South African Journal of Botany 2003, 69(3): 434–445 Printed in South Africa — All rights reserved Copyright © NISC Pty Ltd SOUTH AFRICAN JOURNAL OF BOTANY ISSN 0254–6299

# Recovery of thicket in a revegetated limestone mine

AR Hall, DR du Preez and EE Campbell\*

Department of Botany, University of Port Elizabeth, Port Elizabeth 6031, South Africa \* Corresponding author, e-mail: btaeec@upe.ac.za

Received 5 December 2002, accepted in revised form 6 May 2003

The opencast extraction of limestone at the PPC Cement (Pty) Ltd Loerie quarry in the Eastern Cape, South Africa, has led to disturbance of the immediate environment. Large tracts of thicket have been removed during mining and exhausted quarry areas had to be revegetated. Revegetation commenced 16 years ago and as a result of progressive revegetation efforts since then, five seral stages were available for study. This presented an opportunity to describe the successional progression that occurs where thicket topsoil was used for revegetation. The quarry lies near the Gamtoos fault and both thicket and mountain fynbos is found in proximity to the mine. Before mining, the area was covered by thicket and quarry floors were revegetated by covering

#### Introduction

Plant succession is a directional cumulative change in the species that occupy a given area through time (Barbour *et al.* 1987). Typically successional processes (replacement of some species by others) lead to a climax condition that then remains relatively stable over a substantial period of time. If disturbance causes a regression to an earlier successional stage (sere) and the successional process then follows the same path it did before, a disturbed system should eventually achieve complete recovery (Cairns 1989). These 'Clementsian' ideas do not hold for restoration ecology since in revegetated areas, the species representing the earlier successional stages may no longer be present for re-invasion, and other species not present during the earlier developmental period, may be the post-disturbance colonisers.

Application of successional theory to derelict land has not been easy, as substrates do not always correspond to natural ones (Harris *et al.* 1996). It is difficult to make predictions on the succession of vegetation in highly disturbed environments. For instance, limestone quarries are not alike with respect to the environmental conditions that will direct successional pathways in plant growth. Many attempts at rehabilitating opencast mineral extraction stands have failed because practitioners rigidly followed the methods of past successes (Harris *et al.* 1996). This is especially true when European methods have been used in arid and semi-arid lands in southern Africa. landscaped areas with thicket topsoil. The vegetation that developed in the quarry had a very low floristic relationship to fynbos. After 16 years, the vegetation also had a low similarity to thicket, even though the soils used for revegetation contained thicket propagules. The oldest seral stage (16 years) was a *Rhus incisa– Panicum deustum* thicket in which only 46% of the species were mature thicket species. In order to develop thicket more rapidly, active intervention will be required. This could take the form of planting of saplings of key thicket species. A trial planting of such saplings showed high survival success of most species. Long-term (50 year) monitoring will be required to determine whether this approach was successful.

The opencast extraction of limestone at a guarry near Loerie, about 50km west of Port Elizabeth, has caused severe damage to the natural thicket and underlying soils. Entire hillsides have been cut away in order to access underlying blocks of limestone. The overlying material, or overburden was removed by ripping or blasting. After removal of the limestone, mined areas and hillsides were shaped and terraced with this overburden and then top dressed with a thin (100-200mm) layer of soil taken from thicket areas earmarked for new excavations. This revegetation effort commenced in the early 1980s. After consultation with the Department of Botany at the University of the Witwatersrand it was decided to leave these areas to revegetate through natural succession processes (Shaw and Black 1985). There was thus no irrigation or addition of fertiliser and seed to initiate revegetation in these areas. This method has been used in a number of areas within the quarry over the past 16 years.

If environmental factors such as aspect, slope and macroclimate are similar for all stands, comparison between stands of different age is possible. Further influences on the development of rehabilitated vegetation such as the origin and quality of the topsoil, the distance from an available seed source (MacMahon 1990) and the boundary shape of the rehabilitated site that affects the colonisation pattern (Hardt and Forman 1989) need to be considered. All the revegetated stands at the Loerie quarry showed close similarity in these environmental factors and could thus be used as a chronosequence to study the process of succession in the natural return of indigenous vegetation on the stands. It was hoped that by using topsoil from previously vegetated areas that the natural vegetation would return through succession. Quarry management was under the impression that the natural vegetation of the area was beginning to recover at these stands and this study was initiated to determine if this was so.

It is generally believed that thicket will not recover after massive disturbance. While intact thicket has high stability and resilience (Cowling 1984, Everard 1987) evidence available to date (e.g. Stuart-Hill 1991, Moolman and Cowling 1994) indicates that it is likely that areas cleared of thicket will follow the non-equilibrium model of community dynamics (DeAngelis 1987) rather than develop through to a stable climax state comparable to the intact thicket found prior to disturbance. A number of ecologists have shown that there is little or no regeneration of thicket through the establishment of seedlings (Aucamp and Tainton 1984, Stuart-Hill and Danckwerts 1988, Stuart-Hill 1991, Moolman and Cowling 1994). It is believed that the climate has become drier over the past 6 000 years or so and the lack of a moist and shaded environment inhibits seedling establishment (Stuart-Hill 1991). La Cock (1991) and Thrash (1998) suggest that regeneration through seedlings can only take place under the canopy of certain nurse plant species that provide a suitable microclimate for their establishment. La Cock (1991) believes that it is the distribution pattern of seedlings that is responsible for the failure of the shrub component of thicket to re-colonise poorly vegetated areas rather than the lack of germination and consequent establishment of seedlings.

The use of a chronosequence to study succession has been used extensively in the regeneration of dune thicket after mining by Richards Bay Minerals (Cairns 1989, Moll 1992, Van Aarde and Smit 1997). These studies have been invaluable in the information base that they have provided to the mining company. The advantage of having different aged stands to compare is that predictions can be made as to the development and management of future revegetation trials (Bell 1987, Bradshaw 1990). Key species and successional processes can be identified and manipulated at an early stage thereby speeding up the process of revegetation and reducing costs for the mining company. Cairns (1989) feels that the opportunity offered by rehabilitated areas for the study of ecological processes and functioning cannot be overemphasised.

There is a paucity of succession studies in thicket, probably because of the common belief that the system will not regenerate. Few, if any studies have investigated the regeneration of thicket over a long time period. The primary aim of this study was to assess whether thicket is returning to the revegetated areas through succession in the Loerie quarry. The success of the revegetation programme is assessed and predictions are made as to the climax vegetation expected for the quarry.

#### **Materials and Methods**

#### Study site

Loerie has a temperate climate. Daily summer temperatures for Patensie, a small town 30km from Loerie, range from 16–30°C (means calculated from daily temperatures supplied by the South African Weather Bureau for 1993–1999). Winter temperatures range from 8–21°C. The average annual rainfall is 730mm per year. The area experiences a bimodal rainfall pattern with peaks in the autumn months (March–May), receiving an average of 63mm per month, and in the spring months (September–November) an average of 73mm per month. There are very few incidences of hail on record and virtually no frost.

The natural thicket surrounding the Loerie guarry showed similarities to the Pterocelastrus-Euclea community of Kaffrarian Thicket as well as to the Euclea undulata-Brachylaena ilicifolia community of Kaffrarian Succulent Thicket described by Cowling (1984). The vegetation similarly can be related to Xeric Kaffrarian Thicket or Valley Thicket (Lubke 1996) and Mesic Succulent Thicket as described by Everard (1987). Species such as Aloe africana, Carissa haematocarpa, Euclea undulata var. undulata, Grewia occidentalis. Scutia myrtina and Sideroxylon inerme subsp. inerme found in thicket of the study area, are also listed as dominant in the communities described by these two authors (Cowling 1984, Everard 1987). This vegetation forms a closed low forest with a high proportion of trees forming the canopy between 4m and 6m in height (Everard 1987). The vegetation has a low succulent component and is dominated by a woody canopy with species of strong Afromontane affinity (Cowling 1984). The thicket of the study area is more open within the canopy than Mesic Succulent Thicket as there are fewer spinescent shrubs, woody creepers and succulent species (Everard 1987).

Elements from both Mesic Succulent Thicket (of the lower Gamtoos Estuary) and Xeric Kaffrarian Thicket (of the upper Gamtoos Valley) (Everard 1987) occur at Loerie quarry. This accounts for the high beta diversity in intact thicket at the quarry. Aspect and geology separates thicket types at Loerie. Mesic Succulent Thicket occurs on the upper and drier north facing slopes of valleys and Valley Thicket in pockets in the deeper valleys and on moist, south facing slopes. This gradient has important implications with regards to the succession of the revegetated stands. All revegetation stands are north facing in aspect and have a shallow soil profile that leads to a drier environment similar to that where Mesic Succulent Thicket occurs. It would thus be expected that Mesic Succulent Thicket would revegetate at these stands as opposed to Valley Thicket that requires a deep soil profile, a more shaded southerly aspect and a relatively moist environment.

#### Vegetation assessment

Quadrats were sampled in revegetated areas of one year, two years, six years, 10 years and 16 years old, intact thicket and fynbos. Plant species were recorded with a measure of their canopy cover. Plots were 100m<sup>2</sup> for revegetated areas (Carey and Brooks 1985, Camp and Weisser 1991, Moll 1992),  $10m^2$  for fynbos (Cowling 1984) and  $40m^2$  for thicket (a belt transect of  $20m \times 2m$  wide). Belt transects were selected as the appropriate sampling method in thicket as they provide a less subjective assessment of plant cover than that of a large quadrat (Cowling 1984, Everard 1987, Louw 1993). Access and manoeuvrability within the thicket is also extremely difficult and thus belt transects are an easier way of effectively assessing the composition of the vegetation.

Cover data from the quadrats was used for multivariate analysis. The computer software ordination package CANOCO (Ter Braak 1988) was used to run detrended correspondence analysis (DCA) on the data matrix. Thicket and fynbos were included in the analysis in the first instance. This ordination clearly indicated that the fynbos had little in common with the revegetated stands or thicket and in order to investigate the relationship between revegetated stands and thicket without the polarising effect of fynbos data, a second ordination (DCA) was run that excluded fynbos samples. In all cases the matrix was log-transformed prior to analysis and down-weighting of rare species was applied. The two longest ordination axes were used.

The data were also analysed using Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979).

The cover for the different vegetation strata was measured along two line transects sampled in the quadrats at each site: the tree stratum consisted of single stem woody species forming the upper storey; shrubs were multistemmed species forming the middle storey and grasses and herbs were combined as they formed the understorey. The cover abundance of each species was recorded and these were summed for each stratum (values may exceed 100% due to overlapping of canopies). The results were combined in a stacked bar graph to illustrate the contribution of each vegetation layer to total vegetation cover for each site. Species richness (number of species per site) was also compared for the different stands. Species composition similarity was calculated using Sørensen's similarity index (Mueller-Dombois and Ellenberg 1974) converted to a percentage. Nomenclature follows Arnold and De Wet (1993) and all species authorities are provided in Table 1.

A basic soil analysis was also done to determine whether soils of the revegetated stands have shown an improvement with time in response to revegetation. Twenty soil samples (four from each quadrat) were taken from each stand. Samples were taken by digging out a 100mm by 100mm area to a depth of 100mm. The average soil moisture and organic matter content were determined by weighing the soils after drying and ashing. The results were statistically analysed using SigmaStat Ver 1.0 (Jandel Corporation 1992–1994). A one-way ANOVA was used to determine significance of differences with the All-Pairwise-Multiple-Comparison procedure of the Student-Newman-Keuls method.

In order to determine whether intervention to speed up, or direct succession towards thicket will be possible, saplings of thicket species that were cultivated at the nearby Van Stadens Wildflower Reserve were planted in a recently revegetated area. Seedlings of Acacia karroo, Azima tetracantha, Diospyros dichrophylla, Grewia occidentalis, Olea europaea subsp. africana, Pterocelastrus tricuspidatus, Rhus undulata, Schotia afra var. afra, Schotia latifolia, Sideroxylon inerme subsp. inerme and Tarchonanthus camphoratus were planted in groups of three. Survival of these saplings was monitored.

### Results

#### Comparison to fynbos

Ordination (DCA) of the samples for the revegetated stands shows that thicket and fynbos separate with a group between them that contained the revegetated stands (Figure 1). The fynbos samples plotted separately from the other two groups on the right hand side of the diagram indicating a high degree of dissimilarity from thicket and revegetated samples. The ordination points of revegetated samples lie closer to those of thicket than those of fynbos.

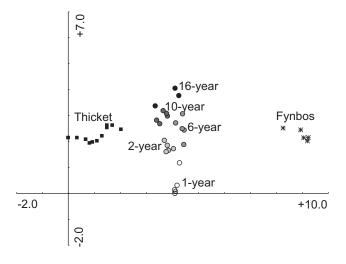
The species ordination of the same analysis showed complete separation of fynbos species from the rest (data not shown). Members of the Proteaceae (*Leucadendron* salignum, Protea exima), Restionaceae (*Hypodiscus striatus*) and Ericaceae (*Erica chamissonis* var. *chamissonis*, *Erica sessiliflora* var. *sessiliflora*) were dominant in the fynbos community.

Classification (TWINSPAN) of the samples indicated a separation of fynbos from the rest at an eigenvalue of over 0.8 (Figure 2). The indicator species for the fynbos community was *Anthospermum aethiopicum*.

Classification (TWINSPAN) of species (Figure 3) also showed high dissimilarity between fynbos and the other communities (an eigenvalue of 0.8).

#### Comparison to thicket

Thicket and revegetated stand species showed some similarity in that they split at the second division level at an eigenvalue of around 0.3 (Figure 3). However, separation between



**Figure 1:** Ordination (DCA) of samples of revegetated stands (circles), thicket (squares) and fynbos (asterisks). Cumulative % variance of species data = 18.6%; sum of unconstrained eigenvalues = 7.178

 Table 1: Species recorded in successional stages, thicket and fynbos at the Loerie Quarry. Species codes used in ordination as well as the community where they were recorded are given. \* indicates exotic species

Species name	Code	1-year	2-year	6-year	10-year	16-year	Fynbos	Thicket
Abutilon sonneratianum (Cav.) Sweet	Abutsonn	1	2	6	10			
* <i>Acacia cyclops</i> A. Cunn ex G. Don	Acaccycl	1	2	6	10	16		
Acacia karroo Hayne	Acackarr		2	6	10	16		Т
*Agrostis montevidensis Spreng. ex Nees	Agromont			6				
Aizoon glinoides L. f.	Aizoglin	1		6	10			
Aizoon rigidum L. f. var. rigidum	Aizorigi	1	2					
Aloe africana Mill.	Aloeafri							Т
Aloe ferox Mill.	Aloefero							Т
Aloe pluridens Haw.	Aloeplur							Т
Anthospermum aethiopicum L.	Anthaeth						F	
*Argemone mexicana L.	Argemexi	1						
Asclepias physocarpa (E. Mey.) Schltr	Asclphys	1	2	6				_
Astephanus marginatus Decne.	Astemarg							Т
Athanasia dentata (L.) L.	Athadent						F	
Atriplex semibaccata R. Br. var. appendiculata Aell.	Atrisemi	1	2	6	10			_
Azima tetracantha Lam.	Azimtetr		2					Т
<i>Berkheya rigida</i> (Thunb.) H. Bol. & Wolley-Dod								
ex Adamson & Salter	Berkrigi			6	10	16		
*Bidens pilosa L.	Bidepilo	1	2		10			
Brachylaena ilicifolia (Lam.) Phill. & Schweick	Bracilic							Т
*Bromus diandrus Roth	Bromdian					16		_
Bulbostylis hispidula (Vahl) R. Haines	Bulbhisp				10			Т
Calpurnia aurea (Ait.) Benth. subsp. aurea	Calpaure				10	16		_
Capparis sepiara L. var. citrifolia (Lam.) Tölken	Cappsepi							Т
Carissa haematocarpa (Eckl.) A. DC.	Carihaem				10			Т
Carpobrous edulis (L.) L. Bol.	Carpedul		2		10			-
Cassine aethiopica Thunb.	Cassaeth							Т
Cassine peragua L.	Casspera							Т
Cassine tetragona (L. f.) Loes.	Casstetr							Т
Celtis africana Burm. f.	Celtafri		0	0				Т
Chamaesyce inaequilatera (Sind.) Sojak	Chaminae	1	2	6				-
Cheilanthes viridis (Forssk.) Swartz var. viridis	Cheiviri							Т
Chironia baccifera L.	Chirbacc							Т
Chrysanthemoides monilifera (L.) T. Norl.	0		0	0	10	40		
subsp <i>monilifera</i>	Chrymoni		2	6	10	16		
Chrysocoma ciliata L.	Chrycili		2	6	10			
* <i>Ciclospermum leptophyllum</i> (Pers.) Eichler	Cicllept	1	2	6	10			
*Cirsium vulgare (Savi) Ten.	Cirsvulg	1	2	6	10		_	
Cliffortia ilicifolia L. var. ilicifolia	Clifilic			0	10	10	F	Ŧ
Clutia daphnoides Lam.	Clutdaph		0	6	10	16		Т
* <i>Conyza albida</i> Spreng.	Conyalbi		2	6	10			
Conyza scabrida DC.	Conyscab		2	6	10			т
Crassula ovata (Mill.) Druce	Crassovat							T T
Crassula tetragona L. subsp. tetragona	Crasstetr							
Cussonia spicata Thunb.	Cussspic		2			16		T T
Cynanchum ellipticum (Harv.) R.A. Dyer	Cynaelli	1	2 2	6	10	10		I
Cynodon dactylon (L.) Pers.	Cynodact	1	2	0	10			
*Datura stramonium L. Dietes iridiodes (L.) Sweet ex Klatt	Datustra Dietirid							т
Digitaria eriantha Steud.							F	1
Digitaria eriantina Steud. Diospyros dichrophylla (Gand.) De Winter	Digieria Diosdich		2		10	16	Г	т
Dipogon lignosus (L.) Verdc.	Dipolign		2 2		10	10		Ť
			2		10			Ť
Dovyalis rotundifolia (Thunb.) Thunb. & Harv. Drosanthemum hispidum (L.) Schwant.	Dovyrotu							I
	Droshisp		2	6	10			
var. <i>platypetalum</i> (Haw.) Schwant.	•		2	6 6	10	16		
Elytropappus rhinocerotis (L.f.) Less. Eragrostis curvula (Schrad.) Nees	Elytrhin Eragoury		0	6 6	10	16		
<b>o</b>	Eragcurv		2 2	0	10	10		
Eragrostis obtusa Munro ex Fical. & Hiern	Eragobtu Ericcham		2				F	
	Fuccham						F	
Erica chamissonis Klotzch ex Benth. var. chamissonis Erica copiosa Wendl. var. copiosa	Ericcopi						F	

Table 1 cont.

Species name	Code	1-year	2-year	6-year	10-year	16-year	Fynbos	Thicket
Erica sp. 1	Ericasp1						F	
Erica sp. 2	Ericasp2						F	
Eriocephalus africanus L.	Erioafri			6	10	16	F	Т
Euclea natalensis A. DC. subsp. capensis F. White	Euclnata							Т
Euclea undulata Thunb. var. undulata	Euclundu							Т
Euphorbia fimbriata Scop.	Euphfimb							Т
Euphorbia kraussiana Bernh. var. kraussiana	Euphkrau			6	10			
Euphorbia triangularis Desf.	Euphtria							Т
Exomis microphylla (Thunb.) Aell.								
var. axyrioides (Fenzl) Aell.	Exommicr		2	6	10	16		
Felicia fasicularis DC.	Felifasi		2		10		_	
Gladiolus sp.	Gladisp						F	
*Gnaphalium pensylvanicum Willd.	Gnappens			6	10			-
Grewia occidentalis L.	Grewocci		2		10			Т
Grewia robusta Burch.	Grewrobu				10			Т
Gymnosporia buxifolia (L.) Szyszyl.	Maythete		2		10		_	Т
Helichrysum anomalum Lees.	Helianom						F	
Helichrysum cymosum (L.) D. Don subsp. cymosum	Helicymo		2	6	10		F	
Helichrysum felinum Lees.	Helifeli						F	
Helichrysum nudifolium (L.) Lees.	Helinudi						F	
Helichrysum petiolare Hilliard & Burtt	Helipeti						F	
Helichrysum rosum (Berg.) Less. var. rosum	Helirosu			6		16		Т
Hermania althaeoides Link	Hermalth		2	6	10	16		Т
Hermania flammea Jacq.	Hermflam			6		16	F	
Hermania mucronulata Turcz	Hermmucr			6		16		
Hippobromus pauciflorus (L. f.) Radlk.	Hipppauc							Т
Hypodiscus striatus (Kunth.) Mast.	Hypostri						F	
*Inula graveolens Desf.	Inulgrav		2					
*Lantana camara L.	Lantcama			6				
* <i>Lantana rugosa</i> Thunb.	Lantrugo		2	6	10	16		_
Ledebouria ensifolia (Eckl.) S. Venter	Ledeensi							Т
Lepidium africanum (Burm. f.) DC. subsp. africanum	Lepiafri		2		10			
Leucadendron salignum Berg.	Leucsali						F	_
Lycium ferocissimum Miers	Lycifero							Т
Maerua cafra (DC.)	Maercafr							Т
Medicago polymorpha L.	Medipoly	1		6				
Melhania didyma Eckl. & Zeyh.	Melhdidy	1		6	10	16		
Melica racemosa Thunb.	Melirace			6				
Merxmuellera disticha (Nees) Conert	Merxdist			6		16		
Mesembryanthemum aitonis Jacq.	Meseaito	1	2				_	
Metalasia muricata (L.) D. Don	Metamuri			6			F	
Mohria caffrorum (L.) Desv. var. caffrorum	Mohrcaff						F	_
Myrsiphyllum asparagoides (L.) Willd.	Myrsapar							Т
*Nicotiana glauca R.C. Grah.	Nicoglau	1	2	6		10		_
Oedera genistifolia (L.) Anderb. & Bremer	Oedegeni			6		16		Т
Olea europaea L. subsp. africana (Mill.) P.S. Green	Oleaeuro			6		16		Т
*Opuntia ficus-indica (L.) Mill.	Opunficu							Т
Panicum deustum Thunb.	Panideus	1	2	6	10	16		Т
Panicum maximum Jacq.	Panimaxi							Т
Pappea capensis Eckl. & Zeyh.	Pappcape						_	Т
Passerina vulgaris Thoday.	Passvulg					16	F	
Pavonia praemorsa (L. f.) Cav.	Pavoprae				10	16		
Pelargonium peltatum (L.) L' Hérit	Pelapelt			_			_	Т
Pelargonium reniforme Curtis.	Pelareni			6			F	Т
Pelargonium urosepalus (L.) L' Hérit	Pelauros		_				F	
*Pennisetum clandestinum Chiov.	Pennclan	1	2					
*Physalis angulata L.	Physangu		2	_		16		
*Picris echioides L.	Picrechi	1		6				_
Pittosporum viridiflorum Sims	Pittviri							Т
*Plantago lanceolata L.	Planlanc			6				
Plumbago auriculata Lam.	Plumauri							Т
Polygala myrtifolia L.	Polymyrt			6	10	16	F	Т

Table	1 cont.
-------	---------

Species name	Code	1-year	2-year	6-year	10-year	16-year	Fynbos	Thicket
Protasparagus africanus (Lam.) Oberm.	Protafri		2		10			
Protasparagus crassicladus (Jessop) Oberm.	Protcras				10			Т
Protasparagus densiflorus (Kunth.) Oberm.	Protdens							Т
Protasparagus denudatus (Kunth.) Oberm.	Protdenu							Т
Protasparagus racemosus (Willd.) Oberm.	Protrace				10	16		Т
Protasparagus setaceus (Kunth.) Oberm.	Protseta				10			Т
Protasparagus suaveolens (Burch.) Oberm.	Protsuav				10			Т
Protasparagus subulatus (Thunb.) Oberm.	Protsubu							Т
Protea exima (Salisb. ex Knight) Fourc.	Protexim						F	
Pseudognaphalium luteo-album (L.) Hilliard & Burtt.	Pseulute		2					
Ptaeroxylon obliquum (Thunb.) Radlk.	Ptaeobli							Т
Pterocelastrus tricuspidatus (Lam.) Sond.	Ptertric							Т
Pteronia incana (Burm.) DC.	Pterinca					16	F	Т
Putterlickia pyracantha (L.) Szyszyl.	Puttpyra							Т
Rhoiacarpos capensis ( Harv.) A. DC.	Rhoicape							Т
Rhoicissus digitata (L. f.) Gilg & Brandt	Rhoidigi							Т
Rhoicissus tridentata (L. f.) Wild & Drum.								
subsp. <i>tridentata</i>	Rhoitrid							Т
Rhus crenata Thunb.	Rhuscren		2				F	
Rhus glauca Thunb.	Rhusglau						F	
Rhus incisa L. f. var. effusa (Presl.) R. Fernandes	Rhusinci		2		10	16		Т
Rhus laevigata L.	Rhuslaev		2	6	10			Т
Rhus pterota Presl.	Rhuspter			6	10			Т
Rhus undulata Jacq.	Rhusundu							Т
*Ricinus communis L.	Ricicomm		2					
Salsola kali L.	Salskali	1						
Salvia triangularis Thunb.	Salvtria			6	10	16		Т
Sarcostemma viminale (L.) R. Br.	Sarcvimi							Т
*Schkuhria pinnata (Lam.) Cabr.	Schkpinn		2	6				
Schotia afra (L.) Thunb. var. afra	Schoafra							T
Schotia latifolia Jacq.	Scholati		2					Т
Scolopia mundii (Eckl. & Zeyh.) Warb.	Scolmund							Т
Scutia myrtina (Burm. f.) Kurz	Scutmyrt					16	_	Т
Selago corymbosa L.	Selacory			6	10	16	F	
Senecio ilicifolius L.	Seneilic	1	2	6				
Senecio inaequidens DC.	Seneinae			6			_	
Senecio linifolius L.	Senelini				10		F	
Sida ternata L. f.	Sidatern		2	6	10			-
Sideroxylon inerme L. subsp. inerme	Sideiner				10			Т
Solanum hermannii Dun.	Solaherm	1	2	6	10			
*Solanum nigrum L.	Solanigr	1						
*Sonchus oleraceus L.	Soncoler	1	0	0	10	10		
Sporobolus africanus (Poir.) Robyns & Tournay	Sporafri	1	2	6	10	16		
Sporobolus fimbriatus (Trin.) Nees	Sporfimb		2	6	10			
Sutherlandia frutescens (L.) R. Br.	Suthfrut	1		0	10			
*Tagetes minuta L.	Tageminu	1	0	6	10			
*Taraxacum officinale Weber	Taraoffi		2		10	10		-
Tarchonathus camphoratus L.	Tarccamp	4	0	0	10	16	-	Т
Tephrosia capensis (Jacq.) Pers.	Tephcape	1	2	6	10	16	F	-
Themeda triandra Forssk.	Themtria					16	F	Т
Viscum rotundifolium L. f.	Viscrotu						-	Т
Watsonia longifolia J.W. Mathews & L. Bol.	Watslong	4	0	0	40	40	F	
Withania somnifera (L.) Dun.	Withsomn	1	2	6	10	16		
*Xanthium spinosum L.	Xantspin	1						-
Zanthoxylum capense (Thunb.) Harv.	Zantcape							Т

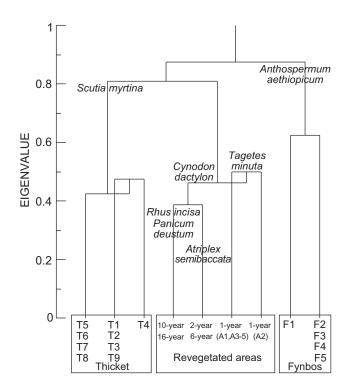
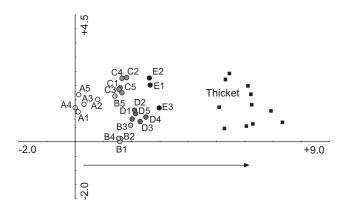


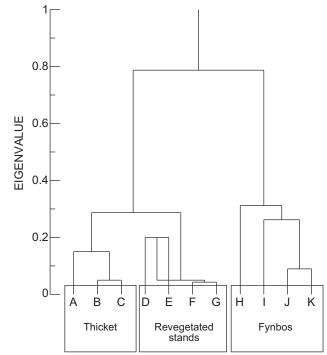
Figure 2: Classification (TWINSPAN) of samples for revegetated stands (A–E are 1–16 years), thicket (T) and fynbos (F)



**Figure 4:** Ordination (DCA) of samples of revegetated stands (A–E are 1–16 years) and thicket vegetation. The arrow represents the successional progression. Cumulative % variance of species data = 17.7%; sum of unconstrained eigenvalues = 6.619

the thicket and the revegetated stand samples occurred at a high eigenvalue of over 0.8 (Figure 2). *Scutia myrtina* serves as the indicator species for the thicket community.

There is a clear separation between the thicket and revegetated stands in ordination space and the revegetated stands generally plot in groups according to their age. The xaxis represents a succession gradient for the revegetated stands that tends towards that of thicket (arrow in Figure 4). There is a progression of samples from the one year stands (labelled A in Figure 4) through the stands of two and six



- A = Polygala myrtifolia
- B = Aloe africana, Cassine aethiopica, Dietes iridiodes, Grewia occidentalis, Euclea undulata var. undulata, Gymnosporia buxifolia, Pappea capensis, Rhoicissus digitata, Scutia myrtina, Sideroxylon inerme subsp. inerme
- C = Dipogon lignosus, Helichrysum rosum var. rosum
- D = Selago corymbosa
- E = Clutia daphnoides, Oedera genistifolia, Rhus incisa var. effusa, Tarchonanthus camphoratus
- F = Acacia karroo, Atriplex semibacata var. appendiculata, Berkheya rigida, Cynodon dactylon, Eragrostis curvula, Felicia fasicularis, Panicum deustum, Sporobolus africanus, Tephrosia capensis, Withania somnifera
- G = Acacia cyclops, Cirsium vulgare, Solanum hermanii, Tagetes minuta
- H = Hermania flammea, Passerina vulgaris
- I = Pelargonium reniforme, Themeda triandra
- J = Cliffortia ilicifolia var. ilicifolia, Erica chamissonis var. chamissonis, Helichrysum cymosum subsp. cymosum
- K = Anthospermum aethiopicum, Erica copiosa var. copiosa, Hypodiscus striatus, Leucadendron salignum

**Figure 3:** Classification (TWINSPAN) of species for revegetated stands (1–16 years) and thicket and fynbos. Only species with abundance over 5% are listed

years (labelled B and C in Figure 4) to the older seral stands of ten and sixteen years (labelled D and E respectively in Figure 4). The wide dispersion of thicket samples suggests high beta diversity.

The species ordination (DCA) of thicket and revegetated stands presents the successional replacement of species (Figure 5). Pioneer species lie to the left of an x-ordination score of 1 (dashed line, Figure 5). Thicket species plot on the right of the x-ordination score of 5 (solid line, Figure 5). The seral species are scattered between these succession-

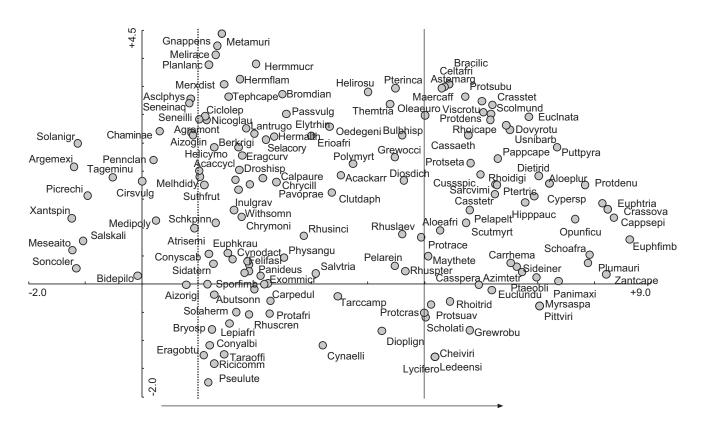


Figure 5: Ordination (DCA) of species of revegetated stands (left) and thicket (right) vegetation. The arrow represents the successional progression. Species codes are listed in Table 1

al extremes indicating gradual replacement of pioneer species with later successional ones, and in the older stands, some climax thicket species are found: e.g. *Grewia occidentalis*; *Olea europaea* subsp. *africana*; *Protasparagus racemosus* and *Schotia latifolia*.

Revegetated stands split at the third classification level where samples of one-year old stands separate from the rest at an eigenvalue of 0.5. *Tagetes minuta* was the indicator for the pioneer successional stage. Classification at the fourth level of division separated two- and six-year stands from older stands. The six- and ten-year stages could not be separated and were indicated by *Cynodon dactylon* while the oldest stage was a *Rhus incisa* var. *effusa–Panicum deustum* community.

Total vegetation cover of the revegetated stands increased with age (Figure 6). The vegetation cover of the 16-year stand was similar to that of thicket. The fynbos community had a lower total percentage cover than that of the thicket and the stands revegetated for 10 years and 16 years. The herbaceous layer had a steady increase in cover from one year to 10 years, after which there was a decline. The total cover of both the tree and shrub strata increased with time up to 16 years corresponding with the reduction in the herbaceous understorey. The thicket community had the highest cover of tree species (150%, Figure 6). By contrast, the fynbos community was composed primarily of a herbaceous layer as well as large contribution (150%) by the shrub component.

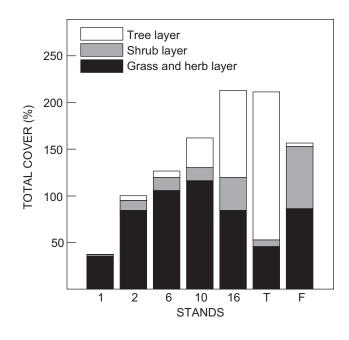
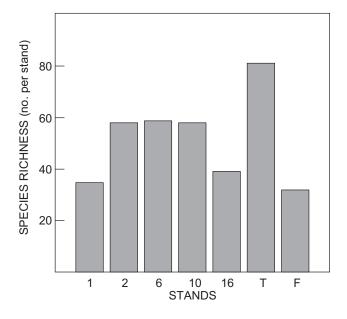


Figure 6: The total cover (as %) of different strata of the revegetated stands (1–16 years), thicket (T) and fynbos (F)



**Figure 7:** Species richness for the revegetated stands (1–16 years), thicket (T) and fynbos (F)

 Table 2: Percentage similarity of different aged revegetated stands to thicket and fynbos

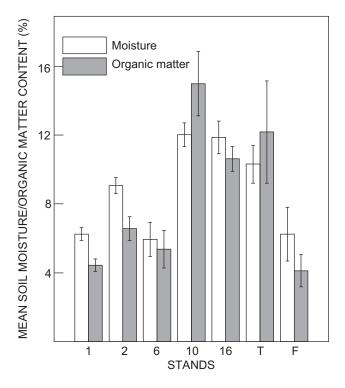
Sites	% similarity to thicket	% similarity to fynbos
1-year	2	2
2-year	20	5
6-year	22	11
10-year	34	6
16-year	46	15
Thicket	100	12
Fynbos	12	100

 
 Table 3: Survival success of thicket saplings planted at the revegetation test site

Tree species planted	Survival after 36 months (%)
Acacia karroo	100
Azima tetracantha	70
Diospyros dichrophylla	40
Grewia occidentalis	40
Olea europaea	25
Pterocelastrus tricuspidatus	0
Rhus undulata	100
Schotia afra	75
Schotia latifolia	50
Sideroxylon inerme	85
Tarchonanthus camphoratus	50

Species richness in the 1-year stand was almost half that found in the 2-year, 6-year and 10-year old stands (Figure 7). Species richness was lower in the 16-year stand. Thicket had the highest species richness (81 species) and fynbos the lowest.

The species similarity of the 16-year old revegetated



**Figure 8:** Average soil moisture and organic matter content for revegetated stands (1–16 years), thicket (T) and fynbos (F). Vertical bars indicate ±1 standard error of the mean

stands showed the highest similarity to thicket (Table 2) with 46% of the species found at the 16-year site being thicket species. Similarity increased with age of the revegetated stands. The 16-year site showed a very low similarity to fynbos (15%).

Soil moisture content and organic matter content increased significantly with the age of the revegetated stands (Figure 8; moisture: F = 7.6; df = 6; P < 0.001; organic matter: H' = 24.4; df = 6; P < 0.001). Early seral stages (1-year, 2-year, 6-year) showed no significant difference for either average soil moisture or organic matter content (P > 0.05). Soil samples taken from the fynbos site had a significantly lower (P < 0.05) soil moisture and organic matter content than thicket, 10-year or 16-year stands. Thicket and older revegetated soils had almost twice the organic matter content of fynbos soils.

Intervention by planting saplings of thicket species appears to be an option as survival rates of over 70% were recorded three years after planting for *Acacia karroo*, *Azima tetracantha*, *Rhus undulata*, *Schotia afra* and *Sideroxylon inerme* (Table 3). With the exception of *Pterocelastrus tricuspidatus*, some saplings of all the other species survived (lowest of 25%, Table 3).

## Discussion

#### Revegetation

The method of revegetation implemented at Loerie quarry in the 1980s was to let the stands revegetate through what Barbour *et al.* (1987) refer to as secondary succession. It was known that the soil used for the revegetation stands was obtained from areas previously covered by thicket and it was presumed that this vegetation type would regenerate through secondary succession as a result. However, the regeneration of thicket through a soil-stored seed bank is considered unlikely based on the findings of Aucamp and Tainton (1984), Stuart-Hill and Danckwerts (1988), Stuart-Hill (1991), Moolman and Cowling (1994).

#### Secondary succession

Using both the ordination and classification of samples and species it was possible to define successional species replacement within the revegetation samples (Figures 1-3). The early successional seral stage consisted of a dominance of weedy annual species (Picris echiodes, Salsola kali, Tagetes minuta and Xanthium spinosum). This was replaced by weedy perennial species (Berkheya rigida, Cirsium vulgare, Nicotiana glauca and Ricinus communis). The third seral stage consisted of grass and ground cover species such as Atriplex semibaccata var. appendiculata, Cynodon dactylon, Mesembryanthemum aitonis, Panicum maximum and Sporobolus africanus. The sub-climax stages (older than 10 years) contained tree and shrub species dominated by Acacia karroo, Clutia daphnoides, Polygala myrtifolia, Rhus incisa, and Rhus laevigata. This successional pathway follows that of Connell and Slayter's (1977) facilitation and tolerance modes of succession: facilitation where early pioneer plants alter the soil and site characteristics so as to make it suitable for other species to establish and tolerance is where the slower growing competitors eventually exclude the early dominant ruderal species.

The cover abundance of the tree and shrub component of revegetated stands increased with age of the stand and corresponds to a decrease in the herbaceous layer (Figure 6). The reduction in the herbaceous layer could be a result of canopy shading in that they are unable to compete for the sub-climax seral species light. This is supported by the decrease in species richness that occurred in the 10-year and 16-year stands (Figure 7) where trees and shrubs became dominant.

The low species richness of the 16-year old thicket (half that of intact thicket) indicates that it does not resemble that of thicket in terms of diversity (Figure 7), however, species composition was 46% similar to thicket.

The reduction in the understorey forb component and the consequent increase in the woody component (Figure 6) suggest that succession at the Loerie quarry is still midway through the facilitation and tolerance modes (Connell and Slayter 1977). An important observation is that the succulent and geophyte component was absent from the 16-year site. Cowling (1984) and Everard (1987) emphasise the importance of the succulent and geophytic components in thicket. Many of the rare and endemic species found in thicket are of these life forms (Dyer 1937, Cowling 1984, Everard 1987). The absence of these components in the 16-year stand further indicates that the revegetation stands have not yet developed into thicket. It is also unlikely that lower-storey succulents and geophytes will return to the system in time.

Resources in the succulent and geophytic life forms are usually allocated towards water storage and the build up of reserves and their reproductive strategy favours asexual rather than sexual reproduction (Cowling 1984). The low production of seed implies that a long time span is needed for the re-colonisation of species through seed. These strategies enable the species to survive adverse climatic conditions such as erratic rainfall (Cowling 1984) but hinder their return to successional areas.

The percentage distribution of the life forms in fynbos in comparison with the 16-year old revegetated stand further excludes fynbos as the vegetation type returning in these stands. There is a very large geophyte component in the fynbos vegetation in comparison with the vegetation from all the other stands analysed (Figure 7). The geophytic life form protects the underground vegetative parts from fire and thus allows the species to flourish after fire events. It is well established that fire is a driving force in the functioning of fynbos vegetation (Cowling 1984, Low and Rebelo 1996) and the absence of this important geophytic component in the 16-year revegetated stand rules out the possibility that the vegetation is developing towards fynbos.

The tree species dominant in the 16-year old revegetated stand were dominated by Acacia karroo, Rhus incisa and Polygala myrtifolia. Moll (1992) had similar findings in a study on the rehabilitation of Dune Thicket at Richards Bay. The dominance of Acacia karroo in 10-year old revegetated Dune Thicket was believed to have caused a reduction in the herb and grass layer of these stands. Although species richness was reduced after ten years it was found that after 50 years the A. karroo trees eventually died and were replaced by Dune Thicket tree and shrub species leaving only a few large individuals. Moll (1992) further reported on the importance of this species as a nurse species allowing shade tolerant thicket species to germinate under the canopy. It is believed that the build-up of organic matter and the retention of moisture under these thickets provides favourable environmental conditions for the establishment and growth of secondary thicket species that will eventually form the climax community in the rehabilitation of Dune Thicket (Moll 1992, Van Aarde and Smit 1997). It is possible that Acacia karroo might fulfil a similar function at Loerie with regards to the re-establishment of key thicket species. The tall A. karroo trees serve as perches for birds that have been recognised as the primary dispersers of seed in thicket (La Cock 1991). Observation suggests that these trees serve a function in this regard, with seedlings of *Clutia daphnoides*, Polygala myrtifolia, Rhus incisa and Scutia myrtina often found at the base of the A. karroo trees. These species are all dominant in Euclea-Pterocelastrus community of Kaffrarian Thicket described by Cowling (1984). It is possible that the microclimate under the canopy of the A. karroo trees is favourable for seed germination and the spinescent nature of the trees may also offer protection to the seedlings from herbivores.

It is interesting to note that this nurse tree association was also found under a few large *Acacia cyclops* trees found on the older revegetated stands. Seedlings of the same species found under *A. karroo* trees were also found under *A. cyclops*. Many large *A. cyclops* individuals had fallen over due to the canopy of the trees becoming top-heavy. Seedlings of *Clutia daphnoides*, *Polygala myrtifolia*, *Rhus incisa* and *Scutia myrtina* were found growing among the recently uprooted roots as well as underneath the branches of the fallen tree. Seeds of thicket species also germinated in the soil around the base of the fallen trees and this could be due to higher nutrient levels in the soil that would be associated with this leguminous alien species. Litter nitrogen inputs are greater for the alien acacias and this leads to an increase in the surface soil and litter layer nitrogen content (Witkowski 1991). It was also interesting to note that very few *A. cyclops* seedlings were found in association with the fallen adult trees indicating that seed from this species is unable to germinate and compete with the vegetation that has re-established.

Soil moisture and organic matter content increased with the age of the revegetated stands to a value similar to that of thicket (Figure 8). This can be attributed to the increase in vegetation cover. As the vegetation re-establishes itself at the revegetated stands, the increase in plant cover provides a favourable microclimate for the retention of moisture in the upper layers of the soil. Soil moisture content in the fynbos areas was low in comparison to the revegetated stands and thicket. The lower soil moisture content in the fynbos area could be attributed to the nature of the soil substrate. The soils of South Eastern Mountain Fynbos at Loerie are of the Oak-leaf soil form (MacVicar et al. 1977) and have a low clay content and are made up of sandy and gravel material that has a lower water holding capacity than the deeper Hutton soil form where thicket is found (Cowling 1984). A higher vegetation cover means that organic matter will be returned to the soil through leaf litter and the senescence of annual and perennial plants (Moll 1992).

#### Predicted climax state

Louw (1993) hypothesised that degraded thicket in the Loerie region would more likely regenerate towards Mountain fynbos rather than to the original thicket. This hypothesis can be rejected on the basis of the data presented. Analysis of the species composition, physiognomy and richness suggests that the vegetation is still in a state of flux and has not reached a climax state.

Although revegetation of the various stands has not returned them to the original vegetation state, vegetation has established and the soil environment has changed over a relatively short period of time. It is clear that the use of topsoil from areas previously covered with thicket provides the physical, chemical and biological attributes necessary for the rapid revegetation of mine areas. It is evident that the soil contains a large seed bank that contributes greatly to the speedy recovery of vegetation of these areas.

The older revegetated stands showed little invasion by exotic species with a few large *Acacia cyclops* individuals being found at the 10-year and 16-year old stands. Many of these individuals have already senesced and may be providing a habitat for the establishment of shrub species. It is evident from the small number of *A. cyclops* seedlings that the ground cover at these stands is preventing the germination of seed and the establishment of thickets. It is important

that the revegetated areas be protected from massive disturbance and fire as this will stimulate the germination of *A. cyclops* seed and the reduction in the ground cover will give the species a chance to establish.

It is widely recognised by many ecologists (Cowling 1984, Everard 1987, Lubke *et al.* 1986, La Cock 1991) that thicket does not recover after massive disturbance. This idea, however, is based on limited research with little data from long term monitoring of disturbed areas. It is imperative that areas such as Loerie be monitored over a long period to test this theory. It is also important that further research into other biological mechanisms such as seed dispersal, plantanimal interactions, soil nutrients and soil mycorrhizae be implemented in order to provide a greater understanding of the process of succession at Loerie quarry and of thicket in general.

Using ordination distance as a measure of successional progression, it can be predicted that the vegetation will require at least 50 years ( $r^2 = 0.874$ , n = 5, P < 0.05) to develop to a state that can be considered to be near-natural thicket (calculated from a power fit of time since rehabilitation against the mean distance of the samples from a 10% fringe around the ordination spread of natural thicket).

Knowledge gained from studying the processes of revegetation and succession at the Loerie quarry may be used to speed up revegetation programmes in the future. By planting some of the indicator and nurse tree species identified in this study it may be possible to revegetate land in a much shorter period of time, with reduced labour and financial input.

Acknowledgements — This study was financed by PPC Cement (Pty) Ltd with an additional contribution from the National Research Foundation's THRIP programme.

#### References

- Arnold TH, De Wet BC (1993) Plants of Southern Africa: Names and Distribution. Memoirs of the Botanical Survey of South Africa No.
  62. National Botanical Institute, Pretoria, 825pp. ISBN 1–874–90703–X
- Aucamp AJ, Tainton NM (1984) Veld Management in the Valley Bushveld of the Eastern Cape. Government Bulletin No. 401. Department of Agriculture, Pretoria, 34pp. ISBN 0–621–08857–9
- Barbour MG, Burk JH, Pitts WD (1987) Terrestrial Plant Ecology (2<sup>nd</sup> edn). Benjamin/Cummings Publishing Company, Menlo Park, 643pp. ISBN 0–805–30541–6
- Bell LC (1987) Before you start think of the finish. In: Mining and the Return of the Living Environment. Australian Mining Industry Council, Canberra, p 26
- Bradshaw AD (1990) The reclamation of derelict land and the ecology of ecosystems. In: Jordan WR, Gilpin ME, Aber JD (eds) Restoration Ecology, a Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, 230pp. ISBN 0–521–33110–2
- Cairns J (1989) Restoring damaged ecosystems: is predisturbance condition a viable option? The Environment Professional **11**: 152–159
- Carey LJ, Brooks DR (1985) Regeneration of tree species by direct seeding on North Stradbroke Island. In: Coleman RJ, Covacevich J, Davie P (eds) Focus on Stradbroke. Boolarang Publications, Brisbane, pp 25–37. ISBN 0–908–17581–7
- Camp P, Weisser PJ (1991) Dune rehabilitation, flora and plant suc-

cession after mining at Richards Bay, South Africa. In: Everard DA, Von Malitz GP (eds) Dune Forest Dynamics in Relation to Land-use Practices. Environmental Forum Report. FRD, Pretoria, p 172. ISBN 0–798–84952–5

- Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. American Naturalist **111**: 1119–1144
- Cowling RM (1984) A syntaxonomic and synecological study in the Humansdorp region of the fynbos Biome. Bothalia **15**: 175–227
- DeAngelis DL (1987) Equilibrium and nonequilibrium concepts in ecological models. Ecological Monographs **57**: 1–21
- Dyer RA (1937) The Vegetation of the Divisions of Albany and Bathurst. Memoirs of the Botanical Society of South Africa No. 17, Pretoria, 138pp
- Everard DA (1987) A classification of the subtropical transitional thicket in the eastern Cape, based on syntaxonomic and structural attributes. South African Journal of Botany **53**: 329–340
- Hardt RA, Forman RTT (1989) Boundary form effects on woody colonisation of reclaimed surface mines. Ecology **70**: 1252–1260
- Harris JA, Birch P, Palmer JP (1996) Land Restoration and Reclamation: Principles and Practice. Addison Wesley Longman Ltd, London, 230pp. ISBN 0–582–24313–0
- Hill MO (1979) TWINSPAN a FORTRAN Program for Arranging Multivariate Data in a Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology and Systematics Section, Cornell University, New York
- La Cock GD (1991) The Conservation Status of Subtropical Transitional Thicket, and the Regeneration Through Seeding of Shrubs in the Xeric Succulent Thicket of the Eastern Cape. MSc Thesis, Rhodes University, Grahamstown, 129pp
- Louw EP (1993) Vegetation analysis across the Gamtoos fault. BSc Honours project, Department of Botany, University of Port Elizabeth, 48pp
- Low AB, Rebelo AG (1996) Vegetation of South Africa, Lesotho and Swaziland: A Companion to the Vegetation Map of South Africa, Lesotho and Swaziland. The Department of Environmental Affairs and Tourism, Pretoria, 85pp. ISBN 0–621–17316–9
- Lubke RA, Everard DA, Jackson S (1986) The biomes of the eastern Cape with emphasis on their conservation. Bothalia **16**: 251–261
- Lubke RA (1996) Mesic Succulent Thicket. In: Low AB, Rebelo AG (eds) Vegetation of South Africa, Lesotho and Swaziland: A Companion to the Vegetation Map of South Africa, Lesotho and Swaziland. The Department of Environmental Affairs and Tourism, Pretoria, p 17. ISBN 0–621–17316–9

- MacMahon JA (1990) Disturbed lands and ecological theory: an essay about mutualistic association. In: Jordan WR, Gilpin ME, Aber JD (eds) Restoration Ecology, a Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, p 230. ISBN 0–521–33110–2
- Macvicar CN, De Villiers JM, Loxton RF, Verster E, Lambrechts JJN, Merryweather FR, Le Roux J, Van Rooyen TH, Harmse, HJ von M (1977) Soil Classification: A Binomal System for South Africa. Department of Agricultural Technical Services, Pretoria, 150pp. ISBN 0–621–03831–8
- Moll JB (1992) Studies on Dune Rehabilitation Techniques for Mined Areas at Richards Bay, Natal. MSc Thesis, Rhodes University. Grahamstown, 102pp
- Moolman HJ, Cowling RM (1994) The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. Biological Conservation **68**: 53–61
- Mueller-Dombois D, Ellenberg H (1974) Aims and Methods of Vegetation Ecology. John Wiley, New York, 547pp
- Shaw EG, Black MA (1985) Loerie Rehabilitation Programme. PPC Cement (Pty) Ltd, Loerie, 12pp
- Stuart-Hill GC (1991) Elephants, the rightful conservators of the Valley Bushveld. Veld and Flora **77**: 9–11
- Stuart-Hill GC, Danckwerts J (1988) Influence of domestic and wild animals on the future of succulent valley bushveld. Pelea 7: 45–56
- Ter Braak CJF (1988) Canonical Correspondence Analysis: a new Eigenvector technique for multivariate direct gradient analysis. Ecology **67**: 1167–1179
- Thrash I (1998) Association of three succulent plant species with woody canopy in the mixed bushveld, South Africa. Koedoe **41**: 95–101
- Van Aarde R, Smit A (1997) The Ecology of Rehabilitating Coastal Dunes at Richards Bay. Faculty of Biological and Agricultural Sciences, University of Pretoria, Pretoria, 68pp
- Witkowski ETF (1991) Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. Journal of Applied Ecology **28**: 1–15