	3%	0%
<i>Peddiea africana</i>	0%	0%	0%	2%	1%
<i>Pinus elliotii</i> *	0%	0%	0%	0%	3%
<i>Scutia myrtina</i>	0%	0%	1%	1%	0%
<i>Ficus burtt-davyi</i>	0%	0%	0%	3%	0%
<i>Rhoicissus digitata</i>	0%	2%	1%	0%	0%
<i>Rhus chirendensis</i>	0%	2%	0%	1%	0%
<i>Diospyros lyciodes</i>	0%	1%	2%	0%	0%
<i>Anisochaeta mikanioides</i>	0%	0%	0%	2%	0%
<i>Eugenia capensis</i>	0%	0%	0%	0%	1%
<i>Acacia karroo</i>	0%	0%	1%	1%	1%
<i>Ozoroa obovata</i>	0%	1%	0%	1%	0%
<i>Grewia occidentalis</i>	0%	0%	0%	1%	1%
<i>Sideroxylon inerme</i>	0%	0%	1%	1%	0%
<i>Tricalysia lanceolata</i>	0%	0%	0%	2%	0%
<i>Vangueria infausta</i>	0%	0%	1%	0%	1%
<i>Xylothea kraussiana</i>	0%	0%	0%	1%	0%
<i>Eriosema psoraleoides</i>	0%	0%	0%	0%	2%
<i>Eugenia woodii</i>	0%	0%	0%	1%	0%
<i>Rauvolfia affra</i>	0%	1%	0%	0%	0%
<i>Tacezea apiculata</i>	0%	0%	0%	2%	0%
<i>Diospyros inhacaensis</i>	0%	0%	1%	0%	0%
<i>Strychnos madagascariensis</i>	1%	0%	0%	0%	0%
<i>Bridelia cathartica</i>	0%	1%	0%	0%	1%
<i>Uvaria affra</i>	0%	1%	0%	0%	0%
<i>Rhus pallens</i>	0%	0%	1%	0%	0%
<i>C23d-t/11-Big tree</i>	0%	0%	1%	0%	0%
<i>Euclea natalensis</i>	0%	0%	0%	1%	0%
<i>Strychnos spinosa</i>	1%	0%	0%	0%	0%
<i>Strychnos usambarensis</i>	0%	1%	0%	0%	0%
<i>Solanum aculeastrum</i>	0%	0%	0%	0%	1%
<i>Trema orientalis</i>	0%	0%	0%	0%	0%
<i>Phyllanthus reticulatus</i>	0%	0%	1%	0%	0%
<i>Hibiscus tiliaceus</i>	0%	0%	0%	0%	1%
<i>Erythroxylum emarginatum</i>	0%	0%	0%	0%	0%
<i>Acokanthera oppositifolia</i>	0%	0%	0%	0%	0%
<i>Chrysanthemoides monilifera</i>	0%	0%	0%	0%	0%
<i>Carissa bispinosa</i>	0%	0%	0%	0%	0%
<i>Rhus dentata</i>	0%	1%	0%	0%	0%
<i>Erythrina lysistemon</i>	0%	0%	0%	0%	1%
<i>Urera trinervis</i>	0%	0%	1%	0%	0%
<i>Eugenia natalita</i>	0%	0%	0%	0%	0%
<i>Teclea gerrardii</i>	0%	0%	0%	0%	0%

The alien, *Psidium guajava*, dominated the understorey in pine plantations and, were it not for alien plant control that occurs at clearfelling, it would dominate clearfelled areas as well. This highlights the importance of post-felling alien plant control.

Apart from *Psidium guajava*, important pioneer or colonizing species in pine plantations opposite grassland with scattered trees are (Table 5.18) *Brachylaena discolor*, *Syzygium cordatum*, *Kraussia floribunda*, *Bridelia micrantha*, *Pteleopsis myrtifolia* and *Rhus nebulosa*. In pine plantations opposite forest, important colonizing species are, *Rhus nebulosa*, *Sapium integerrimum*, *Brachylaena discolor*, *Kraussia floribunda* and *Canthium inerme*. *Rhus nebulosa* is found in large clumps about 0.5 to 1.5 m high in both pine plantations and clearfelled areas. *Pinus* seedlings are less of a problem than the figures portray, because they are mostly found at sites B12 and B13, which came up as outliers in Figure 5.16a and 5.17a. At these sites, *Pinus* profoundly affected the results of the ordination procedure. *Sapium integerrimum* obviously comes into its own after clearfelling, growing rapidly with the new suite of resources available. *Dalbergia armata* and *Adenia gummifera* are both found in plantations but, with clearfelling, are the hardest hit as they are creepers which normally use the pine trees for support. Some damage to other woody species does occur when pines are clearfelled, but they coppice readily (Figure 5.28, p. 126).

Table 5.18 Population structure of key pioneer woody species by size class for all pine plantations.

	< 0.5 m	0.5-1m	1-2 m	2-3 m	>3 m
<i>Brachylaena discolor</i>	5.8	13.5	37.5	15.4	27.9
<i>Bridelia micrantha</i>	0.0	0.0	60.0	10.0	30.0
<i>Canthium inerme</i>	4.3	17.4	31.9	24.6	21.7
<i>Kraussia floribunda</i>	0.0	9.6	58.9	9.6	21.9
<i>Pteleopsis myrtifolia</i>	0.0	0.0	30.3	12.1	57.6
<i>Rhus nebulosa</i>	1.0	33.8	61.7	0.3	3.1
<i>Sapium integerrimum</i>	6.2	5.3	61.1	11.5	15.9
<i>Syzygium cordatum</i>	15.7	10.0	25.7	21.4	27.1

In summary, scattered woody species within the grassland consist of some forest species in low densities and a low species diversity. Within the mature forest, no single species dominates, but the species diversity is high. Pine plantations reflect the species composition of adjacent vegetation (Figures 5.25, 5.26 & 5.27), and clearfelled areas have a similar composition to the pine plantations, but with certain species gaining a competitive advantage.



Figure 5.25 Indigenous understorey within 1st rotation pine plantation. This plantation is located adjacent to indigenous forest (not shown). Note the indigenous understorey. (June 1996)



Figure 5.26 Pine plantation opposite grassland in the process of being cleared. Note lack of indigenous understorey. (April 1997)



Figure 5.27 Comparison between clearfelled area on the left and grassland on the right, with mature dune forest in the background. Grassland has never been planted to pines. (April 1997)

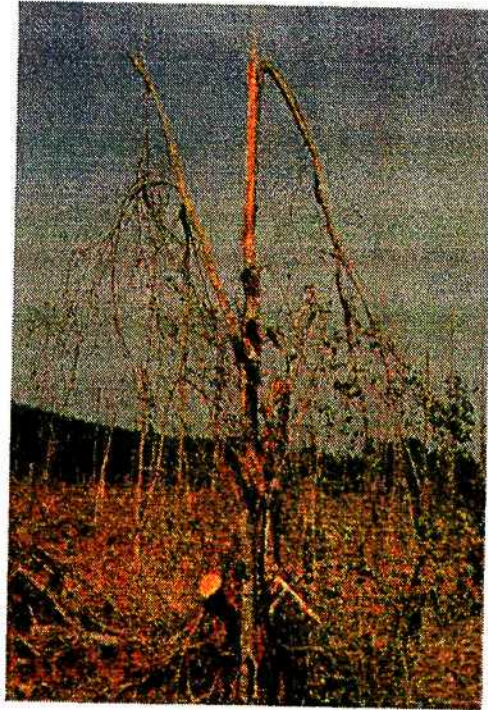


Figure 5.28 Some damage to indigenous understory (this photo - *Annona senagalensis*) does occur with clearfelling, but most of the damaged woody species coppice readily. (April 1997)



Figure 5.29 Animals regularly use the pine plantations as a refuge, thus transporting seeds in their dung. Kudu are common in the dune forests of the Eastern Shores (April 1997). See also Appendix 8.

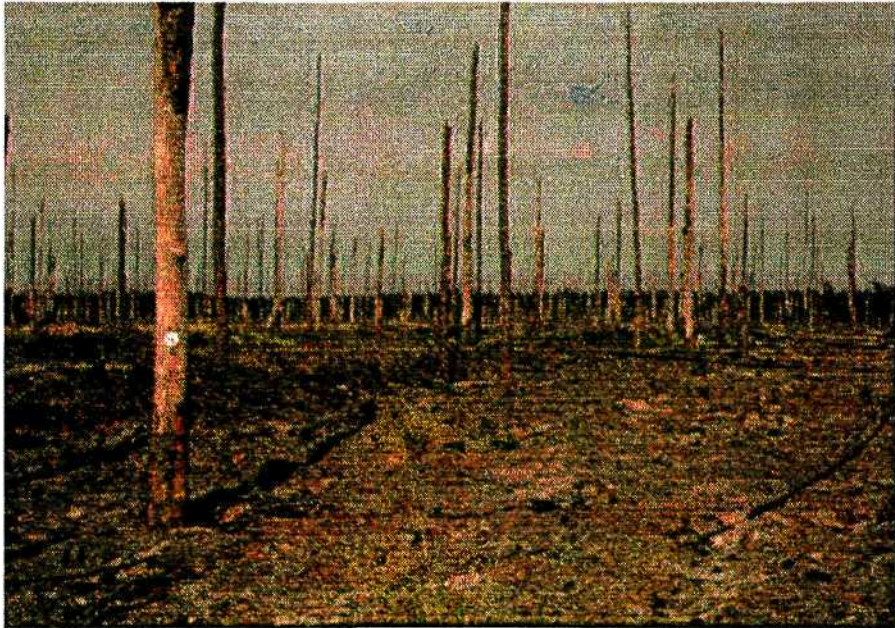


Figure 5.30 This pine plantation was clearfelled as a result of drought damage. Dead pine trees were left standing. The plantation is in Block B, quite a distance from dune forest. Note the lack of indigenous trees. (April 1997)

5.3 HERBACEOUS DATA ANALYSIS

Over the 50 sites sampled, a total of 221 herbaceous species were recorded (Appendix 7). The ordination techniques of CA and CCA were performed using CANOCO (Ter Braak, 1987,1988). These ordinations were related to environmental variables (Appendix 1). As with the woody data analysis, separate ordinations were performed for all sites combined (Figures 5.31 & 5.32), clearfelled sites (Figures 5.34a & b) and pine plantations (Figures 5.36a & b). Species most strongly associated with gradients of change are plotted in Figures 5.33, 5.35 and 5.37.

The first axis of the CA ordination (Eigenvalue: 0.493) describes a gradient from forest to grassland, or sites with high woody species abundance and diversity to sites with low woody species abundance and diversity. This, as elucidated in both the soils and woody data analysis is related to a pH-cation exchange capacity gradient. The second axis (Eigenvalue: 0.354) describes a gradient from first to second rotation pines and from first rotation to clearfelled. It is simultaneously a gradient in phosphorus, pH and cation exchange capacity, although phosphorus is not highly correlated with pH or CEC. It must be remembered that most of the second rotation pine plantations and clearfelled sites were adjacent to undisturbed forest or had at least some forest influence and most of the first rotation pine plantations were adjacent to grassland or grassland with scattered trees. Thus, in ordination space the clearfelled sites tend to be grouped closer to second rather than first rotation pine plantations. The CCA ordination describes, on the first axis (Eigenvalue:0.377) the same gradient in woody diversity and abundance, but with a higher species-environment correlation (0.909, as opposed to 0.819 in CA). Years under pines is part of the same gradient, which is in the same direction as second rotation pines and forest. Second rotation sites have obviously been under pines for longer than first rotation, and most second rotation sites are located close to undisturbed forest, or have some forest influence. Therefore, even the herbaceous component is a product of the influence of adjacent vegetation. The second CCA axis (Eigenvalue:0.236) describes a gradient from first rotation pines and grass with scattered trees to second rotation and forest.

The first four axes for the CA for all sites accounted for 1.5 times the species variance accounted for

by the CCA (Table 5.23, p. 143), whilst the variance of the species-environment relation accounted for by the CCA was 58 % greater than that accounted for by the CA. The overall ordination of the CCA minus outliers was significant ($P = 0.01$: Table 5.22, p.142), therefore the environmental variables chosen explain a significant proportion of the community variation in clearfelled sites. For the first two axes of the CA there is a high (> 0.6) species-environment correlation, and for all four axes of the CCA there is a very high species-environment correlation (> 0.8). The differences between the first and second eigenvalues were 28 % for the CA and 37 % for the CCA, after which differences between subsequent axes are minimal. Therefore, the pattern of floristic variation along the gradient of increasing woody richness and diversity is the primary gradient with a few subsidiary gradients. The species most strongly associated with the gradients of change are listed in Table 5.19.

Table 5.19 Fit per herbaceous species as fraction of variance of species (species most strongly associated with gradients of change) for all sites.

Ref.	CA	Axis 1	Ref.	CCA	Axis 1
91	<i>Digitaria diversinervis</i>	45.47%	171	<i>Phyllanthus meyerianus</i>	35.63%
216	<i>Vernonia natalense</i>	41.15%	23	<i>Asclepias physocarpa</i>	33.97%
23	<i>Asclepias physocarpa</i>	34.97%	216	<i>Vernonia natalense</i>	33.41%
171	<i>Phyllanthus meyerianus</i>	27.24%	91	<i>Digitaria diversinervis</i>	28.36%
16	<i>Agathisanthemum sp.</i>	24.98%	98	<i>Eriosema kraussianum</i>	23.72%
119	<i>Harpochloa falx</i>	22.57%	159	<i>Oxalis sp.</i>	21.80%
86	<i>Desmodium incanum</i>	20.86%	36	<i>Bulbostylis contexta</i>	20.11%
120	<i>Helichrysum cooperi</i>	20.78%			
160	<i>Oxygonum dregeanum</i>	20.00%			
Ref.	CA	Axis 2	Ref.	CCA	Axis 2
211	<i>Tristachya leucothrix</i>	54.33%		Nothing over 20 %	
175	<i>Pteridium aquilinum</i>	22.49%			

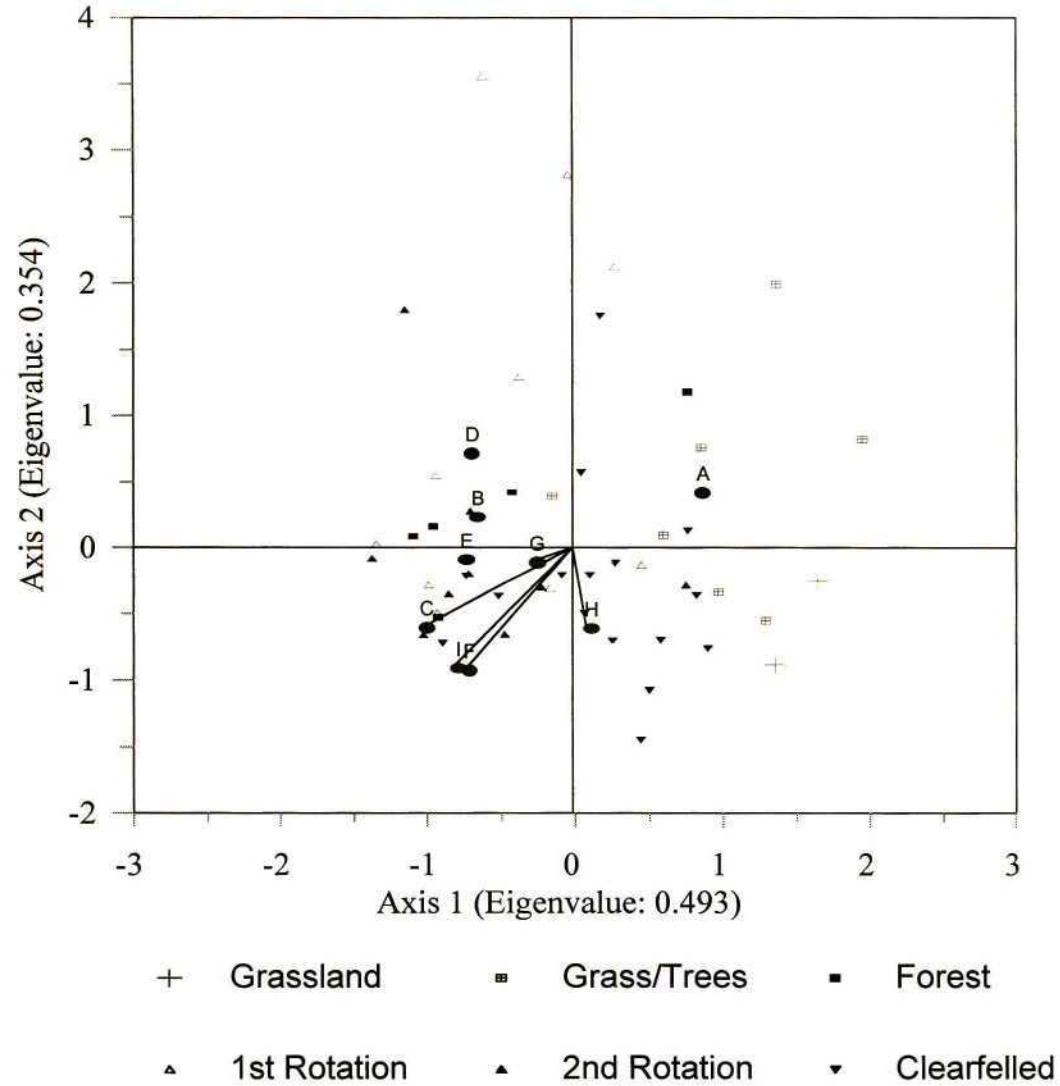


Figure 5.31 Joint plot of sites and environmental variables for the first two axes of correspondence analysis of all sites for herbaceous species. Refer to Table 5.23 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: F = pH measured in KCl; G = Organic carbon; H = Phosphorus; I = Sum of bases; C = Yrs under pines; A (grass with trees), B (forest), D (rotation 1), E (rotation 2) = Centroids for vegetation type.

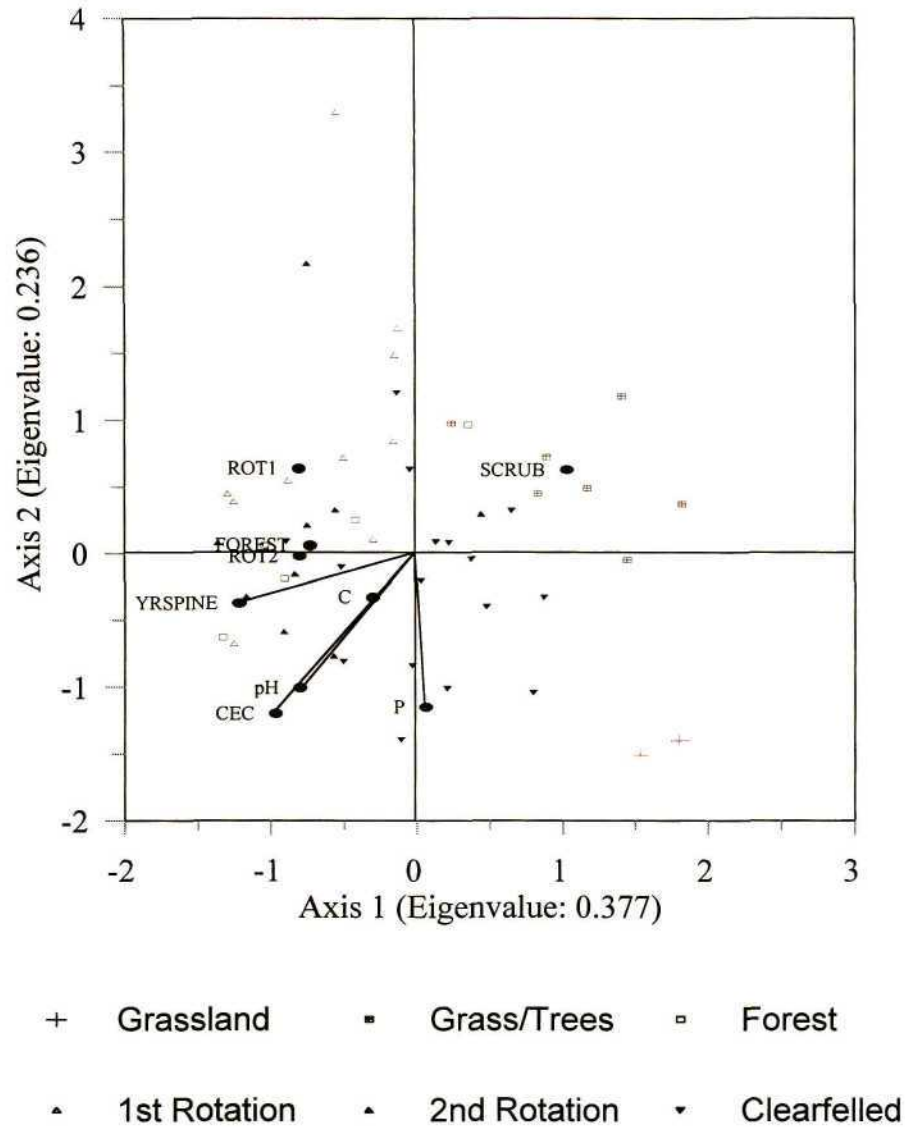
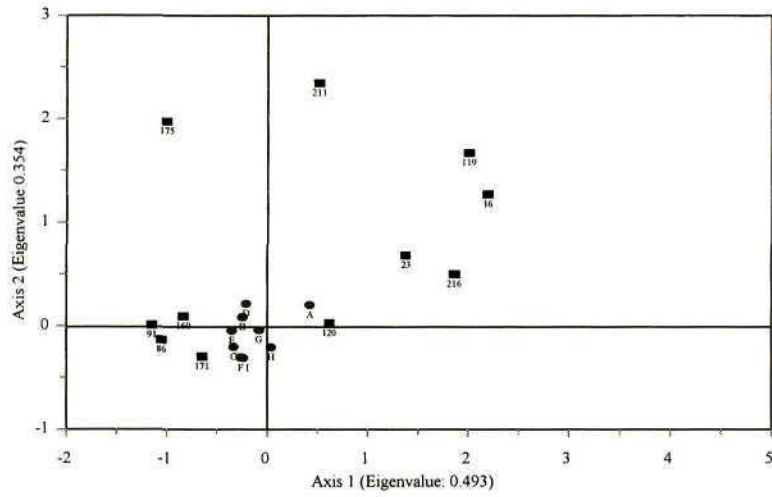
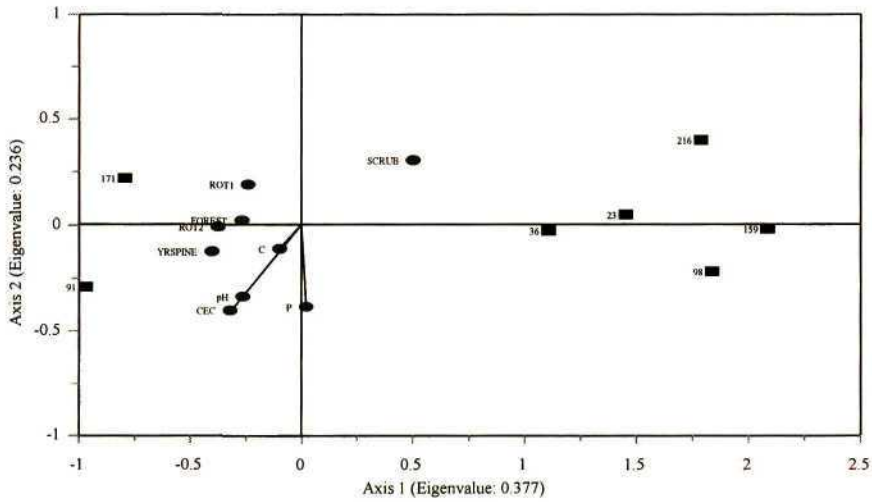


Figure 5.32 Joint plot of sites and environmental variables for the first two axes of canonical correspondence analysis of all sites for herbaceous species. Refer to Table 5.23 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: C = Organic carbon; CEC = Sum of bases; P = Phosphorus; pH = pH measured in KCl; YRSPINE = Yrs under pines; SCRUB, FOREST, ROT1, ROT2 = Centroids for presenting vegetation types.



(a)



(b)

Figure 5.33 Species plots for herbaceous species most strongly associated with environmental gradients in all sites (a) CA, and (b) CCA. - 20 % cutoff as in Table 5.19. Species numbered according to Appendix 7. Environmental variables: C = Years under pine; F = pH; G = Organic carbon; H = Extractable phosphorus; I = Sum of bases; A = Grass/Trees, B = Forest, D = 1st Rotation pine, E = 2nd Rotation pine are all centroids for vegetation types.

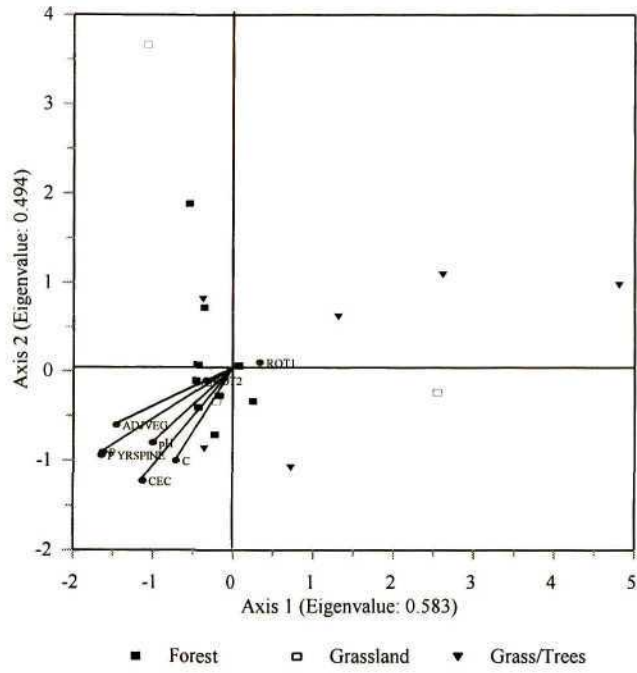
Within the pine plantations both the CA and CCA ordinations show a strong gradient along the first axis (Eigenvalues: 0.583 in CA; 0.468 in CCA) of plantations opposite forest to those opposite grassland, and second rotation to first rotation pines, as in the ordinations for all sites. The second axis (Eigenvalues: 0.494 in CA; 0.362 in CCA) shows a similar gradient.

The first four axes of the CA for all pine plantations accounted for 1.4 times the species variance accounted for by the CCA (Table 5.22), whilst the variance of the species-environment relation accounted for by the CCA was 90 % greater than that accounted for by the CA. The overall ordination of the CCA minus outliers was not significant ($P = 0.29$: Table 5.22), this indicates that the chosen environmental variables explain some of the community variation in clearfelled sites. For the first two axes of the CA there is a high (> 0.6) species-environment correlation, and for all four axes of the CCA there is a very high species-environment correlation (> 0.9). The differences between the first and second axis eigenvalues of the CA was 15 % and between the second and third, 12%, after which differences between subsequent axes are minimal. The differences between the first and second axis eigenvalues of the CCA was 23 %, and between the second and third, 17 %, after which differences between subsequent axes are minimal. Therefore, the pattern of floristic variation along the gradient of the woody component is the primary gradient with a few subsidiary gradients. The species most strongly associated with the gradients of change are listed in Table 5.20. Running the Monte Carlo Test (Table 5.22, p. 142) gave similar erratic results due to small sample size as discussed in the section on woody species analysis.

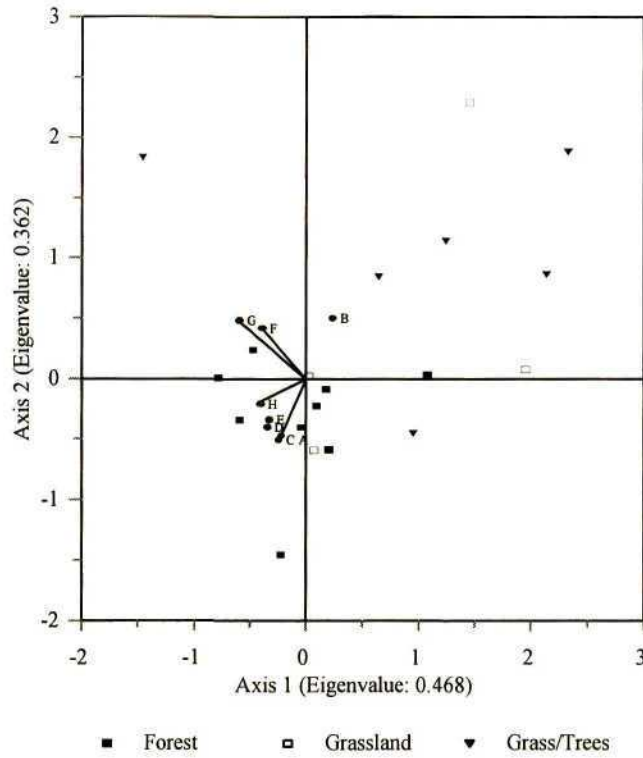
Table 5.20 Fit per herbaceous species as fraction of variance of species (species most strongly associated with gradients of change) for all pine plantations.

Ref.	CA	Axis 1	Ref.	CCA	Axis 1
211	<i>Tristachya leucothrix</i>	83.95%	140	<i>Juncus kraussii</i>	60.94%
117	<i>Grass 6</i>	32.92%	79	<i>D6b/2</i>	45.79%
88	<i>Desmodium setigerum</i>	26.05%	81	<i>D6b/4</i>	45.79%
175	<i>Pteridium aquilinum</i>	21.60%	80	<i>D6b/3</i>	45.79%
164	<i>Pavonia sp.</i>	20.14%	78	<i>D6b/1</i>	45.79%
			173	<i>Protasparagus virgatus</i>	24.22%

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
86	<i>Desmodium incanum</i>	37.17%	35	<i>Bidens pilosa</i>	30.56%
160	<i>Oxygonum dregeanum</i>	37.04%	19	<i>Aneilema aequinoctiale</i>	21.06%
201	<i>Stenochlaena tenuifolia</i>	30.18%	58	<i>Commicarpus sp.</i>	21.06%
91	<i>Digitaria diversinervis</i>	28.83%	110	<i>Grass - A14/2</i>	21.06%
211	<i>Tristachya leucothrix</i>	27.04%	194	<i>Senecio polyanthemoides</i>	21.06%
51	<i>Cissampelos hirta</i>	23.99%	198	<i>Smilax anceps</i>	20.01%
85	<i>Dalechampia volubilis</i>	22.13%			

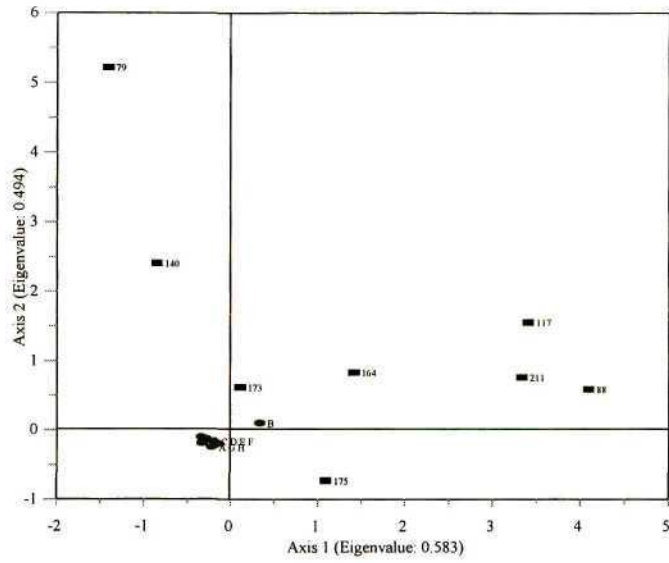


(a)

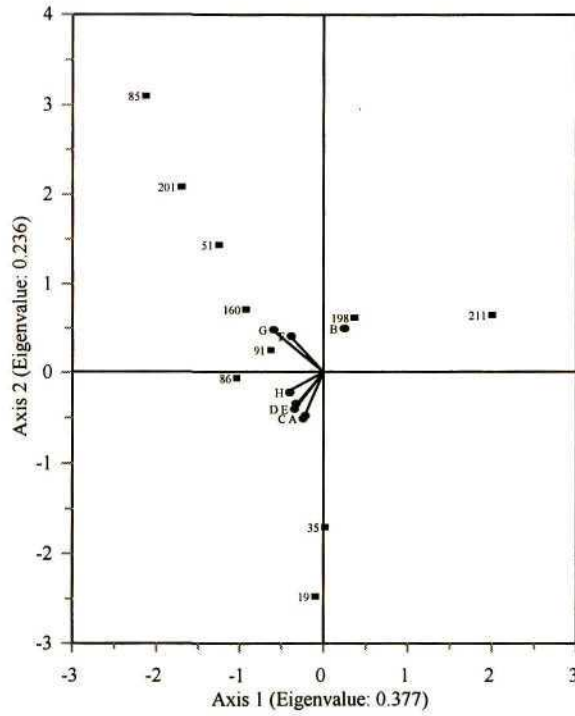


(b)

Figure 5.34 Joint plot of sites and environmental variables for the first two axes of (a) Correspondence analysis, and (b) Canonical correspondence analysis for herbaceous species in pine plantations. Legend describes adjacent vegetation. Refer to Table 5.23 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: A(YRSPINE) = Years under pine; D(ADJVEG) = Degree of woody component in adjacent vegetation; E = pH measured in KCl; F(C) = Organic carbon; G(P) = Extractable phosphorus; H(CEC) = Sum of bases; B & C are centroids for first and second rotation pines respectively.



(a)



(b)

Figure 5.35 Species plots for herbaceous species most strongly associated with environmental gradients in pine plantations (20 % cutoff as in Table 5.20) (a) Correspondence analysis - Species 79 includes 78, 80 & 81, and (b) Canonical correspondence analysis - Species 19 includes 58, 110 & 194. Species numbered according to Appendix 7. Environmental variables: A = Years under pines; D = Degree of woody component in adjacent vegetation; E = pH measured in KCl; F = Organic carbon; G = Extractable phosphorus; H = Sum of bases; B & C are centroids for first and second rotation pines respectively.

The CA ordination for clearfelled areas describes a gradient in phosphorus along the first axis (Eigenvalue: 0.530), which is negatively correlated with a gradient in years under pines, adjacent vegetation and years since clearfelling (Figures 5.36a & b). The CCA first axis (Eigenvalue: 0.442) describes a gradient in time under pines, which is negatively correlated with extractable phosphorus. The second CA axis (Eigenvalue: 0.441) describes the time under pines and the woody component of adjacent vegetation related to pH and sum of bases (CEC). The second CCA axis (Eigenvalue: 0.368) describes a gradient in woody component of the adjacent vegetation, years since clearfelling, pH and sum of bases, i.e. increasing pH and cation exchange capacity related to increasing woody component. Unfortunately, most of the clearfelled sites were located adjacent to undisturbed forest, and most were five years old. Thus, there is not a sufficiently representative spread of sites to make any judgement about time under pines or time since clearfelling. However, the indigenous vegetation adjacent to the clearfelled sites clearly had an influence on the vegetation composition.

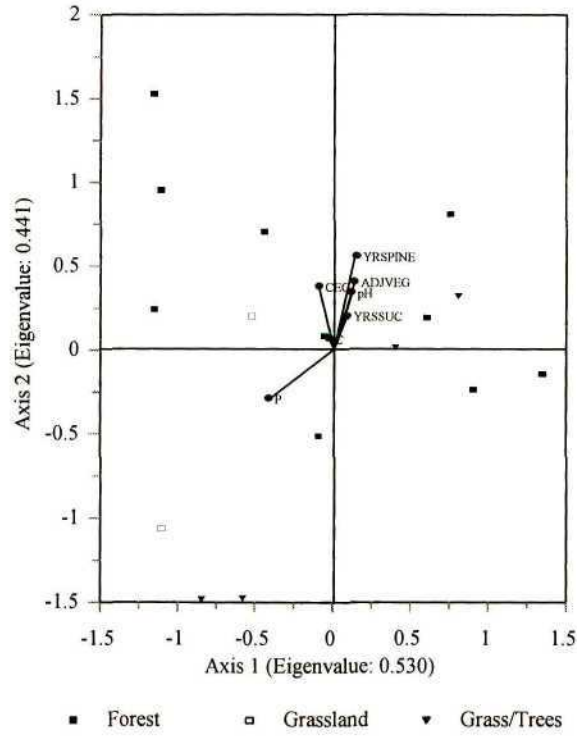
The first four axes for the CA for all clearfelled plantations accounted for 1.2 times the species variance accounted for by the CCA (Table 5.22), whilst the variance of the species-environment relation accounted for by the CCA was 33.3 % greater than that accounted for by the CA. The overall ordination of the CCA minus outliers was not significant ($P = 0.30$: Table 5.22), therefore, the environmental variables chosen do not explain a significant proportion of the community variation in clearfelled sites. The species-environment correlation for the first axis of the CA is 0.563 and that for the second, higher, at 0.955. The remaining two axes have a high species-environment correlation (> 0.9). For all four axes of the CCA there is a very high species-environment correlation (> 0.9). The differences between the first and second axis eigenvalues of the CA was 16 %, and that between the second and third, 12 % after which differences between subsequent axes are minimal. The differences between the first and second axis eigenvalues of the CCA was 16 %, after which differences between subsequent axes are minimal. Therefore, the pattern of floristic variation along the gradient of the woody component is the primary gradient with a few subsidiary gradients. The species most strongly associated with the gradients of change are listed in Table 5.21.

Table 5.21 Fit per herbaceous species as fraction of variance of species (species most strongly associated with gradients of change) for all clearfelled sites.

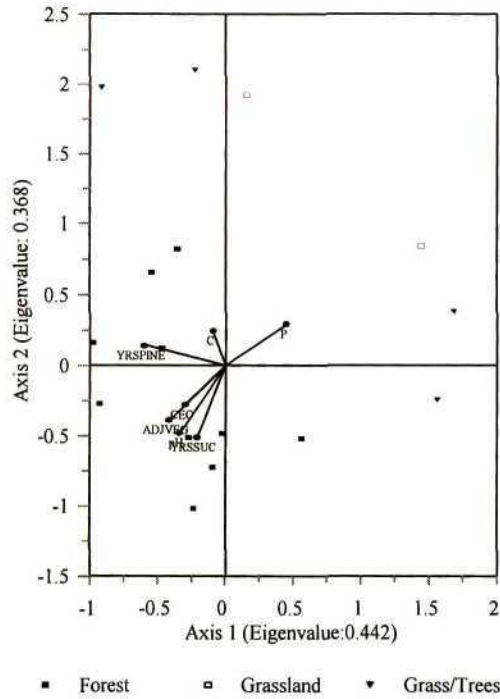
Ref.	CA	Axis 1	Ref.	CCA	Axis 1
57	<i>Commelina erecta</i>	49.17%	85	<i>Dalechampia volubilis</i>	52.72%
179	<i>Richardia brasiliensis</i>	47.50%	60	<i>Conyza sp.</i>	52.72%
210	<i>Triraphis schinzii</i>	46.60%	170	<i>Phyllanthus glaucophyllus</i>	52.72%
177	<i>Rhynchosia sp.</i>	44.02%	195	<i>Senecio serratuloides</i>	50.58%
54	<i>Commelina africana</i>	42.81%	71	<i>Cyperus denudatus</i>	38.30%
91	<i>Digitaria diversinervis</i>	41.07%	49	<i>Cheilanthes viridis</i>	35.63%
82	<i>Dactyloctenium geminatum</i>	38.60%	171	<i>Phyllanthus meyerianus</i>	34.95%
27	<i>Asystasia gangetica</i>	38.26%	154	<i>Oenothera sp.</i>	29.07%
198	<i>Smilax anceps</i>	32.89%	190	<i>Senecio / Conyza sp.</i>	29.07%
14	<i>Achyroopsis sp.</i>	31.84%	153	<i>Mimosa sp.</i>	29.07%
119	<i>Harpochloa falx</i>	31.02%	214	<i>Triumfetta sp.</i>	29.07%
213	<i>Triumfetta rhomboidea</i>	31.02%	127	<i>Hewittia sublobata</i>	29.07%
141	<i>Kyllinga odorata</i>	31.02%	199	<i>Solanum nigrum</i>	29.07%
129	<i>Hibiscus surratensis</i>	31.02%	87	<i>Desmodium repandum</i>	29.07%
151	<i>Mariscus sublimis</i>	31.02%	203	<i>Tephrosia grandiflora</i>	28.45%
201	<i>Stenochlaena tenuifolia</i>	31.02%	220	<i>Wahlenbergia undulata</i>	28.45%
42	<i>Cadaba natalensis</i>	31.02%	57	<i>Commelina erecta</i>	27.40%
158	<i>Osteospermum imbricatum</i>	31.02%	120	<i>Helichrysum cooperi</i>	27.21%
44	<i>Capparis sp.</i>	31.02%	130	<i>Hypoestes aristata</i>	23.02%
109	Grass - A10x/1	31.02%	218	<i>Vernonia sp.</i>	22.74%
83	<i>Dactyloctenium sp.</i>	28.35%	221	<i>Zornia capense</i>	22.66%
196	<i>Senecio sp.</i>	22.58%	46	<i>Centella asiatica</i>	21.99%
73	<i>Cyperus obtusiflorus</i>	22.52%	173	<i>Protasparagus virgatus</i>	21.68%
21	<i>Anthospermum herbaceum</i>	20.76%	77	D1a/2	20.99%
204	<i>Tephrosia sp.</i>	20.16%	9	<i>Abrus sp.</i>	20.99%
122	<i>Helichrysum kraussii</i>	20.15%	176	<i>Pteris vittata</i>	20.99%
			72	<i>Cyperus natalensis</i>	20.99%

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
170	<i>Phyllanthus glaucophyllus</i>	44.49%	140	<i>Juncus kraussii</i>	51.12%
60	<i>Conyza sp.</i>	44.49%	69	<i>Cyperaceae sp.</i>	34.35%
85	<i>Dalechampia volubilis</i>	44.49%	155	<i>Oldenlandia affinis</i>	34.35%
195	<i>Senecio serratuloides</i>	41.51%	86	<i>Desmodium incanum</i>	34.02%
171	<i>Phyllanthus meyerianus</i>	39.78%	211	<i>Tristachya leucothrix</i>	24.49%
130	<i>Hypoestes aristata</i>	33.30%	14	<i>Achyroopsis sp.</i>	21.05%
120	<i>Helichrysum cooperi</i>	29.93%	210	<i>Triraphis schinzii</i>	20.55%
71	<i>Cyperus denudatus</i>	28.91%	36	<i>Bulbostylis contexta</i>	20.50%
49	<i>Cheilanthes viridis</i>	26.36%	65	<i>Cuscuta natalensis</i>	20.29%
107	<i>Gnidia splendens</i>	24.56%			
6	A4/1	24.56%			
68	<i>Cynodon dactylon</i>	24.56%			
167	<i>Pentanissia prunelloides</i>	24.56%			
7	A4/2	24.56%			
215	<i>Vernonia angulifolia</i>	24.56%			
203	<i>Tephrosia grandiflora</i>	23.76%			
220	<i>Wahlenbergia undulata</i>	23.76%			

Ref.	CA	Axis 2	Ref.	CCA	Axis 2
154	<i>Oenothera sp.</i>	22.59%			
190	<i>Senecio / Conyza</i>	22.59%			
199	<i>Solanum nigrum</i>	22.59%			
87	<i>Desmodium repandum</i>	22.59%			
127	<i>Hewittia sublobata</i>	22.59%			
214	<i>Triumfetta sp.</i>	22.59%			
153	<i>Mimosa sp.</i>	22.59%			
173	<i>Protasparagus virgatus</i>	22.16%			
46	<i>Centella asiatica</i>	21.98%			
45	<i>Catharathus roseus</i>	21.98%			

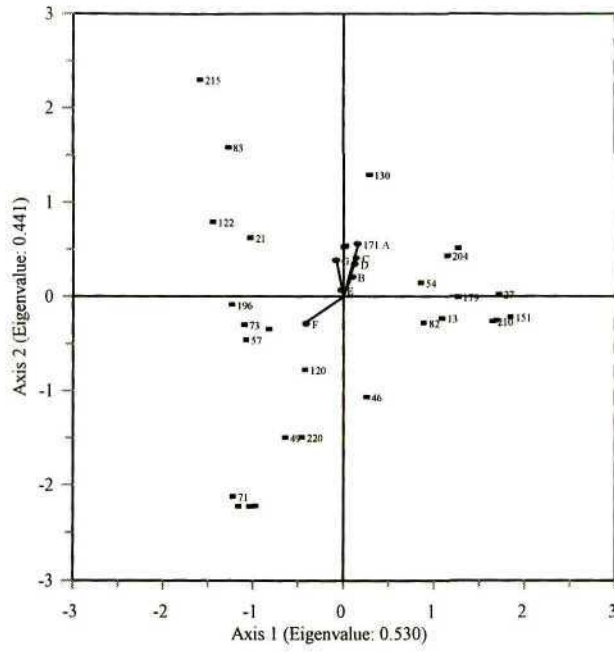


(a)

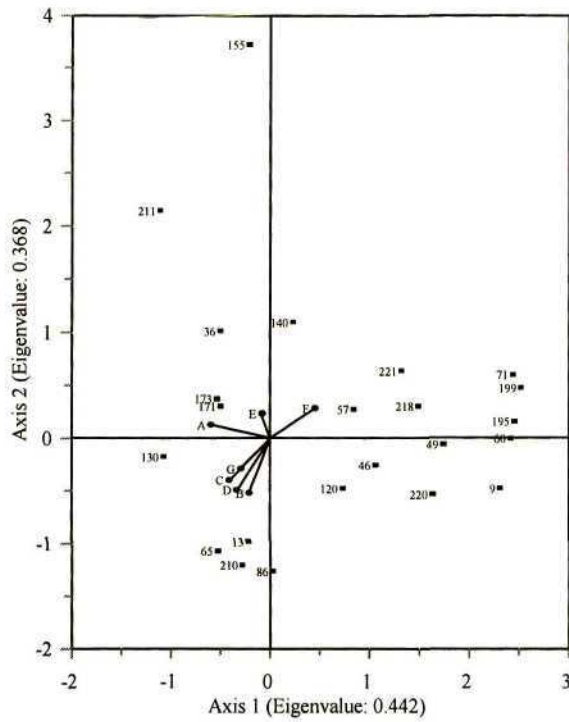


(b)

Figure 5.36 Joint plot of sites and environmental variables for the first two axes of (a) Correspondence analysis, and (b) Canonical correspondence analysis for herbaceous species in clearfelled sites. Legend describes adjacent vegetation. Refer to Table 5.23 for how well the ordinations performed. Environmental variables with the longest arrow relative to an axis have the greatest influence on that axis. If the arrows of two variables subtend a small angle, they are correlated. Environmental variables: ADJVEG = Degree of woody component in adjacent vegetation; C = Organic carbon; CEC = Sum of bases; pH = pH measured in KCl; P = Extractable phosphorus; YRSPINE = Years under pine; YRSSUCC = Years since clearfelling.



(a)



(b)

Figure 5.37 Species plots for herbaceous species most strongly associated with environmental gradients in clearfelled sites (20 % cutoff as in Table 5.20) (a) Correspondence analysis - (215 = 215, 7, 167, 68, 6, 107); (21 = 21, 85, 170, 60, 198); (179 = 179, 91); (71 = 71, 214, 127, 190, 153, 87, 199, 154); (151 = 151, 129, 201, 213, 119, 42, 158, 141, 44, 109); (57 = 57, 195); (220 = 220, 203); (210 = 210, 177); (120 = 120, 171, 173). and (b) Canonical correspondence analysis - (199 = 199, 87, 127, 214, 154, 153, 190); (60 = 60, 85, 170); (9 = 9, 72, 77, 176); (220 = 220, 203). Species numbered according to Appendix 7. Environmental variables: A = Years under pines; B = Years since clearfelling; C = Degree of woody component in adjacent vegetation; D = pH measured in KCl; E = Organic carbon; F = Extractable phosphorus; G = Sum of bases (CEC).

Table 5.22 Monte Carlo Test (No. permutations = 99) for herbaceous species CCA

		All	Pine	Clear
Test of significance of first canonical axis:	Eigenvalue	0.38	0.47	0.44
	F-ratio	2.44	1.16	0.96
	P-value	0.01	0.97	1.00
Overall test	Trace	1.52	2.00	2.01
	F-ratio	1.35	1.08	1.08
	P-value	0.01	0.29	0.30

Table 5.23 Summary of the correspondence (CA) and canonical correspondence (CCA) analyses for the Eastern Shores of Lake St Lucia herbaceous component; axes 1-4 for a) CA - all 50 sites, b) CCA - all 50 sites, c) CA - all pine plantations, d) CCA - all pine plantations, e) CA - all clearfelled sites, f) CCA - all clearfelled sites. Rare species were down-weighted.

		Axis order			
		1	2	3	4
a)	CA - all 50 sites, axis 1-4				
	Eigenvalue	0.493	0.354	0.342	0.332
	Species-environment correlation	0.819	0.682	0.456	0.485
	Cumulative percent variance of:				
	Species data	7.7	13.2	18.5	23.7
	Species environment	21.7	32.6	37.2	42.4
b)	CCA - all 50 sites, axis 1-4				
	Eigenvalue	0.377	0.236	0.220	0.183
	Species-environment correlation	0.909	0.890	0.934	0.883
	Cumulative percent variance of:				
	Species data	5.9	9.6	13.0	15.8
	Species environment	24.8	40.3	54.8	66.9
c)	CA - all pine plantations, axis 1-4 (n = 20)				
	Eigenvalue	0.583	0.494	0.434	0.414
	Species-environment correlation	0.643	0.636	0.598	0.604
	Cumulative percent variance of:				
	Species data	11.9	22.0	30.8	39.3
	Species environment	12.1	22.1	29.8	37.4
d)	CCA - all pine plantations, axis 1-4 (n = 20)				
	Eigenvalue	0.469	0.362	0.299	0.286
	Species-environment correlation	0.969	0.973	0.963	0.970
	Cumulative percent variance of:				
	Species data	9.6	17.0	23.0	28.9
	Species environment	23.5	41.6	56.6	70.9
e)	CA - all clearfelled sites, axis 1-4 (n = 16) minus 1 outlier				
	Eigenvalue	0.530	0.441	0.389	0.362
	Species-environment correlation	0.563	0.955	0.858	0.771
	Cumulative percent variance of:				
	Species data	12.8	23.5	32.9	41.7
	Species environment	8.4	28.4	42.7	53.4
f)	CCA - all clearfelled sites, axis 1-4 (n = 16) minus 1 outlier				
	Eigenvalue	0.442	0.368	0.345	0.276
	Species-environment correlation	0.993	0.985	0.959	0.968
	Cumulative percent variance of:				
	Species data	10.7	19.6	27.9	34.6
	Species environment	22.0	40.3	57.4	71.2

5.3.1 Herbaceous species richness

It is interesting to note that the herbaceous species richness in pine plantations opposite grassland and grassland with scattered trees is very low, whereas plantations opposite forests have a herbaceous species richness very close to that found in the forest (Figure 5.38). This would indicate that there is very little movement of plant propagules from grassland to adjacent pine plantations, but considerable movement from undisturbed forest to adjacent pine plantations.

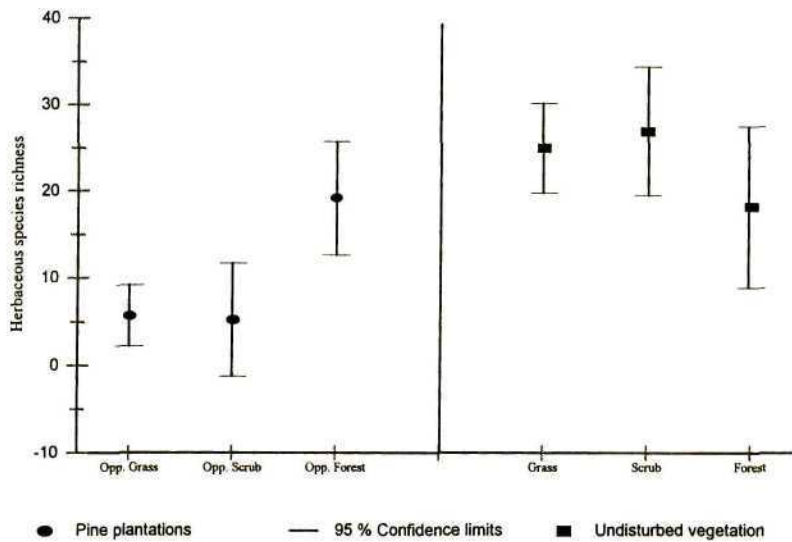


Figure 5.38 Herbaceous species richness in pine plantations and undisturbed vegetation. Pine plantations are divided according to adjacent vegetation type, and undisturbed sites according to vegetation type.

Herbaceous species were mostly found on the edges of pine plantations, with a rapid decrease in number and density towards the centre. They appear to penetrate more in the direction of the prevailing wind and, since few have fleshy fruits or obvious means of attaching seeds to animals, it is assumed that the bulk are wind-dispersed, but this has not been investigated. No increase in herbaceous species richness was observed over successional time. No herbaceous species had a cover of more than 5 % of the total herbaceous composition in any of the vegetation types (Table 5.23). The identification of grasses proved to be a problem as very few were in flower at the time of sampling. The season of sampling of herbaceous species is far more critical than in the sampling of woody species as some are ephemeral, others virtually impossible to identify as seedlings, and others virtually impossible to identify without flowers.

To further consider the effect of adjacent vegetation on pine plantations, the herbaceous species richness, diversity and evenness for each pair of adjacent sites was compared. The correlation co-efficients were calculated for species richness, diversity and evenness across the matched sites. There was no correlation between herbaceous species diversity and richness over paired sites, but the correlation co-efficient for evenness was (0.569). This confirms that very little recruitment of herbaceous species occurs in pine plantations.

Table 5.23 Herbaceous species richness in paired sites. Sites marked with * are opposite forest

PINE PLANTATIONS				UNDISTURBED VEGETATION			
Site No.	Richness	Diversity	Evenness	Site No.	Richness	Diversity	Evenness
B1	3	1.04	0.95	B1x	21	2.74	0.90
B30	2	0.69	1.00	B30x	18	2.62	0.91
B9	2	0.45	0.65	B9x	21	2.72	0.89
B24	5	1.49	0.93	B24x	30	3.18	0.93
B29	8	1.80	0.87	B29x	19	2.72	0.92
B19	4	1.39	1.00	B19x	21	2.72	0.89
A6 *	10	1.98	0.86	A6x	27	3.01	0.91
C6a *	13	2.30	0.90	C6ax	11	2.19	0.91
A1 *	16	2.50	0.90	A1x	23	2.88	0.92
A10 *	14	2.41	0.91	A10x	17	2.59	0.91
A14 *	14	2.29	0.89	A14x	19	2.69	0.92
Mean	8.27	1.67	0.90		20.64	2.73	0.91

5.3.2 Herbaceous successional trajectories

Table 5.24 Herbaceous species proportional composition in undisturbed vegetation

Grass / Trees		Indigenous forest	
<i>Pteridium aquilinum</i>	3%	<i>Digitaria diversinervis</i>	5%
<i>Indigofera filipes</i>	3%	<i>Microsorium scolopendria</i>	5%
B9x/11	3%	<i>Mariscus dubius</i>	4%
<i>Sporobolus africanus</i>	3%	Grass 6	4%
<i>Basanthia polygaloides</i>	2%	<i>Clausena anisata</i>	4%
Grass - B1x/1	2%	<i>Tristachya leucothrix</i>	4%
<i>Smilax anceps</i>	2%	<i>Panicum maximum</i>	3%
<i>Ipomoea sp.</i>	2%	<i>Achyranthus aspera</i>	3%
<i>Hemarthria altissima</i>	2%	<i>Coleotrype natalensis</i>	3%
<i>Microsorium scolopendria</i>	2%	Grass - A10x/1	3%
Grass 7	2%	<i>Dalbergia armata</i>	3%
<i>Helichrysim kraussii</i>	2%	<i>Helichrysim kraussii</i>	3%
<i>Senecio sp.</i>	2%	<i>Desmodium incanum</i>	3%
<i>Salacia kraussii</i>	2%	<i>Pellea viridis</i>	3%
<i>Dactyloctenium geminatum</i>	2%	<i>Asystasia gangetica</i>	2%
<i>Digitaria diagonalis</i>	2%	<i>Ipomoea sp.</i>	2%
<i>Acalypha peduncularis</i>	2%	<i>Dactyloctenium geminatum</i>	2%
<i>Cyperus albostrigatus</i>	2%	<i>Stenochlaena tenuifolia</i>	2%
<i>Panicum parvifolium</i>	2%	<i>Protasparagus virgatus</i>	2%
<i>Harpochloa falx</i>	2%	<i>Secamone delagoense</i>	2%
<i>Tristachya leucothrix</i>	1%	<i>Juncus kraussii</i>	2%
<i>Cyperus sphaerospermus</i>	1%	<i>Smilax anceps</i>	2%
<i>Bulbostylis contexta</i>	1%	<i>Flagellarra guinensis</i>	2%
<i>Lobelia pinifolia</i>	1%	A1x/4	2%
<i>Cuscuta natalensis</i>	1%	Grass 1	2%
<i>Rhynchosia sp.</i>	1%	<i>Cyperus sphaerospermus</i>	2%
B9x/2	1%	<i>Cyperus albostrigatus</i>	2%
<i>Diospyros lyciodes</i>	1%	<i>Commelina africana</i>	2%
<i>Berkheya speciosa</i>	1%	<i>Laportea grossa</i>	2%
<i>Vernonia oligocephala</i>	1%	<i>Desmodium setigerum</i>	1%
<i>Dactyloctenium sp.</i>	1%	<i>Triumfetta pilosa</i>	1%
<i>Achyropsis sp.</i>	1%	<i>Crotalaria dura</i>	1%
<i>Anthospermum herbaceum</i>	1%	<i>Liliaceae sp.</i>	1%
<i>Senecio erubescens</i>	1%	<i>Cyperus obtusiflorus</i>	1%
<i>Alloteropsis semialata</i>	1%	<i>Panicum parvifolium</i>	1%
<i>Cymbapogon validus</i>	1%	<i>Phyllanthus meyerianus</i>	1%
<i>Juncus kraussii</i>	1%	<i>Commelina benghalensis</i>	1%
<i>Imperata cylindrica</i>	1%	<i>Commicarpus sp.</i>	1%
<i>Desmodium sp.</i>	1%	<i>Commelina erecta</i>	1%
<i>Centella glabra</i>	1%	<i>Tecomaria capensis</i>	1%
<i>Ozoroa spherocarpa</i>	1%	<i>Kyllinga odorata</i>	1%
<i>Sebaea sedoides</i>	1%	Grass - A10/2	1%
<i>Eragrostis lappula</i>	1%	<i>Hibiscus surratensis</i>	1%
<i>Diospyros villosus</i>	1%	<i>Sansevieria sp.</i>	1%
<i>Tragia durbanensis</i>	1%	<i>Ricardia brasiliensis</i>	1%
<i>Triumfetta sp.</i>	1%	<i>Pteridium aquilinum</i>	1%
<i>Triraphis schinzii</i>	1%	<i>Isoglossa woodii</i>	1%
<i>Aristea sp.</i>	1%	<i>Senecio deltoides</i>	1%
<i>Thunbergia sp.</i>	1%	<i>Hypoestes aristata</i>	1%
<i>Aeschynemone micrantha</i>	1%	<i>Dracaena altriformis</i>	1%
<i>Tephrosia grandiflora</i>	1%	<i>Capparis sp.</i>	1%
<i>Kyllinga odorata</i>	1%	<i>Abrus sp.</i>	1%
<i>Protasparagus virgatus</i>	1%	<i>Bulbostylis contexta</i>	1%
<i>Indigofera sp.</i>	1%	<i>Aeschynemone micrantha</i>	1%
<i>Centella asiatica</i>	1%	A5/5	1%
	74%		100%

Table 5.25 Herbaceous proportional composition in planted areas

Pine opposite grass/trees		Pine opposite forest		Clearfelled	
<i>Phyllanthus meyerianus</i>	10 %	<i>Phyllanthus meyerianus</i>	6 %	<i>Cyperaceae</i>	3 %
<i>Smilax anceps</i>	8 %	<i>Smilax anceps</i>	5 %	<i>Tendynea sp.</i>	2 %
<i>Pteridium aquilinum</i>	5 %	<i>Protasparagus virgatus</i>	4 %	<i>Dactyloctenium sp.</i>	2 %
<i>Tristachya leucothrix</i>	5 %	<i>Digitaria diversinervis</i>	4 %	<i>Grass - A26/7</i>	2 %
<i>Ipomoea sp.</i>	5 %	<i>Juncus kraussii</i>	3 %	<i>Imperata cylindrica</i>	2 %
<i>Commelina africana</i>	5 %	<i>Secamone delagoensis</i>	3 %	<i>Achyranthus aspera</i>	2 %
<i>Juncus kraussii</i>	3 %	<i>Desmodium incanum</i>	3 %	<i>Aneilema aequinaectiale</i>	2 %
<i>Panicum maximum</i>	3 %	<i>Dactyloctenium geminatum</i>	3 %	<i>Mariscus sublimus</i>	2 %
<i>Stenochlaena tenuifolia</i>	3 %	<i>Helichrysum cooperi</i>	3 %	<i>Cynodon dactylon</i>	2 %
<i>Rhynchosia totta</i>	3 %	<i>Oxygonum dregeanum</i>	3 %	<i>Dalbergia armata</i>	2 %
<i>Digitaria diversinervis</i>	3 %	<i>Senecio deltoideus</i>	2 %	<i>Helichrysim kraussii</i>	2 %
<i>Desmodium setigerum</i>	2 %	<i>Commelina africana</i>	2 %	<i>Rubiaceae sp.</i>	2 %
<i>Desmodium incanum</i>	2 %	<i>Centella asiatica</i>	2 %	<i>Tristachya leucothrix</i>	2 %
<i>Panicum parvifolium</i>	2 %	<i>Panicum maximum</i>	2 %	<i>Anthospermum herbaceum</i>	2 %
<i>Aeschynemone micrantha</i>	2 %	<i>Coleotrype natalensis</i>	2 %	<i>Microsorium scolopendria</i>	2 %
<i>Pavonia sp.</i>	2 %	<i>Asystasia gangetica</i>	2 %	<i>Desmodium sp.</i>	1 %
<i>Dalechampia volubilis</i>	2 %	<i>Achyranthus aspera</i>	1 %	<i>Digitaria diversinervis</i>	1 %
<i>Grass - A10x/1</i>	2 %	<i>Sansevieria sp.</i>	1 %	<i>Dactyloctenium geminatum</i>	1 %
<i>Oxygonum dregeanum</i>	2 %	<i>Pteridium aquilinum</i>	1 %	<i>Panicum maximum</i>	1 %
<i>Osteospermum imbricatum</i>	2 %	<i>Tristachya leucothrix</i>	1 %	<i>Cyperus denudatus</i>	1 %
<i>Cissampelos hirta</i>	2 %	<i>Ornithogallim sp.</i>	1 %	<i>Senecio serratuloides</i>	1 %
<i>D6b/4</i>	2 %	<i>Acalypha peduncularis</i>	1 %	<i>Grass 1</i>	1 %
<i>D6b/3</i>	2 %	<i>Ipomoea sp.</i>	1 %	<i>Vernonia angulifolia</i>	1 %
<i>D6b/2</i>	2 %	<i>Hypoestes aristata</i>	1 %	<i>Gnidia splendens</i>	1 %
<i>D6b/1</i>	2 %	<i>Hibiscus sp.</i>	1 %	<i>Asystasia gangetica</i>	1 %
<i>Grass 6</i>	2 %	<i>Cissampelos hirta</i>	1 %	<i>Crotalaria dura</i>	1 %
<i>Triumfetta sp.</i>	2 %	<i>Grass - A10/2</i>	1 %	<i>Eragrostis ciliaris</i>	1 %
<i>Sansevieria sp.</i>	2 %	<i>Crotalaria dura</i>	1 %	<i>Hibiscus surratensis</i>	1 %
<i>Pentas sp.</i>	2 %	<i>Commelina erecta</i>	1 %	<i>Bulbostylis contexta</i>	1 %
<i>Isoglossa sp.</i>	2 %	<i>Bidens pilosa</i>	1 %	<i>Smilax anceps</i>	1 %
<i>Cyperus sphaerospermus</i>	2 %	<i>Alloteropsis semialata</i>	1 %	<i>Panicum parvifolium</i>	1 %
<i>Cheilanthes viridis</i>	2 %	<i>A5/5</i>	1 %	<i>Triumfetta pilosa</i>	1 %
<i>Grass 1</i>	2 %	<i>Triumfetta pilosa</i>	1 %	<i>Juncus kraussii</i>	1 %
<i>Oenothera sp.</i>	2 %	<i>Aeschynemone micrantha</i>	1 %	<i>Commelina africana</i>	1 %
<i>Cyperus albostriatus</i>	2 %	<i>Abutilon austro-africanum</i>	1 %	<i>Lobelia pinifolia</i>	1 %
<i>Grass - A10/2</i>	2 %	<i>A22/ 4</i>	1 %	<i>Ricardia brasiliensis</i>	1 %
<i>Protasparagus virgatus</i>	2 %	<i>A10/1</i>	1 %	<i>Senecio sp.</i>	1 %
	100 %	<i>Aneilema aequinoctiale</i>	1 %	<i>Hypoestes aristata</i>	1 %
		<i>C23d-i/3</i>	1 %	<i>Hibiscus sp.</i>	1 %
		<i>Anisochaeta mikanioides</i>	1 %	<i>Callocyphala sp.</i>	1 %
		<i>Vigna tenuis</i>	1 %	<i>Helichrysum sp.</i>	1 %
		<i>Cadaba natalensis</i>	1 %	<i>Cuscuta natalensis</i>	1 %
		<i>Callilepis laureola</i>	1 %	<i>Cucumis sp.</i>	1 %
		<i>Capparis sp.</i>	1 %	<i>Desmodium incanum</i>	1 %
		<i>Catharathus roseus</i>	1 %	<i>Achyranthus leptostachya</i>	1 %
		<i>Rubiaceae sp.</i>	1 %	<i>Stenochlaena tenuifolia</i>	1 %
		<i>Ricinis communis</i>	1 %	<i>Senecio madagascariensis</i>	1 %
		<i>Richardia brasiliensis</i>	1 %	<i>Desmodium repandum</i>	1 %
		<i>Cheilanthes viridis</i>	1 %	<i>Rhynchosia sp.</i>	1 %
		<i>Grass 1</i>	1 %	<i>Conyza floribunda</i>	1 %
		<i>Rumex sp.</i>	1 %	<i>Indigofera sp.</i>	1 %
		<i>Elephantorrhiza elephantina</i>	1 %	<i>Protasparagus virgatus</i>	1 %
		<i>Kyllinga odorata</i>	1 %	<i>Helichrysum decorum</i>	1 %
		<i>Drogietia sp.</i>	1 %	<i>Acalypha sp.</i>	1 %
		<i>Isoglossa sp.</i>	1 %	<i>Triraphis schinzii</i>	1 %
		<i>Hewittia sublobata</i>	1 %	<i>Commelina erecta</i>	1 %
		<i>Desmodium sp.</i>	1 %	<i>Centella asiatica</i>	1 %
		<i>Commicarpus sp.</i>	1 %	<i>Asclepias physocarpa</i>	1 %
		<i>Desmodium setigerum</i>	1 %	<i>Secamone delagoense</i>	1 %
		<i>Secamone sp.</i>	1 %		70 %

Pine opposite grass/trees	Pine opposite forest	Clearfelled
	<i>Rhynchosia tosta</i>	1 %
	<i>Phyllanthus glaucophyllus</i>	1 %
	<i>Pavonia sp.</i>	1 %
	<i>Mariscus sublimis</i>	1 %
	<i>Cuscuta natalensis</i>	1 %
	<i>Tragia dioica</i>	1 %
	<i>Stenochlaena tenuifolia</i>	1 %
	<i>Senna petersiana</i>	1 %
	<i>Senecio polyanthemoides</i>	1 %
	<i>Cyperus albobstriatus</i>	1 %
	<i>Hibiscus surratensis</i>	1 %
	<i>Psilotrichum scleranthum</i>	1 %
	<i>Cyperus obtusiflorus</i>	1 %
	<i>Ipomoea ficifolia</i>	1 %
	Grass - A14/2	1 %
	<i>Triumfetta rhomboidea</i>	1 %
	<i>Osteospermum imbricatum</i>	1 %
	<i>Mariscus sp.</i>	1 %
	Leguminosae	1 %
	<i>Jatropha sp.</i>	1 %
		100 %

The high proportion of unidentified herbaceous species prevents full understanding of the vegetation dynamics of the Eastern shores, making it difficult to describe successional trajectories or compile accurate species lists. Nevertheless, with the data available, some useful deductions are still possible: (i) each unidentified species is a unique species, so species diversity and evenness may legitimately be compared; (ii) the presence of identified species in different vegetation types gives an indication of which species found in undisturbed forest and grassland are also found under pine plantations. Therefore, if a species is found only in undisturbed forest, but not undisturbed grassland, then it can be assumed that it is better adapted to forest conditions. If that same species is found consistently within pine plantations, it can be deduced that conditions within the pine plantation are favourable for establishment of forest species.

In summary, the herbaceous species composition in both pine plantations and clearfelled sites is directly related to the nature of the undisturbed vegetation adjacent to that site. Herbaceous species richness and diversity is high in undisturbed grassland and lower in undisturbed forest, while it is low in pine plantations opposite grassland and, opposite forest, converges to the same as that in undisturbed forest, though higher than in pines opposite grassland. This would indicate that herbaceous species adapted to grassland conditions are unable to establish under pine plantations, but the suite adapted to forest conditions are able to establish under pines. In effect then, the pine plantations are mimicking the natural forest environment. Therefore, the nature of the adjacent vegetation, as with the woody component, dictates the character of the herbaceous understorey in pine plantations.

6 DISCUSSION AND CONCLUSIONS

6.1 RESULTS

The results of this study will be summarised and discussed, after which the implications thereof will be explored.

It was found that pine plantations on the Eastern Shores, as with pine plantations worldwide, reduce pH and cation exchange capacity in the soils, relative to adjacent, undisturbed sites, but these effects are short-lived and are ameliorated by the presence of the developing indigenous understorey (Figures 5.6 & 5.7, p.89; Figures 5.8 & 5.9, p.96)

Ordination of both woody and herbaceous plant data indicated that there was a direct relationship between the plant species composition in pine and clearfelled areas, and that of adjacent, undisturbed vegetation. Ordination also showed no direct relationship between age of pine plantations and species composition. The overriding factor was whether or not there was a source of forest species propagules nearby.

Woody species richness and diversity in pine plantations and clearfelled areas was directly proportional to the type of adjacent undisturbed vegetation (Figures 5.22 & 5.23, p.116). Plantations opposite forest had higher woody species richness and diversity than those opposite grassland. Initially after clearfelling, the suite of woody species essentially remained the same as in plantations, but certain species became more dominant and species richness increased with time, or successional age (Figure 5.24, p.116).

Herbaceous species richness and diversity were higher in undisturbed grassland than in undisturbed forest. However, herbaceous species richness in pine plantations opposite grassland and grassland with scattered trees is very low, whereas plantations opposite forests have a herbaceous species richness very close to that found in the forest. No increase in herbaceous species richness was observed over successional time (Figure 5.38, p.139; Table 5.23, p.140).

6.2 TESTING OF HYPOTHESES

Hypotheses generated in the introduction will be tested and discussed in turn.

H1: The nature of adjacent undisturbed vegetation determines the floristic composition and direction of succession.

This was clearly shown in the ordination of woody and herbaceous species data where the spread of points in ordination space was directly related to the nature of the adjacent vegetation. Thus, the initial floristic composition was determined by the adjacent vegetation. Where adjacent vegetation was undisturbed forest, the vegetation within the pine plantations reflected the same composition. Woody species richness within pine plantations was highly correlated with that of the adjacent vegetation, as was species composition over the matched sites. Herbaceous species richness within pine plantations was only correlated with adjacent vegetation when the adjacent vegetation was forest.

H2: The number of rotations of pine plantations affects the soil characteristics and the initial floristic composition (i.e. type of seeds persisting and indigenous species established under the pine canopy).

There was no evidence to suggest that the number of rotations had any significant effect on soil characteristics or initial floristic composition. Initially, it was thought that the second rotation of pines was critical for establishment and consolidation of the indigenous understorey, but it later became clear that it was simply because most second rotation plantations were located adjacent to forest and most first rotation plantations adjacent to grassland. The spread of plantations on the Eastern Shores does not allow adequate investigation of this question.

H3: Pine plantations create a favourable micro-habitat for the establishment of a dune forest understorey.

Woody and herbaceous species associated with dune forest were found within plantations, particularly when a source of propagules was available in adjacent undisturbed forest.

H4: Soil under pine plantations, relative to the soil under adjacent indigenous sites, has lower pH and reduced fertility (in terms of major cations) and reduced extractable phosphorus.

This was clearly shown using the t-test for paired sites.

H5: Soil pH, fertility and extractable phosphorus continue to decline with increased time under pines.

No relationship between time under pines and decreased pH or soil fertility was found.

H6: Pine-induced soil acidity changes texture through increased weathering of particles.

No evidence of changes soil texture due to pine-induced soil acidity was found.

H7: Pine-induced acidity causes aluminium and iron toxicity.

No evidence of pine-induced aluminium or iron toxicity was found.

H8: The presence of pine plantations causes podzolisation of the soil.

No evidence of podzolization due to the presence of pine plantations was found.

6.3 DISCUSSION

Apart from the initial dune building and ongoing shifting of dunes, as well as periodic floods, most disturbance on the Eastern Shores of Lake St Lucia has been medium-term (hundreds of years), anthropogenic disturbance and not in the form of a single catastrophic effect.

Archeological evidence indicates that the first anthropogenic disturbance on the Eastern Shores was clearing of trees for the purposes of iron smelting and shifting agriculture (Hall, 1984; Hall and Vogel, 1978). Since the arrival of colonial settlers in the early 19th Century, there

have been a number of direct and indirect disturbances affecting the integrity of the area now known as the Greater St Lucia Wetland Park. These include: local extinction of animal species which would be important components of the system (eg. elephants); large-scale interference, through various actions, with the hydrology of the Lake and surrounds; military exercises such as missile testing; and, the focus of this study, the establishment of pine plantations on a large part of the secondary grassland.

Grassland that remained after establishment of pines was maintained by regular burning, but conditions changed for the remainder of the area the moment pine plantations were established. Keeping Sousa's (1984) descriptors of disturbance characteristics in mind, this study considered years of growth before clearfelling, number of rotations and time under each rotation to be factors making up the disturbance regime. The regimes of disturbance would then interact with physical factors such as topography, edaphic factors, micro-climate, altitude, hydrology and other factors associated with different spatial scales within Mfabeni. Only the edaphic factors were considered in this study. They would also interact with factors such as proximity of different vegetation types and the consequent availability of plant propagules.

Since amelioration of the effects of pine plantations occurs through the growth of an indigenous understorey, potential negative effects of pine plantations on indigenous trees, as reported by Struhsaker *et al.* (1989), would not be expected. The soils of the Zululand coastal plain are characteristically relatively deep and sandy, with clayey materials being relatively rare (Maud, 1991). Their high permeability and rapid leaching could also be an important factor in reducing the effects of the pines, as there would not be an opportunity for a build-up of acidity.

The direct relationship found between the species composition in pine and clearfelled areas and that of adjacent undisturbed vegetation is consistent with findings of other workers (Chapman and Chapman, 1996). Gleason (1917, 1926, 1927, 1939) took the position that the species that will occur on an available site are substantially a matter of probability depending on the availability of seed and favorable environment. Sturgess and Atkinson (1993) observed that the influence of adjacent vegetation was evident on the composition of establishing communities at some sites. They found that cleared land tended to take on the floristic

character of the nearest vegetation. This study clearly showed that the character of communities under pine plantations and in clearfelled areas was directly related to that of adjacent sites.

Sturges and Atkinson (1993) also found plant species composition was strongly correlated with the age of plantations and the time of felling, but there was no evidence of this on the Eastern Shores. Uhl *et al.* (1981) stated that there is a lack of detailed studies of succession in the lowland tropics and stressed the importance of such studies. Most approaches assume that age is the most important determinant of site floristics and structure, but Uhl *et al.* (1981) state that this may not be the case. They list factors such as type of disturbance (size, duration and seasonal occurrence), composition and seed-dispersal characteristics of the flora and type and abundance of seed-dispersal vectors which could be important. The lack of direct relationship between age of pine plantations and species composition supports Uhl *et al.* (1981). Early in the establishment of the plantations, there may have been observable differences, but they were not evident at the time of the study.

The increase in woody-species richness with time after clearfelling, or successional age does not contradict other workers. In their study on successional process after mining at Richards Bay Minerals, Mentis and Ellery (1994) found that plant species richness increased with time since disturbance, with no significant difference between mined and unmined areas.

Clearly, although trees are found in grassland on the Eastern Shores, succession has been inhibited, or kept as a 'fire climax' grassland by regular burning every three to five years (Blackmore, 1997, *pers comm.*; Conlong, 1986). Plantations facilitate succession but the rate of succession seems to be determined partly by the initial floristic composition (as determined by the seed bank and emerging woody species in grassland prior to planting of pines) and partly by the floristic composition of vegetation units within dispersal range of the plantation.

Matlack (1994a & b) recorded three processes that might impact on the severity and longevity of the effects of historical land use and the recovery from these effects:

- i) dispersal to the disturbed site, i.e. seed dispersal is a major controlling step or limitation;

- ii) ongoing disturbance which can inhibit establishment of forest plants;
- iii) extent of disturbance of soil, as sites within disturbed soil recover quicker than when soil is disturbed.

Tilman's (1982) resource-ratio hypothesis states that through successional time there is an increase in shade and soil nutrients, i.e. an inverse correlation between light availability and nutrient availability. Pine trees have been shown in this study not to significantly change fertility, but they do change light and moisture levels and the fire regime and, therefore, they change resource-ratios. Clearfelling should change the resource-ratios to more light and more nutrients (in the short-term) and less soil moisture (more direct sun) as a result of increased solar radiation and exposure to wind. Whitmore (1975) found that shade is required for successful establishment of seedlings of tropical forest trees therefore, clearfelling may cause a hiatus in the successional process, both through direct damage to trees and through changes in resource ratios.

Luken (1990) stated that it is likely that early stages of succession are more responsive to fertilisation than are later stages. Thus, the pulse of nutrients as a result of pine litter breakdown after clearfelling of plantations on the Eastern Shores (Blackmore, 1993) could have the effect of accelerating succession.

Sturgess and Atkinson (1993) found that woodland plant species, and not necessarily dune specialists, established under the pines, many of which were brought in by birds. In this case, the natural vegetation was not dune forest, but plants adapted to mobile and semi-fixed dunes, i.e. shifting sand. In the case of the Eastern Shores, dune forest is the natural vegetation. Pine stumps were found by Sturgess and Atkinson (1993) to remain intact for 20 years or more, but sometimes after seven to eight years they were sufficiently decomposed to be broken off and removed. On the Eastern Shores the oldest clearfelled site was six years old, and yet virtually all of the stumps in all of the clearfelled sites showed signs of fairly advanced dry rot and yielded to kicking.

Over 86 % of all woody species recorded in this study had fleshy fruit which may be eaten and disseminated by animals. This finding is consistent with other authors discussed in Chapter 1

(Hartshoorn, 1980; Howe, 1980; Uhl *et al.*, 1981; Daubenmire, 1968; Howe and Smallwood, 1982). The role of animal dispersal vectors is crucial to the colonisation of successional sites by many woody species, and tropical forest pioneer trees are widely dispersed by birds and bats (Hartshoorn, 1980). The seeds of the bulk of the tree species observed within the pine plantations are dispersed by frugivorous animals (Coates-Palgrave, 1977; Moll, 1992; Pooley, 1993; Ross, 1972). Animals observed in the pine plantations on the Eastern Shores during this study included kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*), grey duiker (*Sylvicapra grimmia*), samango monkeys (*Cercopithecus mitis*), hippopotamus (*Hippopotamus amphibius*) and waterbuck (*Kobus ellipsiprymnus*) (Skinner and Smithers, 1990). Among the frugivorous birds observed were trumpeter hornbills (*Bycanistes bucinator*), narina trogons (*Apaloderma narina*), purple-crested louries (*Tauraco porphyreolophus*), speckled mousebirds (*Colius striatus*) and black-eyed bulbuls (*Pycnonotus barbatus*) (Maclean, 1993).

The mere presence of pine trees as habitat and as roosting sites for animal vectors for the dispersal of propagules is another important factor to bear in mind. Daubenmire (1968) postulated that the presence of pioneer woody species often increases the rate of colonisation of a site by other woody species whose seeds are dispersed by animals and birds, since the pioneers render the site more attractive to dispersal vectors. The behaviour of the vectors is probably decisive (Hartshoorn, 1980; Howe, 1980; Uhl *et al.*, 1981; Brown and Archer, 1987, 1989).

This study indicated that the pine plantation does not necessarily have to be directly adjacent to indigenous forest for establishment of a well-developed indigenous understorey, but that it would have to be connected to the forest by an unbroken or nearly unbroken canopy. It is probable that many forest vertebrates do not enter open fields or clearings except on brief forays from surrounding forest (Finegan, 1984).

Luken (1990) found that planting or seeding of early-successional tree species does not necessarily guarantee that extended forest development will occur. If sites are well-isolated from forest communities, there may not be a sufficient supply of propagules to establish populations of late-successional trees. Therefore, it may be necessary to augment the propagule

pool of late-successional species at a later stage.

With the above in mind, there is a strong argument for the pines on the Eastern Shores to be considered a dune forest “nursery crop” which simultaneously results in the exclusion of fire, provision of shade and protection from desiccation for emerging forest plant species, and provision of habitat for frugiverous animals which would aid recruitment of plant species.

6.4 REHABILITATION OF MINED DUNES

Comparisons have been made by many people, between the rehabilitation efforts of Richards Bay Minerals and succession within the Mfabeni Section. In the Environmental Impact Assessment (1992) report into mining in the Kingsa/Tojan lease area of the Eastern Shores of Lake St Lucia, it was stated that it would be desirable to conduct the very study that is now being discussed, for the express purpose of understanding successional processes, should mining be allowed on the Eastern Shores. Thus, it is pertinent to compare the Richards Bay Minerals rehabilitation efforts with succession on the Eastern Shores. To an extent, these comparisons are valid, but there are some extremely important differences to keep in mind.

- i) The differences in the successional pathways, as well as differing localities of the Eastern Shores and Richards Bay (Lubke, Moll & Avis, 1992).
- ii) Dune mining implies the complete removal of the existing vegetation the stockpiling of the humus layer, the extraction of heavy minerals and the replacement of the sand tailings to be covered by the humus layer and revegetated (Weisser, 1978).
- iii) Mining through the centrifuge process and the removal of a number of mineral elements changes the particle size distributions as well as the potential for certain nutrients to be released from the soils following weathering. It also changes the topography to a certain extent (Gordon and MacDevette, 1989) as 10 % of the bulk is removed as heavy mineral slag and this will influence material availability for reshaping (Lubke, Moll and Avis, 1992).
- iv) The essential soil structure within the Mfabeni pine plantations has not been disturbed whereas at Richards Bay Minerals, the soil has mostly been placed back in a mixed, compacted, homogenous mass. Richards Bay Minerals does stockpile topsoil prior to

- mining, but does not always have enough to cover all mined areas, thus some areas are rehabilitated without the benefit of original topsoil (P. Camp, 1997, *pers. comm.*). Through stockpiling, the integrity of the topsoil that is available could be compromised (Hargis and Redente, 1984).
- v) Mining of the dunes results in complete destruction of all plants in the area with the exception of some hardy seeds which persist in stockpiled topsoil. Pine plantations, on the other hand, caused very little disturbance to what little dormant seed bank remains within the soil after regular burning, and were, most importantly, often planted adjacent to healthy indigenous dune forest. If mining were to occur on the Eastern Shores, this would mean that all of the vegetation in a 1 436 ha area would be removed (Lubke, Moll & Avis, 1992).
 - vi) After dune mining, a 'virtual moonscape' is the starting point for succession. This, therefore, requires the sowing of a quick growing, annual, nursery crop which aids the establishment of indigenous seedlings and assists with soil formation and stabilization. On the other hand, while pine plantations are growing, they act as a more permanent 'nursery crop' which can fundamentally alter the micro-climate of the area and encourage the growth of indigenous forest species germinating within them. In addition, they may act as a refuge for forest animal species who would transport indigenous plant propagules into the plantations either in dung or carried on their bodies (Hamilton, 1990; Archer and Pyke, 1991; Chapman and Chapman, 1996).
 - vii) After clearfelling of pines, the litter that remains breaks down to release nutrients (Blackmore, 1993) which may aid in promoting succession. Soil analyses performed as part of this study confirm this.
 - viii) The question has been asked whether the predominance of *Acacia karroo* trees at the Richards Bay Mineral site is a result of the harsh growing conditions (loss of soil structure, soil organic carbon and soil fertility; high solar radiation; no shelter from winds and resultant dessication) and whether these trees persist to the virtual exclusion of other tree species because they keep high levels of nitrogen within the soil which inhibits the growth of other species. It is not clear whether this factor has been adequately addressed. However, Weisser (1978) recorded that south of the Umfolozi River, the successional pathway involves predominantly *A. karroo* but further north it involves pioneer scrub. This is clearly the case on the Eastern Shores, since *A.*

- karroo* was virtually non-existent in most of the plantations and clearfelled sites. An additional factor which could count against establishment of the *A. karroo* is that they would probably not establish under the shady conditions created by the pine trees.
- ix) Lubke, Moll and Avis (1992) surmise that the presence of the *Acacia karroo* canopy at Richards Bay could be considered similar to the “climber choke” concept observed in Zululand by Weisser (1989). As in indigenous coastal forests, there is never a uniform cover of trees of the same age, and gap-phase replacement is an important process in “stable” forest communities. The different canopy height and regular spacing of pine trees within plantations possibly inhibits growth of saplings less than a closed, even-aged canopy of *A. karroo*.
 - x) Although there have been questions and studies on the effects of pine plantations on the hydrology of the Eastern Shores, the most dramatic effect they would have on hydrology would be to interrupt ground water flow by increased transpiration. On the other hand, dune mining has the potential to fundamentally alter hydrological regimes within the dune system (Comments by interested and affected parties - Natal Parks Board, 1982).
 - xi) It is possible that the area under the plantations could be restored to a “pristine” state, whereas there is insufficient evidence to indicate that post-mining succession could result in anything more than rehabilitation, ie. a partially restored state (Comments by interested and affected parties - Natal Parks Board, 1982).

Could pine plantations be used as a tool for rehabilitating these mined sites? Can this method be extended to other types of indigenous forest rehabilitation? These are possibilities, and worthy of further investigation.

6.5 RECOMMENDATIONS

It is recommended that the sites sampled in this project be monitored annually until at least the end of the clearfelling, and that as more plantation blocks are felled, these be sampled and added to the database. The study will then gradually evolve from a space-for-time substitution to a valuable real time study of plant succession.

Continuous eradication and follow-up removal of alien plants is essential, as in certain plantations guava (*Psidium guajava*) almost completely dominates the understory. Other aliens observed during this study, that need to be controlled, are triffid weed (*Chromolaena odorata*), prickly pear (*Opuntia ficus indica*), bugweed (*Solanum mauritianum*), and "Todds folly" (*Ageratum houstonianum*) (Arnold and de Wet, 1993; Bromilow, 1995).

Gordon and MacDevette (1989) suggest that if man-induced disturbance ceases once all pine plantations are felled, this will lead to a decrease in species richness of the dunes. They further suggest that techniques to cheaply disturb areas of dune forest need to be explored to manage species diversity. They suggest bombing with the chemical defoliant, Napalm, but possibly the more conservative imminent reintroduction of elephant will suffice. Giving local neighbours limited wood-cutting rights would also serve the same purpose.

For the maintenance of biodiversity, areas of grassland need to be maintained. This could be achieved by regular burning and limited wood-cutting in selected areas.

As a result of this study, the following broad suggestions are made, which could contribute to successful rehabilitation of degraded areas in general.

- i) The nature of the disturbance, extent of damage and probability for reoccurrence would have to be established and steps taken to either halt it, if it is ongoing, or reverse its effects so that natural colonisation, soil formation (if soil integrity has been partially or completely destroyed) and succession can take place.
- ii) Any kind of reclamation or rehabilitation project would have to begin with a benign non-aggressive, nursery species that would assist in recreating favourable soil, micro-habitat and micro-climatic conditions for re-establishment of indigenous successional species. It would be advantageous, from an economical point of view, for the nursery crop to have a commercial value on harvesting, or else it should be an annual species that will die off naturally and not require expensive control once it has fulfilled its function.
- iii) Exotic tree plantations should only be used to rehabilitate forest and not in areas that are naturally grassland or wetland. This is an extremely important point which cannot

- be overstated, as there is a danger that this study could be quoted in the wrong context to justify afforestation of inappropriate areas.
- iv) The proximity of intact seed sources would have to be investigated and the potential for natural seeding considered. If a suitable, natural seed source is within dispersal distance, measures should be taken to encourage animal or wind-dispersal in the degraded area, e.g. the provision of perches for birds, licks for antelope (with or without impregnated seeds) and nets to catch wind-borne seeds (Archer and Pyke, 1991).
 - v) If intact seed sources are not available, seed would have to be collected from areas with similar environmental conditions and a vegetation composition reflecting the desired endpoint. The seeds could then be mechanically sown (the expensive option), or embedded in licks or custom-made bird food (Archer and Pyke, 1991; McClanahan and Wolfe, 1993).
 - vi) To enhance dispersal by animals and birds, the trees should be planted in clumps which will serve as growth nuclei. Artificial perches could also be used to give birds time to “hydroseed” the area.
 - vii) Careful control of alien invaders should be an ongoing exercise (Blackmore, 1993).
 - viii) Monitoring of the process and data collection should be ongoing so that techniques can be refined over time.

6.6 FUTURE RESEARCH

As a result of this study, a number of other possible research projects have been identified.

- i) Although acid soils under coniferous forests preclude the presence of earthworms (*Lumbricus spp.*) which, in turn, would reduce populations of moles (Killham, 1994), there was much evidence of mole (*Chrysochloridae*) activity on the Eastern Shores. Within this study, there was no way to quantify the presence of moles or to say the population had either been reduced or was unaffected by the pine plantations.
- ii) Richards Bay Minerals could establish experimental pine plantations adjacent to unplanted sites, and those planted with *Cassuarina equisetifolia*, to compare the effects of the various post-mining rehabilitation options.

- iii) The viability of seeds in stockpiled topsoil of various depths and for various storage times could be investigated.
- iv) Identification of the important animal vectors responsible for recruitment of plant propagules within the pine plantations.
- v) Micro-meteorological studies of sites under various indigenous vegetation types and under pine plantations, to determine the conditions necessary for the establishment of indigenous forest species.
- vi) To establish whether the simple exclusion of fire and provision of perches for avian seed dispersers would be as effective as afforestation with exotic pines, one could select areas where experimental manipulation using fire and/or perches could be conducted. It has been recorded that in grassy areas of the Mfabeni Section which have been protected from fire, pioneer woody plants quickly invade (Taylor, 1995), and this has also been recorded in Kibale, Uganda (Chapman and Chapman, 1996).

6.7 CONCLUSIONS

Considering the available evidence, and information regarding forest succession in other areas, it is postulated that frugivorous bird, bat and antelope species pass through the pine plantations on the Eastern Shores *en route* to and from adjacent indigenous forests and drop seeds. Due to lack of competition from other tree species and the exclusion of fire, these establish quickly. Many smaller, early successional species produce more seed than a few late-successional species. Therefore, the food supply increases, more birds, bats and antelope visit the area and succession is accelerated further, until a point where plants start competing with one another and slower-growing, longer-lived species with better competitive adaptations start to dominate. On clearfelling, resource-ratios change, i.e. more light and nutrients, some species are inhibited and some species accelerate until their shade and the complete breakdown of pine litter changes ratios again.

To existing succession theory, the following thoughts are offered. Reclamation ecology, to a greater or lesser extent, will never fit into any of the models of succession constructed to date. Succession due to reclamation effort is neither purely autogenic nor allogenic, but driven by a deliberate, calculated effort to accelerate the successional process. It is a form of

anthropogenic succession, that is, succession driven by man but taking advantage of autogenic processes. Bearing in mind that natural succession does not necessarily follow a single pathway, man can facilitate natural succession in a number of ways.

- i) Recreation and stabilisation of a suitable growing substrate (soil) using fertilisation, nursery and/or pioneer species seeding mixtures, geofabrics and mulches. Pickett *et al.* (1987) refer to this as *designed disturbance*.
- ii) Artificial acceleration of succession (leap-frogging) by means of tree plantations or other nursery crops which could attract natural plant dispersers and inhibit ruderal and shade intolerant pioneer species. This effectively cuts out some of the seral stages. Pickett *et al.* (1987) refer to this as *controlled colonisation*.
- iii) Artificial mechanical planting/sowing and hydro seeding; and encouragement of seed dispersal by indigenous animals through provision of licks and seed impregnated foods - *controlled colonisation* and *controlled species performance* (Pickett *et al.*, 1987).
- iv) Seed 'trapping' by means of fine nets for wind-borne seeds or provision of perches and shelters for animal carriers - *controlled colonisation* (Pickett *et al.*, 1987).

Thus, man's efforts would confound such concepts as facilitation, tolerance or competition, although these factors could operate to an extent. Man's efforts could facilitate establishment of certain species and negate or remove competition from other species.

Luken (1990) records that much of what is known about succession can be traced to descriptive and experimental research on a few types of plant communities (e.g. old-fields, glacial moraines). Before succession management moves from the pages of journals or books to actual practice, more research on succession in anthropoeic communities must be done. Therefore, close interaction between ecologists and resource managers is needed.

The results of this study indicate that the presence of the pine plantations on the Eastern Shores of Lake St Lucia have facilitated the re-establishment of indigenous dune forest in areas that were previously secondary grassland. The factors that could have contributed to this re-establishment are exclusion of fire and creation of a favourable forest environment, i.e. shade, protection from wind, provision of a mulch in the form of pine litter, and an attractive habitat

for forest animals. In spite of pine litter being acidic, there did not appear to be inhibition of germination of indigenous seedlings. In the specialist report on rehabilitation ecology in the Environmental Impact Assessment into dune mining, Lubke, Moll and Avis (1992) predicted that rehabilitation after removal of pine plantations may take a long time. They recorded that it is likely that low light intensity and the acidic cushion of pine needles would possibly prevent indigenous species from becoming established. This study shows that the opposite is true.

In general, for exotic plantations to be considered as a management strategy for rehabilitation of indigenous forest, it must be demonstrated that indigenous tree species can become established under the plantations and that subsequent plantation harvesting will not destroy the potential for establishment of indigenous trees, or that the introduced species will not become invasive aliens, as do *Cassuarina equisetifolia* (Lubke, Moll and Avis, 1992). In this study, it was observed that the establishment of indigenous dune forest depended on the floristic composition of adjacent undisturbed land, and that the species composition within the pine plantation mirrored that outside, with the only major difference being size. Indigenous trees within the plantation generally showed the typical etiolated growth form of young trees within established indigenous forests which “wait” for gaps in the canopy to develop as older trees die.

In this study, conditions which favoured re-establishment of dune forest were: (i) creation of a forest environment by the pine plantations; (ii) a well established seed source and the presence of frugivorous birds, antelope and primates; (iii) the exclusion of fire; and a warm climate with high rainfall.

In conclusion, disturbance and successional theory can be useful as a means to manage plant communities and to steer them towards a desired goal, particularly where the integrity of the system has been compromised. Understanding of the successional processes occurring in undisturbed, natural conditions can assist in the monitoring of progress in anthropogenic succession. In this age of large-scale anthropogenic disturbance and the dwindling areas of undisturbed land, the understanding of these processes has become critical.

Thus, this study has direct relevance to future management of the Eastern Shores of Lake St Lucia, practical relevance to post-dune mining rehabilitation, and general relevance to rehabilitation of tropical secondary forests.

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APPENDICES

APPENDIX 1 SAMPLE PLOTS SORTED BY VEGETATION TYPE

SITE NO	SITE CODE	LATITUDE	LONGITUDE	DESCRIPTION	YRS 1ST ROT	YRS 2ND ROT	YRS SINCE FELLING	ADJACENT VEGETATION TYPE
19	B1x	28:06.914	32:29.294	Grass	0	0	0	Grass
35	B30x	28:11.404	32:28.313	Grass	0	0	0	Grass / Trees
6	A6x	28:09.714	32:31.364	Grass / Trees	0	0	0	Wetland & 2nd Rotation
16	A26x	28:11.887	32:30.273	Grass / Trees	0	0	0	Grass & Forest
21	B9x	28:07.714	32:28.906	Grass / Trees	0	0	0	Grass / Trees
23	B12x	28:08.825	32:28.577	Grass / Trees	0	0	0	Grass / Trees
29	B19x	28:07.056	32:30.584	Grass / Trees	0	0	0	Grass / Trees
31	B24x	28:09.420	32:29.610	Grass / Trees	0	0	0	Grass / Trees
33	B29x	28:09.910	32:29.470	Grass / Trees	0	0	0	Grass / Trees
2	A1x	28:09.159	32:32.066	Indigenous forest	0	0	0	Wetland & 2nd Rotation
8	A10x	28:10.719	32:30.790	Indigenous forest	0	0	0	Wetland & 2nd Rotation
10	A14x	28:11.028	32:31.832	Indigenous forest	0	0	0	Forest
13	A22x	28:11.915	32:31.370	Indigenous forest	0	0	0	Forest
38	C6ax	28:16.000	32:28.406	Indigenous forest	0	0	0	Wetland & 2nd Rotation
28	B19	28:07.056	32:30.584	1st Rotation Pine	13	0	0	Grass / Trees
30	B24	28:09.420	32:29.610	1st Rotation Pine	15	0	0	Grass / Trees
32	B29	28:09.910	32:29.470	1st Rotation Pine	16	0	0	Grass / Trees
34	B30	28:11.404	32:28.313	1st Rotation Pine	16	0	0	Grass / Trees
46	C23d-b	28:20.210	32:26.030	1st Rotation Pine	20	0	0	Grass / Trees
47	C23d-t	28:20.417	32:26.469	1st Rotation Pine	20	0	0	Forest
50	D6b	28:17.811	32:26.469	1st Rotation Pine	26	0	0	Pine Plantation / Grass
25	B14	28:08.977	32:29.093	1st Rotation Pine	33	0	0	Pine Plantation / Grass
27	B17	28:09.231	32:29.078	1st Rotation Pine	34	0	0	Pine Plantation / Grass
20	B9	28:07.714	32:28.906	1st Rotation Pine	35	0	0	Grass / Trees
26	B16	28:09.231	32:29.078	1st Rotation Pine	36	0	0	Pine Plantation / Grass
37	C6a	28:16.000	32:28.406	2nd Rotation Pine	30	5	0	Forest
1	A1	28:09.159	32:32.066	2nd Rotation Pine	31	8	0	Forest
17	A18	28:11.629	32:30.744	2nd Rotation Pine	23	9	0	Forest
12	A22	28:11.915	32:31.370	2nd Rotation Pine	28	9	0	Forest
4	A5	28:09.593	32:32.519	2nd Rotation Pine	30	9	0	Pine
9	A14	28:11.028	32:31.832	2nd Rotation Pine	29	10	0	Forest
7	A10	28:10.719	32:30.790	2nd Rotation Pine	35	10	0	Forest
5	A6	28:09.714	32:31.364	2nd Rotation Pine	28	11	0	Grass / Trees
45	C20	28:18.595	32:26.676	2nd Rotation Pine	20	14	0	Pine Plantation / Forest
18	B1	28:06.914	32:29.294	Clearfelled	32	0	0.1	Grass
49	D1d	28:17.622	32:26.697	Clearfelled	18	0	2	Grass / Trees
22	B12	28:08.825	32:28.577	Clearfelled	35	0	2	Grass / Trees
24	B13	28:08.997	32:28.845	Clearfelled	36	0	2	Grass / Trees
15	A26	28:11.887	32:30.273	Clearfelled	24	0	4	Grass & Forest
14	A25	26:11.629	32:30.868	Clearfelled	28	0	5	Forest
36	C4	28:15.286	32:29.056	Clearfelled	28	0	5	Pine Plantation / Forest
40	C8	28:16.694	32:28.324	Clearfelled	29	0	5	Pine Plantation / Forest
39	C7d	28:16.800	32:27.830	Clearfelled	30	0	5	Wetland & Forest
41	C12b	28:17.810	32:27.480	Clearfelled	34	0	5	Pine Plantation / Forest
42	C13a	28:17.560	32:26.820	Clearfelled	34	0	5	Pine Plantation / Forest
3	A4	28:09.593	32:32.519	Clearfelled	35	0	5	Pine
11	A19	28:11.028	32:31.832	Clearfelled	35	0	5	Forest
43	C15	28:18.595	32:26.676	Clearfelled	36	0	5	Pine Plantation / Forest
44	C15(2)	28:17.910	32:27.370	Clearfelled	36	0	5	Pine Plantation / Forest
48	D1a	28:17.515	32:26.909	Clearfelled	34	0	6	Grass / Trees

APPENDIX 2

MINIMUM AREA BLOCK C4

QUADRAT DIMENSIONS	QUADRAT AREA (M2)	SPECIES	ACCUMULATED	ACCUMULATED	ACCUMULATED
			TOTAL ALL SPECIES	HERBACEOUS SPECIES	WOODY SPECIES
0.5 x 0.5	0.25	<i>Cyperus albostrigatus</i>	1	1	X
		<i>Ipomoea sp.</i>	2	2	X
1.0 x 0.5	0.50	nil	2	2	X
1.0 x 1.0	1.00	<i>Senecio polyanthemoides</i>	3	3	X
		<i>Commelina africana</i>	4	4	X
		<i>Unidentified 1</i>	5	5	X
1.0 x 2.0	2.00	<i>Protasparagus virgata</i>	6	6	X
		<i>Phymatodes scolopendria</i>	7	7	X
		<i>Isoglossa sp.</i>	8	8	X
2.0 x 2.0	4.00	<i>Crassula expansa</i>	9	9	X
		<i>Cadaba natalensis</i>	10	10	X
		<i>Vernonia sp.</i>	11	11	X
		<i>Unidentified 2</i>	12	12	X
2.0 x 4.0	8.00	<i>Unidentified 3</i>	13	13	X
		<i>Secamone frutescens</i>	14	14	X
		<i>Trema orientalis</i>	15	X	1
		<i>Clerodendrum glabrum</i>	16	X	2
		<i>Unidentified 4</i>	17	15	X
		<i>Unidentified 5</i>	18	16	X
4.0 x 4.0	16.00	<i>Canthium spinosum</i>	19	X	3
		<i>Sapium intergerrimum</i>	20	X	4
		<i>Landolphia kirkii</i>	21	X	5
4.0 x 8.0	32.00	<i>Unidentified 6</i>	22	17	X
		<i>Desmodium incanum</i>	23	18	X
		<i>Helichrysum kraussii</i>	24	19	X
8.0 x 8.0	64.00	<i>Grewia occidentalis</i>	25	X	6
		<i>Helichrysum mixtum</i>	26	20	X
		<i>Mimusops caffra</i>	27	X	7
		<i>Solanum aculeatissimum</i>	28	X	8
		<i>Rhus pallens</i>	29	X	9
		<i>Albizia adianthifolia</i>	30	X	10
		<i>Acocanthera oppositifolia</i>	31	X	11
		<i>Tragia durbanensis</i>	32	21	X
8.0 x 16.0	128.00	<i>Cyperus obtusiflorus</i>	33	22	X
		<i>Lobelia pinifolia</i>	34	23	X
		<i>Juncus kraussii</i>	35	24	X
		<i>Dietes iridoides</i>	36	25	X
		<i>Tephrosia grandiflora</i>	37	26	X
		<i>Bidens pilosa</i>	38	27	X
		<i>Catunaregam spinosum</i>	39	X	12
16.0 x 16.0	256.00	<i>Desmodium setigerum</i>	40	28	X
		<i>Apodytes dimidiata</i>	41	X	13
		<i>Acalypha spp</i>	42	29	X
		<i>Asclepias physocarpa</i>	43	30	X
16.0 x 32.0	512.00	<i>Scutia myrtina</i>	44	X	14
		<i>Psychotria capensis</i>	45	X	15
		<i>Allophylus natalensis</i>	46	X	16
		<i>Pellaea viridis</i>	47	31	X
		<i>Canthium spp</i>	48	X	17
		<i>Phoenix reclinata</i>	49	X	18
		<i>Rothmania globosa</i>	50	X	19
		<i>Erythrina lysistemon</i>	51	X	20

QUADRAT DIMENSIONS	QUADRAT AREA (M2)	SPECIES	ACCUMULATED	ACCUMULATED	ACCUMULATED
			TOTAL	HERBACEOUS	WOODY
			ALL SPECIES	SPECIES	SPECIES
32.0 x 32.0	1024.00	<i>Senecio deltooides</i>	52	32	X
		<i>Garcinia livingstonia</i>	53	X	21
		<i>Smilax anceps</i>	54	33	X
		<i>Ozoroa obovata</i>	55	X	22
		<i>Antidesma venosum</i>	56	X	23
		<i>Eragrostis ciliaris</i>	57	34	X
		<i>Digitaria eriantha</i>	58	35	X
32.0 X 64.0	2048.00	<i>Brachylaena discolor</i>	59	X	24

AREA vs SPECIES

QUADRAT AREA	ACCUMULATED		
	ALL SPP	TREES	HERB
0.25	2	0	2
0.5	2	0	2
1	5	0	5
2	8	0	8
4	12	0	12
8	19	2	15
16	21	5	17
32	24	5	19
64	32	11	21
128	39	13	27
256	43	13	30
512	52	20	32
1024	58	23	35
2048	59	24	35

APPENDIX 3 LABORATORY ANALYTICAL METHODS FOR SOIL SAMPLES

All samples were air-dried and sieved through a 2 mm mesh and air-dried for at least 48 hours before being analysed. All results were expressed in terms of oven-dry mass which was calculated by drying the soil at 105° C and determining the air-dry water content as a percentage of oven-dried soil. This water content was recorded as moisture content and used to correct soil mass in later calculations.

Sources of error during the soil analysis process were largely due to the extremely high percentage sand and low percentage clay in the samples. For the particle size analysis, the size of the soil sample was increased five-fold in an attempt to reduce the percentage error.

A3.1 Particle size distribution

The pipette method was used to determine particle size distribution (Avery & Bascomb, 1974).

A 100 g soil sample was weighed into a beaker. The soil was dispersed using ultrasound for three minutes in the presence of 10.0 ml of Calgon (40.0 g sodium hexametaphosphate plus 9.1 g of sodium carbonate dissolved in one litre of hot water). A sample of 100 g, as opposed to the usual 20 g for this method, was used because it was found that with the extremely low clay and silt percentages in the soil, 20 g resulted in an unacceptably large percentage error.

Clay (< 0.002 mm) and silt (0.002 to 0.05 mm) fractions were determined by sedimentation and pipette sampling and expressed as a percentage of oven-dried soil (Rowell, 1994). The sand residue (> 0.05 mm) was decanted into a beaker, dried overnight at 105° C and passed through nested sieves. The proportion of coarse (2.0 to 0.5 mm), medium (0.5 to 0.25 mm), and fine (0.25 to 0.05 mm) sand was thus calculated. Particle size classes were according to Rowell (1994).

A3.2 pH

For each soil, two samples of 10 g each were massed and transferred to 50 ml plastic beakers.

The equilibrating solutions used were deionised water and 1 M KCl. In each case, the 10 g of soil was mixed with 25 ml of solution for 30 minutes, with occasional stirring. The pH of the resultant supernatant was read using a glass-calomel electrode pH meter (Rowell, 1994).

A3.3 Organic carbon

The oxidizable organic carbon fraction in the soil was determined using a wet oxidation technique (Walkley, 1935). A 1 g air-dry soil sample was ground to pass through a 0.5 mm screen and then digested in a potassium dichromate / sulphuric acid mixture in which the organic matter is oxidised. Soil organic carbon was then determined by back-titration of the excess dichromate, using a 0.5 M ferrous ammonium sulphate (FAS) solution.

A3.4 Exchangeable cations

A 2.5 g sample of <2 mm soil was weighed and transferred into 100 ml plastic centrifuge tubes. 25 ml of 0.1 M SrCl₂ solution was added to the tube. The tube was stoppered and shaken for 30 minutes on a reciprocal shaker. The samples were then centrifuged for four minutes and the supernatant filtered through 541 filter paper into 100ml volumetric flasks. For a further three times, 25 ml of SrCl₂ was added to the soil, the solution shaken for 15 minutes, centrifuged for four minutes and the supernatant filtered into the 100 ml volumetric flask. Once this process was complete, the volumetric flask was topped up with 0.1 M SrCl₂ to 100 ml. This solution was retained for Ca, Mg, Na and K analysis.

To the soil residue in the centrifuge tube, 25 ml of 70 % alcohol was added. The tube was stoppered and shaken on a reciprocal shaker for five minutes. The supernatant was discarded. For a further three times the residue was washed, shaken and centrifuged with 50 % alcohol.

A 25 ml aliquot of 1 M ammonium acetate was then added to the soil residue. The tube was stoppered and shaken for 30 minutes on a reciprocal shaker. The samples were then centrifuged for four minutes and the supernatant filtered through 541 filter paper into a second set of 100 ml volumetric flasks. For a further three times, 25 ml of 1 M ammonium acetate was added to the tube, the solution shaken for 15 minutes, centrifuged for four minutes and the supernatant filtered into the 100 ml volumetric flask. Once this process was complete, the

volumetric flask was topped up with 0.1 M ammonium acetate to 100 ml. This solution was retained for strontium analysis.

The filtrates were analysed as follows:

Calcium (Ca) and Magnesium (Mg): A 10 ml aliquot of undiluted supernatant were transferred to test tubes for spectroscopy. Standard solutions of 0.0, 1.0, 5.0 and 10.0 mg/l were used.

Sodium (Na): A 9 ml aliquot of supernatant was added to 1 ml potassium (KCl) suppressant in a test tube to make a concentration of 2000 ppm K. This was analysed using flame emission spectroscopy. Standard solutions of 0.0, 1.0, 5.0, 10.0 and 30.0 mg/l were used.

Potassium (K): A 9 ml aliquot of supernatant was added to 1 ml caesium (CsCl) suppressant in a test tube to make a concentration of 2000 ppm Cs. This was analysed using flame emission spectroscopy. Standard solutions of 0.0, 1.0, 5.0 and 10.0 mg/l were used.

All results were expressed in $\text{cmol}_c \text{kg}^{-1}$ soil.

The two methods of determining CEC are (i) to add the values obtained experimentally for the exchangeable bases (Ca, Mg, Na, K) plus exchangeable acidity, and (ii) to use the value for strontium obtained at the end of the analysis. The value for strontium was not used because it was considerably lower than that of the calculated CEC in the preliminary analysis. This could have occurred as a result of unavoidable loss of fine particles each time a sample being analysed was rinsed and the supernatant poured off. The calculated exchangeable acidity was extremely low in the initial analysis, therefore, the sum of bases (Ca, Mg, Na, K) was used as an indicator of cation exchange capacity.

A3.5 Exchangeable acidity

The method used involved the displacement of exchangeable and solution acidity (H^+ and Al^{3+} ions) and their determination by titration with a base. A 10 g soil sample was equilibrated with 50 ml of unbuffered 1 M potassium chloride (KCl) and centrifuged at 3000 rpm for two

minutes. The solution was filtered through a Whatman 541 filter paper. A 25 ml aliquot was titrated against a 0.001 M NaOH solution. A 25 ml aliquot of 1 M KCl served as a blank and was titrated first. Five drops of phenolphthalein was used as an indicator and the titration continued until the solution turned pink and stayed stable for at least 30 seconds. Exchangeable acidity is expressed in terms of $\text{cmol}_c \text{H}^+ \text{kg}^{-1}$ soil.

A3.6 Effective cation exchange capacity (ECEC)

The effective cation exchange capacity (ECEC) was calculated as the sum of the exchangeable cations plus the exchangeable acidity measured above.

A3.7 Extractable phosphorus

The molybdenum blue method (Avery and Bascomb, 1974) was used to determine extractable phosphate.

A 2.5 g soil sample was weighed into 100 ml conical flasks. A 5 ml aliquot of 1M ammonium bicarbonate solution was dispensed into each flask. The flasks were shaken on a reciprocal shaker for 15 minutes at 180 cycles per second. The extracts were then filtered through Whatman No. 541 filter paper into glass bottles.

A 2.0 ml aliquot of the extract was placed into a 50 ml beaker. To this was added 8 ml distilled water. Standard solutions of known concentrations were prepared in the same manner. To each beaker, 10 ml of colour reagent was added slowly, while swirling the solutions to mix them. During the process, the room temperature was kept at a constant 25°C . After 45 minutes the absorbance for each was read at 670 nm on a UV spectrophotometer.

From the absorbance values of the standard solutions, a standard curve was plotted. The value for each sample was compared to the standard curve, and the concentration of phosphorus in mg P/kg soil was calculated.

A3.8 Extractable iron and aluminium

Three different extraction procedures were used to provide a basis for an approximate differentiation of the forms of Fe, and Al in the soils.

Dithionite-citrate-bicarbonate (Mehra & Jackson, 1960) removes finely divided haematite and goethite, amorphous inorganic Fe and Al oxides and organic-complexed Fe and Al. It extracts Fe and Al from most silicate minerals only slightly. This procedure is often used to remove the sesquioxide coatings from soils and clays prior to X-ray analysis. It provides an estimate of “free” (non-silicate) Fe in soils, but sand-sized goethite and haematite are not dissolved completely, and magnetite is not dissolved.

Acid ammonium oxalate (Schwertmann, 1973) dissolves amorphous inorganic Fe and Al and organic complexed Fe and Al from soils. It attacks most silicate minerals and goethite and haematite only slightly, but it dissolves magnetite and finely divided, easily-weathered silicates such as olivine to a considerable extent.

Sodium pyrophosphate (Loveland & Digby, 1984) extracts organic-complexed Fe and Al from soils. It dissolves amorphous inorganic forms only slightly and silicate minerals and crystalline Fe and Al oxides are not attacked to any significant extent.

Thus, an estimate of three forms of Fe in soil can be made as follows:

- (a) Finely divided haematite and goethite: (dithionite Fe - oxalate Fe)
- (b) Amorphous inorganic Fe: (oxalate Fe - pyrophosphate Fe)
- (c) Organic complexed Fe: (pyrophosphate Fe)

Relationship (b) and (c) hold approximately for Al also. Aluminium in (a) is an indicator of Al-substitution in the Fe minerals.

Standard atomic absorption procedures were used. Standard solutions containing Fe and Al were prepared in a matrix of the extracting solution. An air-acetylene flame was used for the determination of Fe, and a nitrous-oxide acetylene flame was used for Al. Sodium at 2000ppm was used as suppressant.

A3.8.1 Dithionite

A 0.5 g sample of soil was weighed into a 15 ml test tube marked at 10 ml. To the sample was added 10 ml of sodium-citrate-bicarbonate solution. Approximately 0.2 g of Sodium dithionite ($\text{Na}_2\text{S}_2\text{O}_4$) was added. The solution was well mixed and the tube put into a water bath at 80°C for 15 minutes, stirring every two to three minutes.

After removal from the bath, 1 ml of saturated NaCl was added and the tube centrifuged for five minutes. The centrifugate was poured off into a 50 ml volumetric flask. The extraction procedure was repeated after loosening the soil with a vortex mixer.

The soil was then washed with 10 ml of citrate-bicarbonate buffer solution and 1 ml of saturated NaCl, and then centrifuged. The wash solution was then added to the volumetric flask.

The extract was made to volume with citrate-bicarbonate buffer. This solution was transferred into a test tube for iron and aluminium determinations.

A3.8.2 Sodium Pyrophosphate

A 1 g soil sample was added to a 125 ml capacity centrifuge tube. A 100 ml 0.1 mol/l sodium pyrophosphate solution was added to the soil and shaken overnight on a horizontal shaker. A 0.4 cm^3 superfloc solution was added and the tube was shaken and centrifuged at 2 000 rpm. The clear supernatant was transferred into a test tube for iron and aluminium determinations.

A3.8.3 Oxalate

A 0.25 g soil sample was weighed into a 15 ml centrifuge tube after which 10 ml of acid ammonium oxalate solution was added and the stoppered tubes placed in an end-over-end shaker and shaken for two hours in the dark. The tubes were centrifuged and the clear centrifugate decanted into another tube for the aluminium determination.

APPENDIX 4

A4.1 SOIL ANALYSIS SUMMARY - 1 Preliminary analysis (3-depths for 16 sites)

(Details of sites can be found in Appendix 1)

SAMPLE No. AND DEPTH	CLAY	SILT	SAND	ORG. C	MOIST.	pH (H ₂ O)	pH KCl	EXCH. P	EXCH. ACID.	EXCH. Ca	EXCH. Mg	EXCH. Na	EXCH. K	CEC	ECEC
	%	%	%	%	%			mg/kg	cmol.kg ⁻¹	cmol.kg ⁻¹	cmol.kg ⁻¹	cmol.kg ⁻¹	cmol.kg ⁻¹	cmol.kg ⁻¹	cmol.kg ⁻¹
1 A1:1-14 cm	0.373	1.437	98.190	0.80	0.403	5.83	4.19	12.70	0.25	0.81	0.40	0.32	0.09	0.91	1.87
2 A1:28-42 cm	0.849	1.910	97.241	0.48	0.353	5.83	4.74	2.34	0.04	0.97	0.59	0.29	0.03	0.98	1.91
3 A1:112-126 cm	1.170	2.340	96.490	0.08	0.308	6.21	4.98	0.73	0.03	0.70	0.38	0.31	0.04	0.80	1.46
4 A1X:1-14 cm	0.320	1.332	98.349	0.20	0.451	5.33	4.27	2.52	0.22	0.46	0.30	0.27	0.05	0.69	1.30
5 A1X:28-42 cm	1.011	1.596	97.393	0.20	0.314	5.14	4.54	3.24	0.04	0.34	0.25	0.30	0.06	0.66	1.00
6 A1X:112-126 cm	1.169	1.754	97.077	0.00	0.228	5.23	4.65	0.90	0.28	0.23	0.14	0.28	0.05	0.36	0.98
7 A4:1-14 cm	0.213	0.907	98.880	0.27	0.594	5.96	4.98	9.07	0.03	1.55	0.72	0.31	0.16	1.05	2.76
8 A4:28-42 cm	0.533	1.119	98.348	0.26	0.461	6.11	4.88	3.45	0.05	0.60	0.46	0.23	0.07	0.66	1.41
9 A4:112-126 cm	0.106	0.691	99.203	0.13	0.200	6.23	4.93	3.81	0.06	0.30	0.24	0.25	0.06	0.35	0.92
10 A5:1-14 cm	0.319	0.851	98.830	0.22	0.280	5.79	4.55	0.36	0.10	0.70	0.44	0.32	0.08	0.70	1.63
11 A5:28-42 cm	0.798	1.968	97.234	0.18	0.295	6.19	4.97	1.44	0.03	0.75	0.51	0.27	0.05	0.66	1.61
12 A5:112-126 cm	1.063	1.329	97.608	0.12	0.236	6.21	4.93	3.27	0.07	0.45	0.27	0.27	0.02	0.42	1.09
13 A25:1-14 cm	0.799	1.597	97.604	0.44	0.407	5.92	5.08	5.40	0.03	1.67	0.60	0.32	0.07	1.00	2.69
14 A25:28-42 cm	1.329	1.169	97.502	0.24	0.233	5.98	4.95	5.42	0.04	0.66	0.29	0.23	0.03	0.57	1.25
15 A25:112-126 cm	1.967	1.063	96.970	0.12	0.243	5.65	5.15	1.08	0.08	0.36	0.18	0.35	0.11	0.42	1.06
16 A26(2):1-14 cm	1.224	1.437	97.340	0.39	0.341	5.78	5.48	1.45	0.05	0.85	0.36	0.32	0.07	0.70	1.64
17 A26(2):28-42 cm	1.647	0.478	97.874	0.16	0.261	5.42	4.54	3.78	0.15	0.31	0.17	0.26	0.04	0.41	0.93
18 A26(2):112-126 cm	1.806	1.381	96.812	0.12	0.265	5.13	4.46	1.61	0.38	0.25	0.09	0.27	0.03	0.41	1.02
19 B9:1-14 cm	0.956	0.956	98.088	0.31	0.220	4.09	3.87	5.78	0.54	0.19	0.06	0.24	0.03	0.42	1.06
20 B9:28-42 cm	0.638	1.275	98.087	0.43	0.205	4.72	4.42	4.12	0.44	0.18	0.03	0.21	0.02	0.40	0.87
21 B9:112-126 cm	0.426	0.213	99.361	0.10	0.375	4.75	4.91	3.43	0.16	0.18	0.01	0.20	0.01	0.17	0.56
22 B9X:1-14 cm	0.319	0.585	99.095	0.42	0.382	4.97	4.27	0.18	0.17	0.45	0.20	0.30	0.07	0.57	1.19
23 B9X:28-42 cm	0.319	0.744	98.937	0.24	0.229	5.40	4.51	0.73	0.20	0.27	0.13	0.23	0.06	0.36	0.90
24 B9X:112-126 cm	1.329	0.585	98.086	0.16	0.327	5.30	4.81	1.99	0.24	0.21	0.06	0.22	0.02	0.38	0.74
25 B12:1-14 cm	0.532	0.957	98.511	0.63	0.317	4.38	3.74	6.27	0.40	0.42	0.19	0.25	0.04	0.66	1.29
26 B12:28-42 cm	0.956	0.584	98.459	0.15	0.202	4.83	4.24	4.16	0.40	0.23	0.07	0.21	0.04	0.30	0.95
27 B12:112-126 cm	1.331	1.011	97.658	0.16	0.394	4.77	4.79	0.54	0.29	0.20	0.03	0.22	0.31	0.37	1.05
28 B12X:1-14 cm	0.319	0.585	99.095	0.43	0.329	6.38	4.26	2.89	0.26	0.34	0.16	0.15	0.05	0.52	0.95
29 B12X:28-42 cm	0.532	0.585	98.884	0.27	0.259	5.55	4.69	1.45	0.23	0.31	0.12	0.22	0.05	0.33	0.93
30 B12X:112-126 cm	0.959	1.492	97.549	0.20	0.480	5.64	4.84	1.61	0.24	0.23	0.05	0.23	0.04	0.35	0.78
31 B13:1-14 cm	0.745	0.373	98.882	0.44	0.370	3.36	3.62	6.48	0.52	0.31	0.13	0.22	0.03	0.44	1.21
32 B13:28-42 cm	1.010	-0.479	99.468	0.08	0.271	4.68	4.41	3.98	0.38	0.24	0.07	0.27	0.03	0.36	0.98
33 B13:112-126 cm	0.850	-0.744	99.894	0.00	0.222	5.05	4.69	2.52	0.49	0.21	0.06	0.19	0.02	0.25	0.97
34 B14:1-14 cm	0.214	1.552	98.233	0.83	0.951	4.51	3.76	7.35	0.62	0.40	0.39	0.23	0.02	0.97	1.66
35 B14:28-42 cm	2.235	0.160	97.605	0.20	0.380	5.16	4.63	3.08	0.34	0.24	0.13	0.29	0.04	0.40	1.05

A4.2

SOIL ANALYSIS SUMMARY - 2 (Topsoil for 50 sites)

(Details of sites can be found in Appendix 1)

		C	P	Ca	Mg	Na	K	Sum of bases
	pH	%	mg/kg	cmolc/kg	cmolc/kg	cmolc/kg	cmolc/kg	cmolc/kg
A1	4.19	0.80	8.40	0.81	0.40	0.32	0.09	1.62
A1x	4.27	0.20	10.54	0.46	0.30	0.27	0.05	1.08
A4	4.98	0.27	12.68	1.55	0.72	0.31	0.16	2.74
A5	4.55	0.22	14.20	1.03	0.46	0.18	0.00	1.67
A6	4.17	0.27	2.14	0.34	0.13	0.17	0.00	0.64
A6x	3.93	0.31	1.99	0.29	0.13	0.16	0.01	0.59
A10	4.34	0.27	12.22	0.70	0.22	0.17	0.03	1.12
A10x	4.51	0.19	6.42	0.70	0.35	0.19	0.10	1.33
A14	4.33	1.34	6.57	1.34	1.05	0.21	0.07	2.67
A14x	4.85	0.25	3.06	2.06	1.19	0.24	0.13	3.62
A19	4.77	1.21	9.32	1.47	1.17	0.21	0.24	3.10
A22	4.61	0.12	9.62	1.09	0.77	0.24	0.06	2.17
A22x	5.52	0.92	5.50	2.66	1.19	0.17	0.01	4.03
A25	5.08	0.44	11.91	1.67	0.60	0.32	0.07	2.66
A26	3.26	1.34	26.12	0.57	0.24	0.18	0.01	1.00
A26x	4.03	0.12	8.86	0.49	0.27	0.14	0.06	0.96
A18	5.48	0.39	10.23	0.85	0.36	0.32	0.07	1.60
B1	3.69	0.13	6.11	0.22	0.09	0.15	0.00	0.47
B1x	4.33	0.35	10.69	0.62	0.25	0.22	0.01	1.10
B9	3.87	0.31	6.87	0.19	0.06	0.24	0.03	0.52
B12	3.74	0.42	8.71	0.45	0.20	0.30	0.07	1.03
B12x	4.26	0.63	7.79	0.42	0.19	0.25	0.04	0.89
B9x	4.27	0.43	10.08	0.34	0.16	0.15	0.05	0.69
B13	3.62	0.44	10.84	0.31	0.13	0.22	0.03	0.69
B14	3.76	0.82	3.67	0.40	0.39	0.23	0.02	1.04
B16	4.33	0.08	4.89	0.48	0.28	0.16	0.00	0.92
B17	4.42	0.36	11.30	0.61	0.48	0.16	0.03	1.29
B19	4.05	0.15	11.61	0.34	0.19	0.28	0.05	0.86
B19x	4.40	0.39	11.30	0.54	0.26	0.30	0.07	1.18
B24	4.70	0.12	9.16	0.60	0.34	0.18	0.00	1.11
B24x	4.65	0.31	10.08	0.70	0.25	0.17	0.03	1.15
B29	4.13	0.10	3.06	0.75	0.32	0.19	-0.01	1.25
B29x	4.63	0.47	2.16	0.88	0.40	0.18	0.07	1.53
B30	4.02	0.19	9.62	0.44	0.20	0.17	0.06	0.87
B30x	4.62	0.96	11.46	1.48	0.62	0.17	0.09	2.37
C4	4.01	0.76	13.90	0.60	0.30	0.16	0.06	1.13
C6a	3.48	0.42	3.36	0.38	0.22	0.18	0.02	0.79
C6ax	4.36	0.31	3.97	0.43	0.25	0.18	0.08	0.94
C7d	4.62	0.53	4.49	1.17	0.49	0.20	0.05	1.91
C8	4.82	0.44	11.46	0.73	0.42	0.15	0.04	1.35
C12b	4.56	0.00	2.70	0.51	0.25	0.20	0.07	1.04
C13a	3.15	2.93	12.04	1.06	0.57	0.18	0.00	1.81
C15	4.41	0.33	18.18	0.91	0.37	0.26	0.15	1.69
C15(2)	4.58	0.35	4.13	0.90	0.06	0.20	0.07	1.24
C20	4.46	0.52	11.61	1.34	0.51	0.27	0.02	2.14
C23d-b	3.90	4.95	28.93	0.83	0.87	0.50	0.04	2.24
C23d-t	4.51	0.08	6.29	0.87	0.63	0.23	0.01	1.74
D1a	4.31	0.16	11.76	1.34	0.51	0.27	0.02	2.14
D1d	3.86	0.50	15.43	0.48	0.19	0.14	0.00	0.82
D6b	3.63	0.67	12.83	0.23	0.16	0.18	0.02	0.58

APPENDIX 5

SOIL PARTICLE SIZES

SAND FRACTION BREAKDOWN

SAMPLE #	% 2000-1000µm	% 1000-710µm	% 710-500µm	% 500-425µm	% 425-355µm	% 355-250µm	% 250-212	% 212-125µm	% 125-106µm	% 106-90µm	% 90-63µm	% 63-53µm	% coarse	% med.	% fine
A1:1-14 cm	0.001	0.233	1.677	4.633	10.757	41.906	21.808	12.086	1.767	1.360	0.624	0.335	1.911	57.296	37.980
A1:28-42 cm	0.001	0.099	1.745	4.372	10.595	41.247	20.421	13.115	1.931	1.532	0.498	0.216	1.845	56.214	37.713
A1:112-126 cm	0.022	0.042	1.287	4.362	14.484	31.715	20.359	14.920	1.936	2.785	1.305	0.543	1.351	50.561	41.848
A1X:1-14 cm	0.001	0.036	1.498	4.791	11.166	43.650	17.955	12.958	0.681	1.846	0.684	0.313	1.535	59.607	34.437
A1X:28-42 cm	0.000	0.088	1.560	4.862	10.475	41.622	19.793	13.926	1.358	1.698	0.497	0.284	1.648	56.959	37.556
A1X:112-126 cm	0.000	0.092	1.411	5.388	9.612	39.150	20.200	14.661	2.235	2.369	0.615	0.335	1.503	54.150	40.415
A4:1-14 cm	0.032	0.726	3.830	6.511	12.890	39.274	19.255	12.338	1.415	1.020	0.346	0.204	4.588	58.675	34.578
A4:28-42 cm	0.033	0.505	3.182	5.810	10.580	40.091	18.290	15.385	1.229	1.576	0.355	0.166	3.720	56.481	37.001
A4:112-126 cm	0.020	0.318	3.470	7.344	12.360	42.212	19.138	11.884	0.508	0.741	0.160	0.049	3.808	61.916	32.480
A5:1-14 cm	0.034	0.669	6.539	11.551	15.993	36.852	13.669	10.490	0.595	0.755	0.279	0.084	7.242	64.396	25.872
A5:28-42 cm	0.063	0.617	5.782	10.290	15.031	36.023	16.199	11.170	0.986	0.893	0.324	0.096	6.462	61.344	29.668
A5:112-126 cm	0.198	1.294	5.209	9.521	13.482	37.735	15.035	12.493	0.931	1.027	0.330	0.083	6.701	60.738	29.899
A25:1-14 cm	0.073	0.521	2.121	4.116	7.468	38.987	26.140	16.187	0.765	0.564	0.425	0.153	2.715	50.571	44.234
A25:28-42 cm	0.072	0.240	1.691	3.738	6.681	38.419	27.468	16.646	0.650	1.073	0.348	0.147	2.003	48.838	46.332
A25:112-126 cm	0.006	0.113	1.988	3.309	7.749	37.523	28.531	14.933	1.063	0.872	0.506	0.134	2.107	48.581	46.039
A18:1-14 cm	0.012	0.064	0.455	0.794	2.401	34.872	35.206	20.994	0.826	0.909	0.275	0.150	0.531	38.067	58.360
A18:28-42 cm	0.001	0.011	0.149	0.641	2.141	43.007	29.436	2.076	0.664	0.495	0.257	0.035	0.161	45.789	32.963
A18:112-126 cm	0.001	0.025	0.541	1.537	3.994	33.417	29.220	24.779	0.920	1.282	0.730	0.214	0.567	38.948	57.145
B9:1-14 cm	0.004	0.058	0.910	3.195	7.742	42.247	25.154	17.540	0.346	0.274	0.200	0.087	0.972	53.184	43.601
B9:28-42 cm	0.003	0.050	0.737	2.458	6.092	39.877	30.154	17.725	0.389	0.238	0.216	0.075	0.790	48.427	48.797
B9:112-126 cm	0.005	0.076	1.196	3.559	8.001	42.214	25.959	15.637	0.220	0.157	0.070	0.018	1.277	53.774	42.061
B9X:1-14 cm	0.303	0.244	0.399	1.052	4.234	39.069	33.169	18.976	0.320	0.205	0.175	0.095	0.946	44.355	52.940
B9X:28-42 cm	0.012	0.110	0.455	0.895	3.255	37.460	37.198	18.069	0.373	0.273	0.141	0.058	0.577	41.610	56.112
B9X:112-126 cm	0.009	0.019	0.248	1.114	4.155	35.464	35.956	19.485	0.388	0.291	0.145	0.043	0.276	40.733	56.308
B12:1-14 cm	0.133	0.344	2.415	5.032	10.561	38.656	25.413	13.887	0.547	0.398	0.183	0.085	2.892	54.249	40.513
B12:28-42 cm	0.009	0.170	2.020	3.668	8.541	39.518	26.060	16.696	0.534	0.333	0.214	0.074	2.199	51.727	43.911
B12:112-126 cm	0.011	0.177	2.597	5.280	9.290	34.369	25.732	17.153	0.550	0.556	0.270	0.117	2.785	48.939	44.378

SAMPLE #	% 2000-1000µm	% 1000-710µm	% 710-500µm	% 500-425µm	% 425-355µm	% 355-250µm	% 250-212	% 212-125µm	% 125-106µm	% 106-90µm	% 90-63µm	% 63-53µm	% coarse	% med.	% fine
B12X:1-14 cm	0.508	0.218	0.494	1.673	7.294	47.743	23.699	15.034	0.560	0.508	0.334	0.171	1.220	56.710	40.306
B12X:28-42 cm	0.050	0.225	0.537	0.958	4.571	37.920	29.460	22.400	0.620	0.559	0.403	0.163	0.812	43.449	53.605
B12X:112-126 cm	0.002	0.075	0.522	1.619	5.338	38.382	26.428	20.937	0.859	1.079	0.659	0.362	0.599	45.339	50.324
B13:1-14 cm	0.021	0.191	0.891	1.238	3.549	33.240	32.484	24.863	0.722	0.490	0.239	0.081	1.103	38.027	58.879
B13:28-42 cm	0.015	0.075	0.445	1.024	3.691	37.632	32.748	21.044	0.493	0.588	0.238	0.043	0.535	42.347	55.154
B13:112-126 cm	0.000	0.016	0.251	0.821	2.592	40.019	36.180	18.368	0.227 ?		0.128	0.012	0.267	43.432	54.915
B14:1-14 cm	0.141	0.998	3.129	5.355	8.679	39.510	25.516	11.825	0.468	0.500	0.190	0.122	4.268	53.544	38.621
B14:28-42 cm	0.055	0.426	2.931	4.991	8.258	42.251	23.218	13.730	0.384	0.329	0.174	0.039	3.412	55.500	37.874
B14:112-126 cm	0.154	0.707	3.012	3.772	7.700	35.471	26.323	15.937	0.393	0.429	0.191	0.044	3.873	46.943	43.317
B19:1-14 cm	0.031	0.279	0.762	1.179	2.563	23.093	36.872	31.479	0.698	0.571	0.171	0.061	1.072	26.835	69.852
B19:28-42 cm	0.011	0.118	0.975	1.539	2.960	25.955	35.741	29.015	0.705	0.417	0.181	0.047	1.104	30.454	66.106
B19:112-126 cm	0.029	0.117	0.935	1.577	3.172	27.022	38.656	24.375	0.437	0.387	0.164	0.028	1.081	31.771	64.047
B19X:1-14 cm	0.133	0.413	1.856	1.907	3.723	27.156	35.655	25.735	0.616	0.605	0.154	0.077	2.402	32.786	62.842
B19X:28-42 cm	0.017	0.351	1.885	1.871	3.549	26.580	34.871	26.737	0.626	0.639	0.159	0.059	2.253	32.000	63.091
B19X:112-126 cm	0.014	0.072	0.546	0.855	0.185	15.784	44.567	32.063	0.721	0.735	0.136	0.030	0.632	16.824	78.252
C15:1-14 cm	0.095	0.469	3.801	6.071	10.942	46.192	22.610	6.975	0.235	0.238	0.154	0.096	4.365	63.205	30.308
C15:28-42 cm	0.050	0.330	3.680	6.566	12.654	47.372	18.650	7.810	0.250	0.251	0.155	0.040	4.060	66.592	27.156
C15:112-126 cm	0.014	0.075	1.508	2.609	6.186	43.155	33.363	10.916	0.175	0.188	0.085	0.019	1.597	51.950	44.746
C20:1-14 cm	0.057	0.740	5.142	8.209	13.948	45.255	17.038	5.688	0.249	0.293	0.150	0.119	5.939	67.412	23.537
C20:28-42 cm	0.002	0.343	3.868	7.287	13.216	47.687	17.767	7.008	0.145	0.200	0.097	0.050	4.213	68.190	25.267
C20:112-126 cm	0.056	0.515	4.929	6.878	13.415	43.015	19.863	8.420	0.295	0.260	0.145	0.044	5.500	63.308	29.027
D1A:1-14 cm	0.010	0.055	0.597	1.343	3.604	37.866	34.123	19.257	0.457	0.607	0.289	0.062	0.662	42.813	54.795
D1A-2 m	0.022	0.062	1.105	2.470	6.014	40.934	31.760	14.138	0.481	0.629	0.234	0.055	1.189	49.418	47.297
D1A-3 m	0.029	0.130	1.344	3.098	6.471	44.761	24.738	15.136	0.555	0.700	0.322	0.057	1.503	54.330	41.508
D1A-3.8 m	0.001	0.086	0.940	2.161	4.483	38.311	32.637	17.256	0.861	0.782	0.288	0.070	1.027	44.955	51.894

APPENDIX 6

IRON AND ALUMINIUM

SAMPLE No.	DITHIONITE		PYROPHOSPHATE		OXYLATE	
	Fe %	Al %	Fe %	Al %	Fe %	Al %
1 A1:1-14 cm	2.50	0.69	0.67	0.80	0.05	0.10
2 A1:28-42 cm	3.81	0.83	0.77	0.72	0.11	0.16
3 A1:112-126 cm	2.18	0.65	0.99	0.89	0.13	0.24
4 A1X:1-14cm	1.91	0.66	0.95	0.66	0.02	0.04
5 A1X:28-42 cm	2.20	0.79	1.49	0.82	0.07	0.12
6 A1X:112-126 cm	1.78	0.66	1.43	0.77	0.08	0.12
7 A4:1-14 cm	2.18	0.51	0.58	0.35	0.07	0.07
8 A4:28-42 cm	2.42	0.75	0.77	0.42	0.07	0.08
9 A4:112-126 cm	2.20	0.53	0.55	0.23	0.05	0.08
10 A5:1-14 cm	2.23	0.58	0.53	0.21	0.06	0.05
11 A5:28-42 cm	2.11	0.52	0.62	0.51	0.07	0.09
12 A5:112-126 cm	2.00	0.59	0.64	0.28	0.12	0.19
13 A25:1-14 cm	1.36	0.46	0.49	0.12	0.09	0.19
14 A25:28-42 cm	1.73	0.47	0.83	0.41	0.07	0.11
15 A25:112-126 cm	2.47	0.69	1.24	0.70	0.11	0.22
16 A18:1-14 cm	1.73	0.61	0.50	0.37	0.05	0.12
17 A18:28-42 cm	1.48	0.53	0.74	0.59	0.09	0.19
18 A18:112-126 cm	2.13	0.54	0.83	0.90	0.08	0.20
19 B9:1-14 cm	0.20	0.33	0.32	0.68	0.01	0.08
20 B9:28-42 cm	0.11	0.37	0.13	0.72	0.02	0.07
21 B9:112-126 cm	0.48	0.76	0.31	1.83	0.00	0.12
22 B9X:1-14 cm	0.78	0.46	0.37	0.56	0.05	0.11
23 B9X:28-42 cm	0.83	0.45	0.64	1.08	0.02	0.05
24 B9X:112-126 cm	0.90	0.77	0.74	1.64	0.03	0.13
25 B12:1-14 cm	0.48	0.50	0.33	0.62	0.01	0.04
26 B12:28-42 cm	0.34	0.69	0.33	0.76	0.02	0.12
27 B12:112-126 cm	0.64	0.94	0.84	1.73	0.04	0.13
28 B12X:1-14 cm	0.30	0.60	0.31	0.62	0.02	0.05
29 B12X:28-42 cm	0.14	0.69	0.13	0.71	0.02	0.09
30 B12X:112-126 cm	0.25	1.73	0.26	1.82	0.04	0.15

SAMPLE No.	DITHIONITE		PYROPHOSPATE		OXYLATE	
	Fe %	Al %	Fe %	Al %	Fe %	Al %
31 B13:1-14 cm	1.17	0.85	0.43	0.58	0.05	0.07
32 B13:28-42 cm	1.58	0.96	0.65	0.77	0.08	0.18
33 B13:112-126 cm	1.88	0.99	0.37	0.44	0.05	0.10
34 B14:1-14 cm	1.51	1.09	1.28	0.65	0.04	0.14
35 B14:28-42 cm	1.93	1.38	0.71	0.67	0.10	0.32
36 B14:112-126 cm	3.66	1.48	0.13	0.22	0.00	0.02
37 B19:1-14 cm	2.15	1.30	0.38	0.43	0.05	0.09
38 B19:28-42 cm	1.73	1.36	0.41	0.80	0.24	0.33
39 B19:112-126 cm	2.58	1.91	0.74	0.91	0.10	0.25
40 B19X:1-14 cm	2.10	0.45	0.39	0.90	0.02	0.03
41 B19X:28-42 cm	2.72	0.54	0.52	0.71	0.03	0.06
42 B19X:112-126 cm	2.65	0.41	0.52	0.97	0.07	0.17
43 C15:1-14 cm	1.08	0.45	0.42	1.09	0.03	0.05
44 C15:28-42 cm	1.34	0.41	0.73	1.00	0.06	0.15
45 C15:112-126 cm	1.30	0.48	0.63	1.44	0.05	0.12
46 C20:1-14 cm	1.02	0.54	0.63	0.97	0.03	0.10
47 C20:28-42 cm	0.96	0.75	0.53	0.60	0.03	0.12
48 C20:112-126 cm	0.39	0.91	0.23	0.85	0.02	0.17
49 D1A-1m	0.90	1.00	0.41	0.55	0.01	0.03
50 D1A-2m	0.96	0.98	0.40	0.79	0.02	0.09
51 D1A-3m	0.65	1.23	0.29	0.76	0.03	0.17
52 D1A-3.8m	0.40	1.11	0.17	0.65	0.04	0.20

APPENDIX 8

WOODY SPECIES LIST

	ABBREVIATION	WOODY SPECIES	DISPERSAL MECHANISM	ANIMAL
1	Acackar	<i>Acacia karroo</i>	Pod browsed by antelope	Y
2	Acacmea	<i>Acacia mearnsii</i>	Pod browsed by antelope	Y
3	Acokopp	<i>Acokanthera oppositifolia</i>	Fleshy fruit eaten by birds & bats	Y
4	Adengum	<i>Adenia gummifera</i>	Fleshy fruit	Y
5	Albiadi	<i>Albizia adianthifolia</i>	Pod browsed by antelope	Y
6	Allonat	<i>Allophylus natalansis</i>	Fleshy fruit eaten by birds & bats	Y
7	Aloethr	<i>Aloe thraskii</i>	Birds	N
8	Anismik	<i>Anisochaeta mikanioides</i>	?	N
9	Annosen	<i>Annona senegalensis</i>	Fleshy fruit - monkeys, antelope	Y
10	Antiven	<i>Antidesma venosum</i>	Fleshy fruit - birds & monkeys	Y
11	Apoddim	<i>Apodytes dimidiata</i>	Fleshy fruit - birds & bats	Y
12	Bersluc	<i>Bersama lucens</i>	Fleshy fruit - birds, monkeys & bats	Y
13	Bracdis	<i>Brachylaena discolor</i>	Nutlet with bristly hairs - adheres to animals	Y
14	Bridcat	<i>Bridelia cathartica</i>	Fleshy fruit - birds & monkeys	Y
15	Bridmic	<i>Bridelia micrantha</i>	Fleshy fruit - birds & monkeys	Y
16	Burbub	<i>Burchellia bubalina</i>	Fleshy fruit - birds	Y
17	C23dBig	<i>C23d-t/YY-Big tree</i>	?	N
18	Cantcil	<i>Canthium ciliatum</i>	Fleshy fruit - birds & monkeys	Y
19	Cantine	<i>Canthium inerme</i>	Fleshy fruit - birds & monkeys	Y
20	Cantvan	<i>Canthium vanwykii</i>	Fleshy fruit - birds & monkeys	Y
21	Captom	<i>Capparis tomentosa</i>	Fleshy fruit - monkeys, antelope & bushpig	Y
22	Caribis	<i>Carissa bispinosa</i>	Fleshy fruit - birds & monkeys	Y
23	Carimac	<i>Carissa macrocarpa</i>	Fleshy fruit - birds & monkeys	Y
24	Casspap	<i>Cassine papillosa</i>	Fleshy fruit - birds & monkeys	Y
25	Catuspi	<i>Catunaregam spinosa</i>	Fleshy fruit - monkeys	Y
26	Celtafr	<i>Celtis africana</i>	Fleshy fruit - birds & monkeys	Y
27	Chroodo	<i>Chromolaena odorata</i>	Wind dispersed	N
28	Chrymon	<i>Chrysanthemoides monilifera</i>	Fleshy fruit - birds & monkeys	Y

	ABBREVIATION	WOODY SPECIES	DISPERSAL MECHANISM	ANIMAL
29	Clauani	<i>Clausena anisata</i>	Fleshy fruit - birds	Y
30	Clergla	<i>Clerodendrum glabrum</i>	Fleshy fruit - birds	Y
31	Commwoo	<i>Commiphora woodii</i>	Hard fruit - birds especially parrots	Y
32	Crotsyl	<i>Croton sylvaticus</i>	Fleshy fruit - monkeys, birds, antelope & bushpig	Y
33	Cussspi	<i>Cussonia spicata</i>	Fleshy fruit - birds	Y
34	Dalbarm	<i>Dalbergia armata</i>	Pod - wind dispersed & browsed by antelope	Y
35	Dichcin	<i>Dichrostachys cinerea</i>	Pod browsed by antelope	Y
36	Diosdic	<i>Diospyros dichrophylla</i>	Fleshy fruit	Y
37	Diosinh	<i>Diospyros inhacaensis</i>	Fleshy fruit	Y
38	Dioslyc	<i>Diospyros lyciodes</i>	Fleshy fruit - birds, dogs (jackal?)	Y
39	Diossca	<i>Diospyros scabrida</i>	Fleshy fruit - birds	Y
40	Diossim	<i>Diospyros simii</i>	Fleshy fruit	Y
41	Diovill	<i>Diospyros villosa</i>	Fleshy fruit	Y
42	Dodoang	<i>Dodonaea angustifolia</i>	Capsule with wings - wind dispersed	N
43	Dovyluc	<i>Dovyalis lucida</i>	Fleshy fruit	Y
44	Drypnat	<i>Drypetes natalensis</i>	Fleshy fruit - monkeys	Y
45	Ekebcap	<i>Ekebergia capensis</i>	Fleshy fruit - birds & monkeys	Y
46	Eriopso	<i>Eriosema psoraleoides</i>	?	N
47	Erytlys	<i>Erythrina lysistemon</i>	Fleshy fruit - birds & monkeys	Y
48	Erytdel	<i>Erythroxylum delagoense</i>	Fleshy fruit	Y
49	Erytema	<i>Erythroxylum emarginatum</i>	Fleshy fruit	Y
50	Eucleri	<i>Euclea crispa</i>	Small, hard fruit - birds, rats, mongoose, antelope	Y
51	Eucldiv	<i>Euclea divinorum</i>	Small, hard fruit - birds	Y
52	Euclnat	<i>Euclea natalensis</i>	Fleshy fruit - birds & monkeys	Y
53	Euclrac	<i>Euclea racemosa</i>	Fleshy fruit - birds	Y
54	Eugecap	<i>Eugenia capensis</i>	Fleshy fruit	Y
55	Eugeery	<i>Eugenia erythrophylla</i>	Fleshy fruit - birds & genets	Y
56	Eugemos	<i>Eugenia mossambicensis</i>	Fleshy fruit	Y
57	Eugenat	<i>Eugenia natalita</i>	Fleshy fruit - birds	Y
58	Eugewoo	<i>Eugenia woodii</i>	Fleshy fruit	Y
59	Ficubur	<i>Ficus burtt-davyi</i>	Fleshy fruit - birds	Y

	ABBREVIATION	WOODY SPECIES	DISPERSAL MECHANISM	ANIMAL
60	Ficunat	<i>Ficus natalensis</i>	Fleshy fruit - birds, fruit bats & antelope	Y
61	Ficutri	<i>Ficus trichopoda</i>	Fleshy fruit - birds	Y
62	Garcliv	<i>Garcinia livingstonei</i>	Fleshy fruit	Y
63	Gardthu	<i>Gardenia thunbergia</i>	Fleshy fruit - antelope	Y
64	Grewlas	<i>Grewia lasiocarpa</i>	Fleshy fruit	Y
65	Grewmic	<i>Grewia microthyrsa</i>	Fleshy fruit - birds & mammals	Y
66	Grewocc	<i>Grewia occidentalis</i>	Fleshy fruit - birds & mammals	Y
67	Hibitil	<i>Hibiscus tiliaceus</i>	Fleshy fruit	Y
68	Hypeamo	<i>Hyperacanthus amoenus</i>	Fleshy fruit - birds & monkeys	Y
69	Jatrvar	<i>Jatropha variifolia</i>	?	N
70	Krauflo	<i>Kraussia floribunda</i>	Fleshy fruit - birds & monkeys	Y
71	Landkir	<i>Landolphia kirkii</i>	Fleshy fruit - monkeys & antelope	Y
72	Macacap	<i>Macaranga capensis</i>	Capsule, hard seed - birds	Y
73	Manidis	<i>Manilkara discolor</i>	Fleshy fruit - birds & animals	Y
74	Maytund	<i>Maytenus undata</i>	Fleshy fruit	Y
75	Mimucaf	<i>Mimusops caffra</i>	Fleshy fruit - birds & monkeys	Y
76	Monacaf	<i>Monanthes caffra</i>	Fleshy fruit	Y
77	Monojun	<i>Monodora junodii</i>	Fleshy fruit	Y
78	Nectzul	<i>Nectaropetalum zuluense</i>	Fleshy fruit	Y
79	Nuxicon	<i>Nuxia congesta</i>	Small, hairy capsule	N
80	Ochnarb	<i>Ochna arborea</i>	Fleshy fruit - monkeys	Y
81	Onciten	<i>Oncinotis tenuiloba</i>	?	N
82	Opunfic	<i>Opuntia ficus-indica</i>	Fleshy fruit	Y
83	Ozoreng	<i>Ozoroa engleri</i>	Fleshy fruit	Y
84	Ozorobo	<i>Ozoroa obovata</i>	Fleshy fruit - birds, esp. hornbills	Y
85	Ozorsph	<i>Ozoroa sphaerocarpa</i>	Fleshy fruit	Y
86	Passrig	<i>Passerina rigida</i>	Small fruit	N
87	Pavecoo	<i>Pavetta cooperi</i>	Fleshy fruit	Y
88	Peddafr	<i>Peddiea africana</i>	Fleshy fruit - birds	Y
89	Phoerec	<i>Phoenix reclinata</i>	Fleshy fruit - birds & monkeys	Y
90	Phylret	<i>Phyllanthus reticulatus</i>	Fleshy fruit - birds, monkeys & antelope	Y

	ABBREVIATION	WOODY SPECIES	DISPERSAL MECHANISM	ANIMAL
91	Pinus	<i>Pinus elliotii</i>	Hard seed - birds	Y
92	Pleucap	<i>Pleurostyliia capensis</i>	Fleshy fruit	Y
93	Polymyr	<i>Polygala myrtifolia</i>	Winged fruit - wind	N
94	Psidcat	<i>Psidium cattleianum</i>	Fleshy fruit - birds, monkeys & antelope	Y
95	Psidgua	<i>Psidium guajava</i>	Fleshy fruit - birds, monkeys & antelope	Y
96	Psyccap	<i>Psychotria capensis</i>	Fleshy fruit - birds	Y
97	Ptelmyr	<i>Pteleopsis myrtifolia</i>	Winged fruit - wind	N
98	Rapamel	<i>Rapanea melanophloeos</i>	Fleshy fruit - birds, monkeys & bushpig	Y
99	Rauvcaf	<i>Rauvolfia caffra</i>	Fleshy fruit - birds, monkeys & bushbabies	Y
100	Rawsluc	<i>Rawsonia lucida</i>	Fleshy fruit	Y
101	Rhoidig	<i>Rhoicissus digitata</i>	Fleshy fruit - birds	Y
102	Rhoirev	<i>Rhoicissus revoilii</i>	Fleshy fruit - birds	Y
103	Rhoitri	<i>Rhoicissus tridentata</i>	Fleshy fruit - birds	Y
104	Rhuschi	<i>Rhus chirindensis</i>	Fleshy fruit - birds & monkeys	Y
105	Rhusden	<i>Rhus dentata</i>	Fleshy fruit - birds	Y
106	Rhusnat	<i>Rhus natalensis</i>	Fleshy fruit	Y
107	Rhusneb	<i>Rhus nebulosa</i>	Fleshy fruit	Y
108	Rhuspal	<i>Rhus pallens</i>	Fleshy fruit	Y
109	Rhuspyr	<i>Rhus pyroides</i>	Fleshy fruit - birds	Y
110	Salakra	<i>Salacia kraussii</i>	Fleshy fruit	Y
111	Sapiint	<i>Sapium integerrimum</i>	Fleshy fruit - birds & antelope	Y
112	Schrala	<i>Schrebera alata</i>	Winged seeds - wind dispersed	Y
113	Sclebir	<i>Sclerocarya birrea</i>	Fleshy fruit - birds, monkeys, antelope & bushpig	Y
114	Scutmyr	<i>Scutia myrtina</i>	Fleshy fruit - birds	Y
115	Sennpet	<i>Senna petersiana</i>	Fleshy fruit - birds & monkeys	Y
116	Sideine	<i>Sideroxylon inerme</i>	Fleshy fruit - birds, bats, monkeys & bushpig	Y
117	Solaacu	<i>Solanum aculeastrum</i>	Fleshy fruit	Y
118	Solamau	<i>Solanum mauritianum</i>	Fleshy fruit - birds	Y
119	Strenic	<i>Strelitzia nicolai</i>	Seed with woolly aril - birds & monkeys	Y
120	Strymad	<i>Strychnos madagascariensis</i>	Fleshy fruit - monkeys & antelope	Y
121	Strymit	<i>Strychnos mitis</i>	Fleshy fruit - birds & monkeys	Y

	ABBREVIATION	WOODY SPECIES	DISPERSAL MECHANISM	ANIMAL
122	Stryspi	<i>Strychnos spinosa</i>	Fleshy fruit - birds, monkeys	Y
123	Stryusa	<i>Strychnos usambarensis</i>	Fleshy fruit - birds	Y
124	Synakir	<i>Synaptolepis kirkii</i>	?	N
125	Szyzycor	<i>Syzygium cordatum</i>	Fleshy fruit - birds, monkeys & bushpig	Y
126	Tacaapi	<i>Tacazzea apiculata</i>	?	N
127	Tarelit	<i>Tarenna littoralis</i>	Fleshy fruit - birds	Y
128	Tarepav	<i>Tarenna pavettoides</i>	Fleshy fruit	Y
129	Teclger	<i>Teclea gerrardii</i>	Fleshy fruit - birds, monkeys	Y
130	Tecocap	<i>Tecomaria capensis</i>	?	N
131	Tremori	<i>Trema orientalis</i>	Fleshy fruit - birds & fruit bats	Y
132	Triccap	<i>Tricalysia capensis</i>	Fleshy fruit	Y
133	Triclan	<i>Tricalysia lanceolata</i>	Fleshy fruit - birds	Y
134	Tricson	<i>Tricalysia sonderiana</i>	Fleshy fruit - birds	Y
135	Urertri	<i>Urera trinervis</i>	Small nut - birds ?	Y
136	Uvarcaf	<i>Uvaria caffra</i>	Fleshy fruit - monkeys	Y
137	Vanginf	<i>Vangueria infausta</i>	Fleshy fruit - birds, monkeys, antelope, tortoises	Y
138	Veprlan	<i>Vepris lanceolata</i>	Fleshy fruit - birds	Y
139	Veprref	<i>Vepris reflexa</i>	Fleshy fruit - birds	Y
140	Vernang	<i>Vernonia angulifolia</i>	Wind dispersed	N
141	Xylokra	<i>Xylothea kraussiana</i>	Woody capsule - birds	Y
142	Zantcap	<i>Zanthoxylum capense</i>	Fleshy fruit - birds	Y
143	Zizimuc	<i>Ziziphus mucronata</i>	Fleshy fruit - birds, mammals, rats	Y

Animal dispersed > 8.9%

Arnold and de Wet (1993); Coates-Palgrave (1977); Hennesy (1974); Moll (1992); Pooley (1993); Ross (1972); Walker (1996); van Wyk and Smith (1996).

APPENDIX 12 SPECIES RICHNESS AND EVENNESS - WOODY AND HERBACEOUS

SITE NO	SITE CODE	DESCRIPTION	ADJACENT VEGETATION	WOODY			HERBACEOUS		
				INDEX	EVENNESS	No. OF SPECIES	INDEX	EVENNESS	No. OF SPECIES
1	A1	2nd Rotation Pine	Forest	2.59	0.75	32	2.50	0.9	16
2	A1x	Indigenous forest	Wetland & 2nd Rotation	2.69	0.74	38	2.88	0.92	23
3	A4	Clearfelled	Pine	3.00	0.89	29	2.66	0.89	20
4	A5	2nd Rotation Pine	Pine	1.57	0.55	17	2.73	0.91	20
5	A6	2nd Rotation Pine	Grass / Trees	2.07	0.70	19	1.98	0.86	10
6	A6X	Grass / Trees	Wetland & 2nd Rotation	1.93	0.66	19	3.01	0.91	27
7	A10	2nd Rotation Pine	Forest	2.68	0.80	29	2.41	0.91	14
8	A10x	Indigenous forest	Wetland & 2nd Rotation	2.96	0.78	44	2.59	0.91	17
9	A14	2nd Rotation Pine	Forest	2.56	0.83	22	2.29	0.87	14
10	A14x	Indigenous forest	Forest	3.17	0.89	36	2.69	0.92	19
11	A19	Clearfelled	Forest	2.35	0.77	21	2.73	0.93	19
12	A22	2nd Rotation Pine	Forest	2.41	0.71	30	2.95	0.93	24
13	A22x	Indigenous forest	Forest	2.90	0.85	30	2.16	0.90	11
14	A25	Clearfelled	Forest	2.23	0.80	16	3.39	0.93	38
15	A26	Clearfelled	Grass & Forest	1.49	0.62	11	2.61	0.90	18
16	A26x	Grass / Trees	Grass & Forest	0.69	1.00	2	2.94	0.93	24
17	A18	2nd Rotation Pine	Forest	2.12	0.75	17	3.05	0.95	25
18	B1	Clearfelled	Grass	1.68	0.81	8	1.04	0.95	3
19	B1x	Grass	Grass	0.00	0.00	0	2.74	0.90	21
20	B9	1st Rotation Pine	Grass / Trees	0.45	0.65	2	0.45	0.65	2
21	B9x	Grass / Trees	Grass / Trees	0.00	0.00	0	2.72	0.89	21
22	B12	Clearfelled	Grass / Trees	0.92	0.51	6	1.69	0.87	7
23	B12x	Grass / Trees	Grass / Trees	0.00	0.00	0	2.57	0.91	17
24	B13	Clearfelled	Grass / Trees	0.60	0.37	5	1.99	0.86	10
25	B14	1st Rotation Pine	Pine Plantation / Grass	0.00	0.00	0	0.66	0.95	2
26	B16	1st Rotation Pine	Pine Plantation / Grass	2.11	0.82	13	0.00	0.00	1
27	B17	1st Rotation Pine	Pine Plantation / Grass	2.25	0.81	16	1.95	0.85	10
28	B19	1st Rotation Pine	Grass / Trees	2.27	0.77	19	1.39	1.00	4
29	B19x	Grass / Trees	Grass / Trees	2.07	0.72	18	2.72	0.89	21
30	B24	1st Rotation Pine	Grass / Trees	2.14	0.86	12	1.49	0.93	5
31	B24x	Grass / Trees	Grass / Trees	1.47	0.71	8	3.18	0.93	30
32	B29	1st Rotation Pine	Grass / Trees	1.51	0.61	12	1.80	0.87	8
33	B29x	Grass / Trees	Grass / Trees	2.04	0.82	12	2.72	0.92	19
34	B30	1st Rotation Pine	Grass / Trees	0.69	1.00	2	0.69	1.00	2
35	B30x	Grass	Grass / Trees	0.00	0.00	0	2.62	0.91	18
36	C4	Clearfelled	Pine Plantation / Forest	2.38	0.72	28	3.11	0.92	30
37	C6a	2nd Rotation Pine	Forest	2.23	0.76	19	2.30	0.90	13
38	C6ax	Indigenous forest	Wetland & 2nd Rotation	1.54	0.86	6	2.19	0.91	11
39	C7d	Clearfelled	Wetland & Forest	2.09	0.66	24	2.68	0.93	18
40	C8	Clearfelled	Pine Plantation / Forest	1.91	0.70	15	1.94	0.88	9
41	C12b	Clearfelled	Pine Plantation / Forest	2.09	0.67	23	2.74	0.92	20
42	C13a	Clearfelled	Pine Plantation / Forest	2.15	0.84	13	2.49	0.92	15
43	C15	Clearfelled	Pine Plantation / Forest	3.00	0.83	38	2.56	0.90	17
44	C15(2)	Clearfelled	Pine Plantation / Forest	2.19	0.70	23	2.66	0.90	19
45	C20	2nd Rotation Pine	Pine Plantation / Forest	2.84	0.85	28	1.75	0.9	7
46	C23d-b	1st Rotation Pine	Grass / Trees	1.73	0.75	10	1.94	0.88	9
47	C23d-t	1st Rotation Pine	Forest	2.98	0.84	35	2.43	0.92	14
48	D1a	Clearfelled	Grass / Trees	2.44	0.83	19	2.73	0.91	20
49	D1d	Clearfelled	Grass / Trees	2.49	0.86	18	2.82	0.91	22
50	D6b	1st Rotation Pine	Pine Plantation / Grass	0.00	0.00	0	1.15	0.83	4

Note: Index = Shannon-Weaver Diversity Index (Zar, 1996)