REGENERATION FAILURE AND THE *ACACIA KARROO* SUCCESSIONAL PATHWAY IN COASTAL DUNE FORESTS IN KWAZULU-NATAL, SOUTH AFRICA

L.J. Boyes, M.J. Lawes and M.E. Griffiths
Forest Biodiversity Research Unit, School of Biological and Conservation Sciences
University of KwaZulu-Natal, Pietermaritzburg

Abstract

The *Acacia karroo* successional pathway is currently used to rehabilitate mined dunes near Richards Bay, South Africa. At Cape Vidal, however, relatively low forest tree diversity and slow natural regeneration of coastal dune forests in areas dominated by *A. karroo* has cast doubt on the efficacy of this restoration strategy. Three hypotheses have been proposed to explain the relatively slow rate of regeneration at Cape Vidal. First, a dispersal limitation may exist, preventing forest tree seeds from reaching the *A. karroo* stands, resulting little seedling recruitment and low species diversity in the stands. Second, the abundance of nitrogen-fixing *A. karroo* in these stands may indicate that this species is exploiting an area of low soil nutrients, particularly nitrogen, from which forest species are excluded. Third, higher levels of herbivory and trampling in the *A. karroo* stands may reduce growth and survival of tree species, inhibiting natural forest succession. Greenhouse, laboratory and field experiments have been conducted to examine these hypotheses for the low species diversity and apparent regeneration failure of the coastal dune forests in *A. karroo* stands at Cape Vidal. Results suggest that: (1) a seed dispersal limitation may exist, preventing tree communities between forest and *Acacia* stands from converging; (2) soil nitrogen was not a limiting factor to seedling growth in the *Acacia* stands; and (3) seedling growth and survival is increased in the *A. karroo* stands when herbivores are excluded. This indicates that herbivores are negatively affecting the rate of succession at Cape Vidal. This study provides a broader understanding of the *A. karroo* successional pathway, and enables more informed decisions to be made in management and rehabilitation of anthropogenically disturbed regions such as Cape Vidal.

1. Introduction

The A*cacia karroo* successional pathway is initiated by the establishment of cohorts of even-aged stands of *A. karroo* trees in areas of recent disturbance (Camp & Weisser, 1991). After approximately 25 years, the *A. karroo* trees begin to senesce and die, and are replaced by forest pioneer and climax forest species. Recent studies show that *A. karroo* stands lead to fully restored climax dune forest within 25 – 60 years (Mentis & Ellery, 1994), and it is currently thought to be the easiest secondary pathway to rehabilitate these regions following disturbance. As a result of such studies, the *A. karroo* successional pathway is currently being successfully used by mining companies to rehabilitate mined dunes.

Acacia karroo is a natural vegetation type of coastal dunes in KwaZulu-Natal, often associated with former human settlements, wind blows and sites of anthropogenic disturbance (Weisser & Muller 1983). Such stands are present in areas surrounded by climax coastal dune forest at Cape Vidal, South Africa. A recent study in this area has shown that although *A. karroo* does establish, it does not lead to a fully restored climax dune forest (West *et al*., 2000). *A. karroo* stands at Cape Vidal are quite species-poor even through it is 50 years after disturbance, and the canopy is dominated by mature *A. karroo* individuals.

The aim of this study is to investigate mechanisms proposed to explain the low diversity of forest species in *A. karroo* stands and the apparent regeneration failure of the *A. karroo* pathway at Cape Vidal. In particular, we wanted to determine the factors driving the relatively slow rate of dune forest recovery in the Greater St. Lucia Wetland Park compared to the rapid recovery, via the *A. karroo* successional pathway, of mined dune sites near Richards Bay. Three potential explanations for the arrested nature of succession will be examined. These are: (1) a seed dispersal limitation preventing forest tree propagules from reaching the *A. karroo* stands; (2) low soil nitrogen levels in the *A. karroo* stands in which *A. karroo* can thrive, but forest tree species are excluded; and (3) higher levels of herbivory and trampling in the *A. karroo* stands reduce growth and survival of forest tree species here.

2. Methods

2.1 Study sites

The Cape Vidal coastal dune forest is located in the Greater St. Lucia Wetland Park in northern KwaZulu-Natal. The forest is bounded by the Indian Ocean in the east and Lake St. Lucia in the west. *Acacia karroo* stands typically form 50-100 m wide longitudinal strips in the dune slacks. Climax forest grows on the coastal dunes between these *A. karroo* stands. The stands thus occur as isolated, longitudinal patches surrounded by coastal dune forest vegetation.

The Richards Bay Minerals mined dune sites are situated approximately 13 km north-east of Richards Bay along the northern coast in KwaZulu-Natal. Mining of the dunes at Richards Bay, which began in 1977, involves the removal of existing vegetation, and the extraction of heavy metals from the dune sands. Following mining, the dune sand is returned and reshaped to approximately its original topography, followed by the spreading of topsoil collected prior to mining. Regeneration from this topsoil has resulted in a series of known aged stands dominated by *A. karroo*, which in time (approximately 25 yrs) begin to senesce and die, giving way to forest tree species (van Aarde *et al.*, 1996). At present, the landscape includes a series of stands at various stages of rehabilitation, varying from immediately post-mining to 27 year old stands, and provides an opportunity to compare stands of similar vegetation and varying ages. Three stands of increasing age since mining, those rehabilitated in 1978, 1991 and 1998, were selected for investigation.

2.2 Seed dispersal limitation

Soil samples were collected from *A. karroo* stands and the adjacent forest at Cape Vidal, as well as from the three selected *A. karroo* stands at Richards Bay Minerals. These were potted in the greenhouse and seedling emergence monitored. Once all germination ceased, soils were sieved and all ungerminated seeds identified and counted.

Seed density and total number of species present in the various habitats were analysed using ANOVA (SPSS 13.0), and community relationships compared using nonmetric multidimentional scaling (NMDS) and multi-response permutation procedures (MRPP; PC-Ord).

2.3 Soil nitrogen limitation

Soil samples were collected from *A. karroo* stands, adjacent forest, and from dune slacks vegetated with undisturbed forest at Cape Vidal, and from four different age classed stands at Richards Bay. These were tested at Cedara Agricultural College for general fertility and nutrient content, as well as for nitrate, ammonium, and levels of mineralization. Soils were collected from a depth of 0-5 cm and nutrient levels were compared between the two habitats. Differences in soil nutrient levels were analyzed using MANOVA (SPSS 13.0), and relationships between the habitats compared using NMDS and MRPP (PC-Ord).

Fifteen paired sites in the *A. karroo* stands and adjacent forest were set up at Cape Vidal. Two 1 m^2 plots were cleared of all vegetation and 5 seedlings of *A. karroo* (a pioneer species), *C. africana* (a pioneer forest species) and *Diospyros natalensis* (a climax forest species) were randomly planted in each plot. Nitrogen-based fertilizer (Limstone Ammonium Nitrate) was applied annually to one of these plots, and the other served as a control. Growth in height was monitored over a two-year period to determine the affect of nitrogen enrichment on growth of these species. Analysis of variance (SPSS 13.0) was used to analyse the difference in growth between the treatments.

2.4 Herbivory

Paired sites, similar to the fertilizer addition treatments, were set up in the forest and *A. karroo* stand habitats. The treatment plot was fenced to exclude large mammalian herbivores, and the control plot was left unfenced. Growth was again monitored over a 2 year period to determine the effect of browsing and trampling on the growth of *A. karroo*, *C. africana* and *D. natalensis* individuals. The difference in growth between the protected and unprotected seedlings was analysed using ANOVA (SPSS 13.0).

Herbivore density transects were conducted in order to estimate herbivore traffic and densities in the *A. karroo* stand and forest habitats at Cape Vidal. King's strip transect method was used. Transects were walked slowly (1-2 km/hr) in the early morning and late afternoon when animals are most active. All herbivores sighted and their distance from the observer was recorded. At Richards Bay, small numbers of bush buck are present but wild herbivores are very rare due to hunting pressures (A. Haagner, pers coms).

For this reason, driven transects were conducted through the stands and herbivore sightings in the different aged stands recorded.

3. Results

3.1 Seed dispersal limitation

At Cape Vidal, both the total seed bank density and the mean number of species present were significantly higher in the forest habitat ($F_{1,28}$ = 35.458, $p < 0.001$; and $F_{1,28}$ = 11.349, $p = 0.002$ respectively). Although seed bank community composition of these two habitats differ significantly (MRPP; $p < 0.001$) and the within group homogeneity is low (A = 0.210), the NMDS ordination analysis (Figure 1) shows that a small degree of overlap does occur. Additionally, 80% of the seeds in the forest seed bank were *C. africana* seeds and the remaining 20% comprised a number of different forest species, whereas in the *A. karroo* stands 30% of the seeds were those of *A. karroo*, 30% were *C. africana*, and the remaining 40% was composed of a variety of different species.

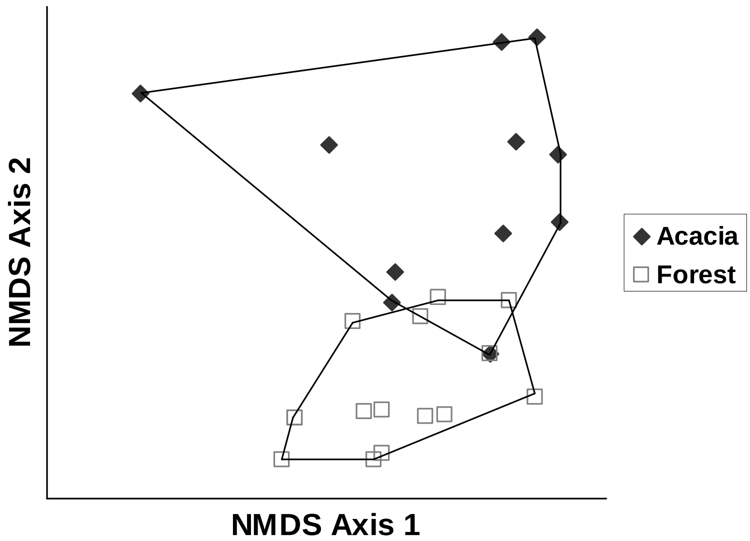

Figure 1. Nonmetric-multidimensional scaling (NMDS) graph showing the relationship between seed bank community composition of the forest and *A. karroo* stands habitats at Cape Vidal.

The different aged stands at Richards Bay have a significant difference in total seed bank density between the different aged stands ($F_{2,42}$ = 9.546, $p < 0.001$). The seed bank in stand 1978 was significantly larger than 1991 and 1998 (Tukey HSD; $p = 0.001$). No statistical difference occurs in the total number of species present in the three stands ($F_{2,42}$ = 2.444, $p = 0.099$). The NMDS ordination analysis (Figure 2) shows a large degree of overlap in seed bank communities of the older two stands (1978 and 1991), but the youngest stand is significantly different as the seed bank is still predominantly composed of herbaceous and early successional species. Despite the overlap between the older stands, the seed bank community composition of these stands is still significantly different (MRPP $p < 0.001$), and the within-group homogeneity is small (*A* = 0.236).

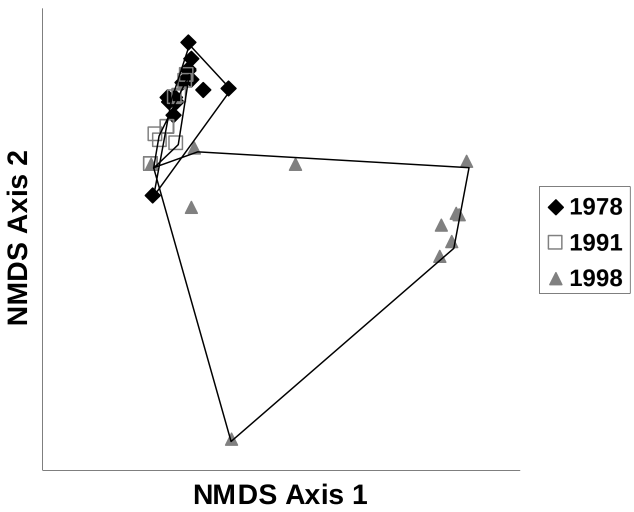

Figure 2. Nonmetric-multidimensional scaling (NMDS) graph showing the relationship between seed bank community composition of the varying aged *A. karroo* stands at Richards Bay.

3.2 Soil nitrogen limitation

Analysis of soil samples showed a significant difference exists in the nutrients found in soils from the *A. karroo* stands, forest and forested dune slacks at Cape Vidal (MRPP; $p < 0.001$) and the within-group homogeneity was low ($A = 0.316$). However, nitrogen itself did not differ between the habitats (MANOVA; $p = 0.090$), and NMDS ordination analysis (Figure 3) indicates that a large degree of overlap occurs in the nutrient content between the forest and *A. karroo* stand soils.

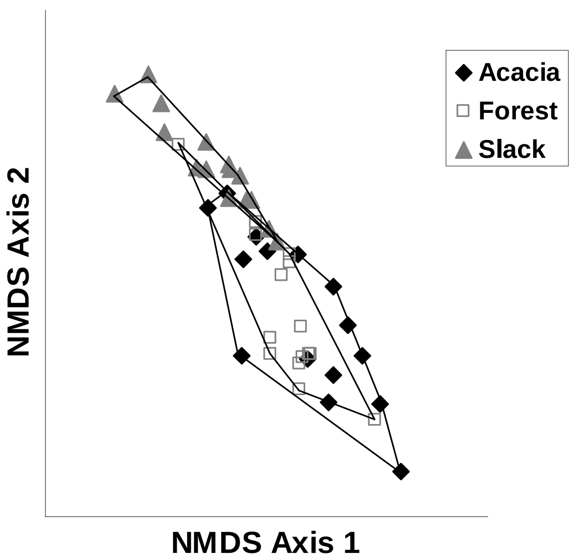

Figure 3. Nonmetric-multidimensional scaling (NMDS) graph showing the relationship between soil nutrient levels in the *A. karroo* stand, forest and dune slack habitats at Cape Vidal.

The nutrient content of Richards Bay soils also differed in different aged stands (MRPP; $p < 0.01$) and had similarly low within-group homogeneity ($A = 0.153$). Nitrogen did differ between the stands (MANOVA; $p < 0.001$), with the older two stands having the highest nitrogen levels. The NMDS ordination analysis (Figure 4) indicates a large degree of convergence in the nutrient levels between the older two stands.

The nitrogen-addition treatment plots showed no difference in growth between the species in the two habitats at Cape Vidal when nitrogen was added (Figure 5; ANOVA; $p = 0.090$).

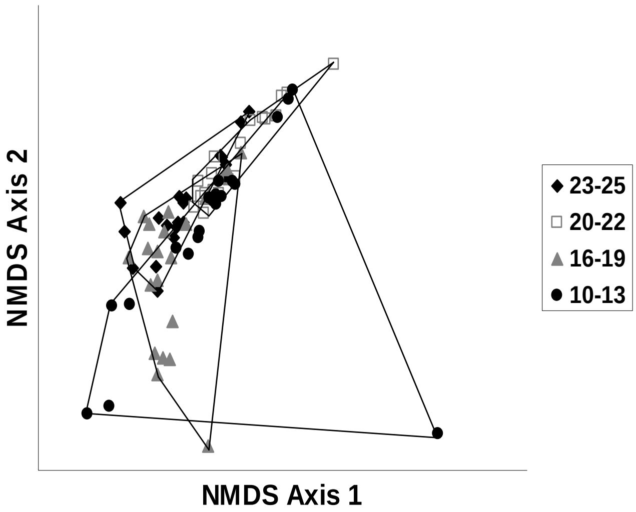

Figure 4. **Nonmetric-multidimensional scaling (NMDS) graph showing the relationship between soil nutrient levels in the four selected age category *A. karroo* stands at Richards Bay.**

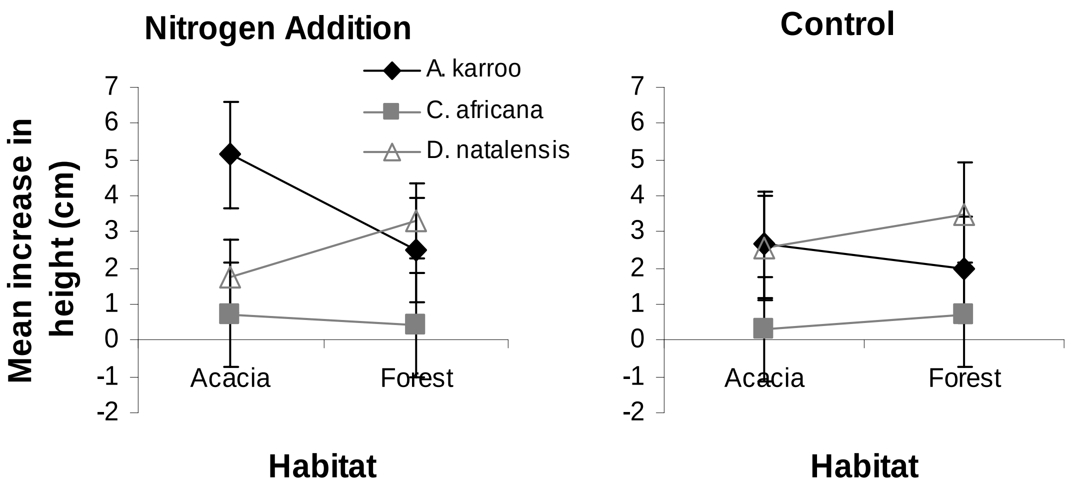

Figure 5. **Mean growth in height of *A. karroo*, *C. africana* and *D. natalensis* in nitrogen treated and control plots in the forest and *A. karroo* stand habitats.**

3.3 Herbivory

A significant difference in the growth of *A. karroo*, *C. africana* and *D. natalensis* was found between the herbivore exclosure plots and the control plots (Figure 6; ANOVA; $p < 0.001$). All species showed an increase in growth in the *A. karroo* stands when herbivores were excluded. In the unfenced control plots, growth was low in all species.

At Cape Vidal, herbivore densities were found to be dramatically higher in the *A. karroo* stands. A mean herbivore density of 185.2 ± 41.4 individuals /km^2 was recorded in the *A. karroo* stands, whereas only 13.7 ± 3.1 individuals /km^2 were encountered in the forest. At Richards Bay a total of 27.3 km were driven through *Acacia* stands aged from directly post-mining to 27 years since mining, but no sightings of herbivores were made.

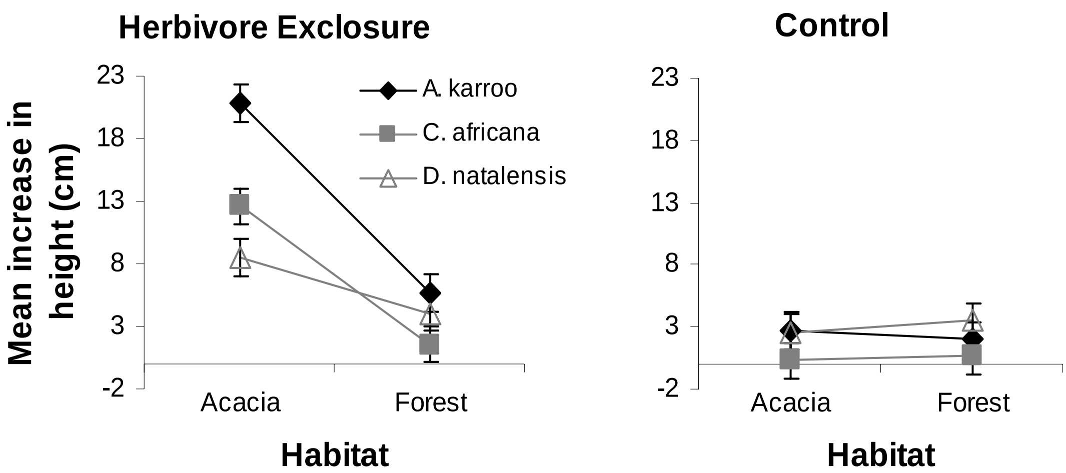

Figure 6. Mean growth in height of *A. karroo*, *C. africana* and *D. natalensis* in herbivore exclosure and control plots in the forest and *A. karroo* stand habitats at Cape Vidal.

4. Discussion

4.1 Seed dispersal limitation

A seed dispersal limitation may exist at Cape Vidal. The *A. karroo* stand seed bank shows a lower number of species present, as well as a lower seed density than that of the forest. Although a degree of overlap does occur between the habitats, the compositions are still different 50 years post-disturbance. The difference in the seed densities is mainly due to large numbers of *C. africana* seeds present in the forest seed bank. Eighty percent of the forest seed bank is composed of this species' propagules, whereas it only comprises 30% of the seed bank in the *A. karroo* stands. This is a reflection of the mature canopy composition of the two habitats: *C. africana* is very common in the forest, but occurs less frequently in the *A. karroo* stands.

At Richards Bay, the older stand (1978) was found to have both more species present, as well as a greater seed density. This is likely a result of this stand having had a longer time period in which to accumulate seeds. Convergence of the stands begins to occur after 14 years.

4.2 Soil nitrogen limitation

Although soil nutrients differ between the forest, *A. karroo* stands, and dune slacks, nitrogen itself is not limiting in any of these habitats. The forest and *A. karroo* stand habitats overlap to a large degree (Figure 3), indicating that in the 50 years since disturbance, the *A. karroo* stand soils have had a chance to accumulate soil nutrients and return to pre-disturbance levels.

Richards Bay soils also show a significant difference in nutrient levels. The large degree of overlap between the older stands indicates that accumulation of soil nutrients is occurring, which supports trends previously demonstrated here (van Aarde *et al.*, 1996).

4.3 Herbivory

The negative impact of herbivores on unfenced seedlings in the *A. karroo* stands at Cape Vidal is evident from this study. When protected from mammalian herbivores, all species doubled their growth, and the largest increase in height occurred in the *A. karroo* stands when fenced. This indicates that herbivory plays a large role in shaping community structures in this particular habitat. Additionally, herbivore density was found to be 13 times greater in the *A. karroo* stands than in the forest. The large numbers of herbivores observed utilizing this habitat at Cape Vidal gives insight into the impact of these animals on the vegetation in the *Acacia* stands.

At Richards Bay, where regeneration is successfully occurring as predicted, herbivore density is negligible. This implies that in the absence of large numbers of wild herbivores, succession via the *A. karroo* pathway on coastal dunes is effective.

5. Conclusions

This study indicates that although a seed dispersal limitation may prevent forest tree propagules from reaching the *A. karroo* stands at Cape Vidal, the major factor reducing growth of forest tree species in these disturbed habitats is the harmful effect of large numbers of herbivores browsing and trampling the germinating seedlings. Soil nitrogen does not limit seedling growth and can be excluded as a factor affecting succession.

Numerous studies at Richards Bay Minerals show that succession facilitated by the *A. karroo* pathway leads to climax dune forest within 54-80 years on mined dunes (Mentis and Ellery, 1994; West *et al*., 2000) Although tree species richness does increase with time since disturbance at Cape Vidal (Wassenaar, 2003), the natural *A. karroo* successional pathway does not lead to fully rehabilitated dune forests in this region, as a large amount of the diversity is lost. None of the studies to date have allowed for the harmful effects of herbivores and how they may be affecting the successional process here. Thus, it would seem that in the absence of large numbers of mammalian herbivores, the *Acacia karroo* successional pathway does successfully rehabilitate disturbed coastal dune forests.

Acknowledgements

This project was made possible by funding and logistical support provided by Ezemvelo KwaZulu-Natal Wildlife, the SA National Research Foundation and the Mazda Wildlife Fund.

References

CAMP, P. & WEISSER, P.J. (1991). Dune rehabilitation, flora and plant succession after mining at Richards Bay, South Africa. In: EVERARD, D.A. & VON MALTITZ, G.P. (eds.). *Dune Forest Dynamics in Relation to Land-Use Practices*. Pretoria. pp. 106-123.

MENTIS, M.T. & ELLERY, W.N. (1994). Post-mining rehabilitation of dunes on the north-east coast of South Africa. *South African Journal of Science* 90: 69-74.

VAN AARDE, R.J., FERREIRA, S.M. & KRITZINGER, J.J. (1996). Successional changes in rehabilitating coastal dune communities in northern KwaZulu-Natal, South Africa. *Landscape and Urban Planning* 34: 277-286.

WASSENAAR, T.D. & VAN AARDE, R.J. (2005). *The Ecology of Coastal Dune Forest Restoration*. University of Pretoria, Pretoria, South Africa.

WEISSER, P.J. & MULLER, R. (1983). Dune vegetation dynamics from 1937 to 1976 in the Mlalazi-Richards Bay area of Natal, South Africa. *Bothalia* 14: 661-667.

WEST, A., BOND, W. & MIDGLEY J.J. (2000). Dune forest succession on old lands: implications for post-mining restoration. In: SEYDACK, A.H.W., VERMEULEN, W. J. & VERMEULEN, C. (eds.). *Towards Sustainable Management Based on Scientific Understanding of Natural Forests and Woodlands*. Department of Water Affairs and Forestry, Knysna. pp. 35-39.