

THE CONSERVATION STATUS OF SUBTROPICAL TRANSITIONAL
THICKET, AND REGENERATION THROUGH SEEDING OF SHRUBS IN
THE XERIC SUCCULENT THICKET OF THE EASTERN CAPE.

THESIS

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CONTENTS

	<u>Page</u>
CHAPTER 1. Introduction.	1
CHAPTER 2. Re-assessment of the area and conservation status of subtropical transitional thicket in the eastern Cape, South Africa.	14
CHAPTER 3. Germination and establishment of selected shrubs in the xeric succulent thicket of the eastern Cape.	23
CHAPTER 4. An <i>ad hoc</i> study of a black rhinoceros dung midden as a germination site for <i>Pappea capensis</i> seeds in xeric succulent thicket.	74
CHAPTER 5. Occurrence of saplings in the xeric succulent thicket of the eastern Cape.	84
CHAPTER 6. Conclusions and management proposals.	108
REFERENCES.	116
APPENDICES.	129

LIST OF TABLES.

<u>Table</u>	<u>page</u>
Table 1.1. Syntaxonomic and synecological relationships of higher vegetation units of subtropical transitional thicket in the eastern Cape.	1
Table 2.1. Listing of the five Landsat images which cover the subtropical transitional thicket in the eastern Cape.	17
Table 2.2. Conservation status of subtropical transitional thicket in the eastern Cape.	18
Table 2.3. Area of subtropical transitional thicket per 1: 250 000 topographical map: Acocks (1970) versus this survey.	19
Table 2.4. Area of subtropical transitional thicket in conservation areas in the eastern Cape.	20
Table 3.1. Tree and shrub species used in germination survey, their mean radius, the quadrat size used in sampling beneath them, and their primary dispersal mechanisms.	31
Table 3.2. Breakdown of number of plots surveyed, the starting date for each survey, and the surveys allocated to each season.	41
Table 3.3. Number of seedlings of each species at each site.	50
Table 3.4. Number of newly germinated seedlings under each nurse species at each site, the total seedling density (seedlings m ⁻²) under each species, and the mean seedling density under nurse species.	51
Table 3.5. Number of newly germinated seedlings at each site for each season.	54
Table 3.6. Number of newly germinated seedlings at each side of tree at each site.	59
Table 3.7. Soil properties of soil samples collected at the Andries Vosloo Kudu Reserve.	62
Table 5.1. Number of saplings of each species occurring at each site.	91
Table 5.2. Nurse plants under which saplings occurred for each site.	94
Table 5.3. Nurse plant - sapling relationships for the most commonly occurring nurse plants and	95

saplings.

	<u>page</u>
Table 5.4. Percentage open area and canopy cover for each site, and the relative dominance of each species.	98
Table 5.5. Level of protection from herbivory by large herbivores of saplings at each site.	99

LIST OF FIGURES.

<u>Figure</u>	<u>Page</u>
Figure 1.1. Map showing the extent of the four suborders of subtropical transitional thicket in the eastern Cape.	2
Figure 1.2. Map showing the boundaries of the three reserves.	9
Figure 1.3. The climate diagram for the Andries Vosloo Kudu Reserve.	11
Figure 1.4. Monthly rainfall at the Andries Vosloo Kudu Reserve for January 1989 to December 1990.	12
Figure 2.1. South African 1: 250 000 topographical sheets referred to in the text.	14
Figure 3.1. Examples of the vegetation sampled in open habitats.	32
Figure 3.2. Map showing the localities of survey sites at Andries Vosloo Kudu Reserve.	36
Figure 3.3. Examples of the vegetation at the six survey sites.	37
Figure 3.4. Examples of positioning of plots around tree.	39
Figure 3.5. Field map of north well vegetated site, showing random plot distribution.	43
Figure 3.6. Examples of the quadrat sizes and the grid system annotation used in each.	44
Figure 3.7. Joint cluster analysis of site and season of germination, showing decompositions of the chi-square at the two sets of nodes, and the cut-off point for significant clustering at the 95 % level.	56
Figure 3.8. Joint cluster analysis of side of tree and site of germination, showing decompositions of the chi-square at the two sets of nodes, and the cut-off point for significant clustering at the 95 % level.	58

page

Figure 3.9. Cluster analysis of site of germination versus seedling species, showing decompositions of the chi-square for the site of germination, and the cut-off point for significant clustering at the 95 % level.	60
Figure 3.10. Plot of the first and second principal components for the twelve soil variables (a) and the twenty-four soil samples (b).	63
Figure 4.1. Mean density of <i>Pappea capensis</i> seedlings in black rhinoceros midden and in control under canopy of <i>P. capensis</i> tree.	78
Figure 5.1. Basal diameter size class distribution for saplings of the three most commonly occurring species of saplings.	92

LIST OF APPENDICES

APPENDIX 1. BRIERS, J. H. & LA COCK, G. D. *submitted*. Tree successional dynamics of xeric Kaffrarian Thicket in an old land on the Thomas Baines Nature Reserve. *Journal of the Grassland society of southern Africa*.

APPENDIX 2. LA COCK, G. D., PALMER, A. R. & EVERARD, D. A. 1990. Re-assessment of the area and conservation status of subtropical transitional thicket (valley bushveld) in the eastern Cape, southern Africa. *South African Journal of Photogrammetry, Remote Sensing and Cartography* 15: 231-235.

APPENDIX 3. Assembled data of each seedling occurrence for successive surveys.

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ABSTRACT

The historically poorly conserved subtropical transitional thicket (STT) of the eastern Cape is overutilised by domestic stock and game in the more xeric areas, and has shown no signs of recovery from this grazing pressure. It has been postulated that no regeneration through seeding occurs.

This project was undertaken to determine: 1) how much STT has disappeared between 1950 and present, and what the current conservation status is; and 2) whether regeneration of the xeric succulent thicket is taking place through seeding, and if so, where. The study was conducted at the Andries Vosloo Kudu Reserve near Grahamstown.

Approximately one-third less STT was mapped in this study, based on 1981 Landsat images, than was mapped in 1950. Approximately 10 % of all remaining STT is conserved. The order Kaffrarian thicket is poorly conserved.

Newly germinated seedlings of a wide range of shrub species occurred under the canopies of a wide range of shrubs which served as nurse plants, throughout a gradient of veld condition. Seedlings of *Portulacaria afra*, the dominant shrub in xeric succulent thicket, were most common. Similarly all saplings recorded in a survey of saplings were associated with bushclumps. One-third of all saplings have the potential to contribute to the spread of bushclumps. Regeneration of xeric succulent thicket through seeding probably does occur, contrary to current ideas.

Ptareaoxylon obliquum was the most common sapling, despite mature trees now being scarce following earlier heavier utilisation. *P. obliquum* was also the nurse plant which

supported the highest density of newly germinated seedlings. The possible role of *P. obliquum* in the functioning of xeric succulent thicket is discussed.

The confinement of seedlings and saplings to areas under the canopies of trees and shrubs implies that the xeric succulent thicket will not recover rapidly if allowed to rest. Active management techniques will be necessary if rapid recovery is required. Bare areas between bushclumps may no longer be suitable germination habitats because of high Al concentrations.

There was no evidence to support the idea that germination and establishment of shrubs in clear areas is linked to episodic climatic events. Dung middens of recently reintroduced black rhinoceros may however aid in germination of seeds and establishment of seedlings under certain climatic conditions.

Recommendations for further studies, based on the findings of this project, are made. Possible management techniques aimed at the rapid recovery of this veld are suggested, and management proposals for the Sam Knott Nature Reserve/Andries Vosloo Kudu Reserve complex are made.

EXPLANATION OF TERMINOLOGY USED BY AUTHORS WHEN REFERRING TO SUBTROPICAL TRANSITIONAL THICKET.

Various authors or groups of authors have used different terminology for what is now referred to by botanists as subtropical transitional thicket. Certain authors refer to the sub-orders of subtropical transitional thicket. This different terminology may create confusion. The terminologies used by certain authors or groups will be explained below. These terminologies are especially relevant to Chapters 1 and 2.

Valley bushveld. Acocks (1988) Veld Type 23.

Subtropical transitional thicket. Cowling (1984), Everard (1987). This is essentially Acocks's valley bushveld, with portions of similar adjacent Acocks veld types included. Portions of coastal forest and thornveld (Acocks veld type = 1), Alexandria forest (2), noorsveld (24), and spekboomveld (25). The portions of these veld types included are very small, therefore subtropical transitional thicket and valley bushveld are essentially the same. Everard (1985, 1987) classified this vegetation into two orders each with two suborders, based on syntaxonomic and synecological relationships of higher vegetation units (see Chapter 1 for more detail).

Subtropical thicket. Lubke et al. (1986). This comprises valley bushveld, noorsveld, spekboomveld and dune thicket, in the eastern Cape.

Succulent valley bushveld. This is the term used by agriculturalists for the more xeric forms of subtropical transitional thicket (Everard's (1987) xeric succulent thicket and mesic succulent thicket), which can be used for small and large stock farming. The work of authors such as Aucamp and Stuart-Hill refer specifically to this region, although Aucamp & Tainton (1984) do use the term valley bushveld.

Palmer (1982) and Hoffman (1989a) worked in the xeric succulent thicket.

CHAPTER 1.

INTRODUCTION.

The subtropical transitional thicket (STT, sensu Everard 1987), essentially Acocks's (1988) valley bushveld, is the dominant vegetation type in the eastern Cape, comprising approximately 15 % of the region (Everard 1985, 1987, Palmer 1990a). It does not occur in one solid block, but is distributed along the coast, and up the river valleys and basins into the dry mountainous areas of the south-west (Aucamp & Tainton 1984, Lubke et al. 1988; Figure 1.1). The STT is a dense impenetrable thicket dominated by spiny woody shrubs and leaf and stem succulents. It has a wealth of growth forms, including evergreen, deciduous and succulent shrubs, geophytes, lianas, herbs, and grasses (Hoffman & Everard 1987). In more mesic areas the canopy can reach 5 m, but in xeric areas the canopy is 2 - 2,5 m (Everard 1987), with occasional larger canopy trees reaching up to 5 m.

Everard (1987) classified the STT into two orders and four suborders (Table 1.1; Figure 1.1), based on syntaxonomic and structural units which comply with those of

Table 1.1. Syntaxonomic and synecological relationships of higher vegetation units of subtropical transitional thicket in the eastern Cape (from Everard 1987).

Rank	Name	Structural characterization ¹	Distribution	Rainfall
Class	Subtropical thicket	Closed (mid-dense) large-leaved (succulent) shrubland	Kei to Gouritz Rivers	300-850
Order	Kaffrarian succulent thicket	Tall (mid-high) closed (mid-dense) large-leaved and succulent shrubland	Fish to Gouritz	300-450
	Xeric succulent thicket	Tall (mid-high) semi-closed (mid-dense) large-leaved and succulent shrubland	Fish to Bavinanskloof (inland areas)	300-400
	Mesic succulent thicket	Tall (mid-high) closed (dense) large-leaved and succulent shrubland	Sundays to Gamtoos River valleys	400-450
Order	Kaffrarian thicket	Tall (mid-high) closed (mid-dense) large-leaved (semi-succulent) shrubland	Kei to Gouritz in more mesic sites	550-850
	Xeric kaffrarian thicket	Tall (mid-high) closed (mid-dense) large-leaved and semi-succulent shrubland	Kei to Groot Brak River	550-700
	Mesic kaffrarian thicket	Tall (mid-high) closed (mid-dense) large-leaved shrubland	Kei to Buffalo River valleys	700-850

¹Structural characterization after Campbell *et al.* 1981

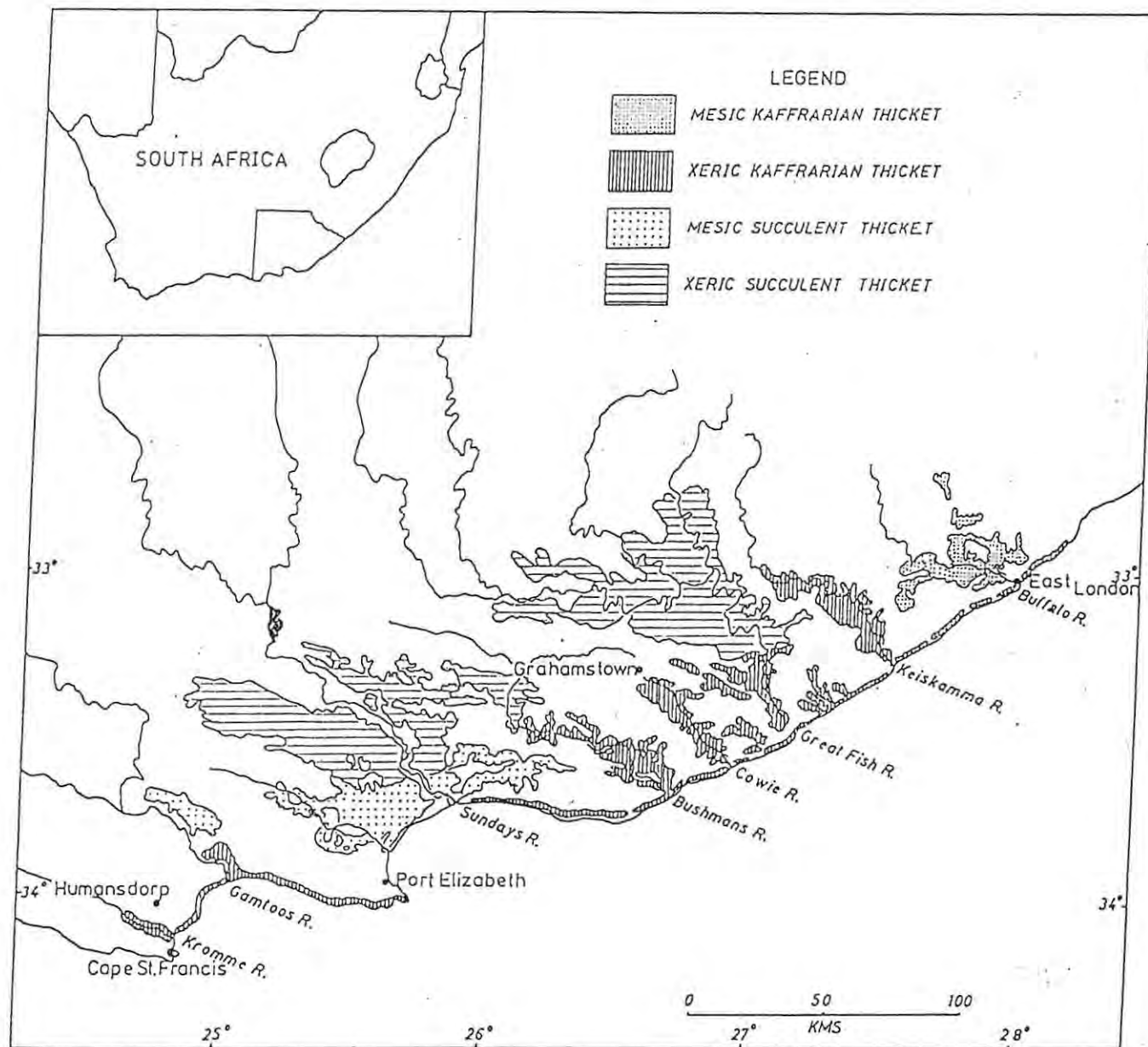


Figure 1.1. Map showing the extent of the four suborders of subtropical transitional thicket in the eastern Cape (from Everard 1987).

Cowling (1984).

The STT is subjected to a range of agricultural practices, ranging from bushclearing for crops such as chicory, pineapples and wheat in the more mesic areas (e.g. Hoffman & Everard 1987, Malan 1988) to intensive small and large stock farming in the more xeric areas. The boom in the mohair industry resulted in overutilisation of the veld by Angora goats in many areas.

The production base of this veld is the bush component (Stuart-Hill 1989). The annual productivity of this veld in the more xeric areas used for stock farming is low (Aucamp 1979), but there is a large accumulation of browse. Goats are able to destroy this accumulation without losing condition, therefore management based on animal condition can result in severe degradation of the veld. Veld denuded of shrubs by excessive grazing and browsing is not replaced by a more productive grass component as in other bushveld types, but rather by a form of false dwarf karroid veld comprising Karoo shrublets (Aucamp & Tainton 1984, Stuart-Hill 1989, pers obs).

Little is known about the dynamics of disturbed and undisturbed STT and its post-disturbance recovery, but it has been considered to be stable, with a low resilience (Cowling 1984, Hoffman & Cowling 1990). Post-disturbance recovery following overutilisation has been considered to be extremely slow to non-existent (e.g. Aucamp & Tainton 1984, Hoffman & Everard 1987, Stuart-Hill & Danckwerts 1988,

Stuart-Hill 1989). Stuart-Hill & Danckwerts (1988) and Stuart-Hill (1989) have postulated that there is little or no recruitment of woody species through seeding. Stuart-Hill (1989) suggested that seedling establishment may occur after episodic events, and data are needed to back up these statements.

Lubke et al. (1986) rated the subtropical thicket (= STT) as the vegetation type most in need of further investigation in the eastern Cape, based on the number of threatened taxa, threat to and uniqueness of the vegetation, conservation status, and past study. The area of conserved valley bushveld in southern Africa (Edwards 1974, Scheepers 1983) and the eastern Cape (Lubke et al. 1986, Palmer 1990) has generally been considered to be less than 2 %. These figures are based on the area of valley bushveld as mapped by Acocks in 1950 (Acocks 1970). Subsequently extensive bushclearing has taken place and large tracts of STT have been degraded through mismanagement of stock. Simultaneously new conservation areas have been established. The conservation status of STT was therefore in need of review.

At a meeting between parties interested in or working in the STT held in March 1988 it was decided that this project should concentrate on aspects of the regeneration of xeric succulent thicket, as opposed to the regeneration of old lands in xeric kaffrarian thicket. Aspects of the regeneration of old lands in the xeric kaffrarian thicket at the Thomas Baines Nature Reserve have, however, been studied

with J Briers (Appendix 1). It was decided that xeric succulent thicket should be a priority, because it has become degraded in large areas throughout its range through overutilisation by stock, and because it comprises approximately half of all the STT in the eastern Cape. The primary problem in xeric kaffrarian thicket is bushclearing for the planting of crops. This results in total destruction of all components of xeric Kaffrarian thicket at cleared sites, whereas components of the original vegetation may remain in the overutilised xeric succulent thicket.

On the basis of this preliminary analysis of the status of STT the major aims of this study were formulated as:

- 1.) to determine what effect the destruction of the veld has had on the extent and distribution of STT in the eastern Cape, and to determine its present conservation status (Chapter 2);
- 2.) to determine whether germination of seeds and subsequent establishment of seedlings of the shrub component does take place in the xeric succulent thicket, and if so, where and when (Chapters 3 & 4);
- 3.) to determine whether saplings occur in the xeric succulent thicket, and if so, where (Chapter 5);
- 4.) to provide managers with advice on the future management of their veld, based primarily on the findings of this study (Chapter 6).

The extent of xeric succulent thicket presently remaining, compared to the STT as mapped by Acocks in 1950 (Acocks 1970), and the current conservation status of STT, were studied and are presented as Chapter 2 and also in La Cock et al. (1990; Appendix 2).

Seed production does occur in the xeric succulent thicket (Palmer 1982, Hoffman 1989a, b), and seeds did germinate under nursery conditions. Seeds are therefore viable and would possibly germinate under field conditions. There is however no scientific information on the occurrence of seedlings in xeric succulent thicket. Further, post-disturbance recovery following heavy utilisation has been considered to be extremely slow to non-existent in the more xeric suborders of subtropical transitional thicket (e.g. Aucamp & Tainton 1984, Hoffman & Everard 1987, Stuart-Hill & Danckwerts 1988, Stuart-Hill 1989). This extremely slow recovery rate could therefore be as a result of a lack of, or alternatively a very low incidence of seed germination and seedling establishment. The hypothesis to be tested was therefore that seeds do germinate and that seedlings do become established in the xeric succulent thicket. This question of whether seed germination and seedling establishment of shrubs do in fact take place in the xeric succulent thicket, or whether germination failure is responsible for the failure of this vegetation type to recover from disturbance, was the subject of the second objective (Chapter 3).

The specific incidence of germination of Pappea capensis seeds in a black rhinoceros midden under a P. capensis tree was studied as an extension of the second objective (Chapter 4). Speculation on the possible role of episodic climatic events in the dynamics of the xeric succulent thicket also forms part of this chapter. This was an *ad hoc* study, but because of envisaged high populations of black rhinoceros in the xeric succulent thicket as a result of a reintroduction campaign, and a lack of knowledge on their influence on the vegetation, this study was considered worthy of inclusion. It must however be seen as once-off study of a possibly rare sequence of events. Detailed surveys of the role of rhino dung middens in seedling establishment will therefore need to be conducted once the black rhinoceros population has increased at the Andries Vosloo Kudu Reserve.

As a continuation of the rationale for the seedling survey, if seeds do germinate and seedlings do become established, the reason for a lack of recovery could be that seedlings do not survive to enter the system as saplings, ultimately recruiting to the reproductively active vegetation. The hypothesis to be tested was that saplings do occur. A sapling survey was therefore conducted to determine whether seedlings have in the past survived to become saplings, and thus potentially recruit to the system, and what role these saplings may play in the recovery of this vegetation (Chapter 5). The distribution of these

saplings could be a result of establishment coupled to episodic events, as postulated by Stuart-Hill (1989).

Management proposals aimed at improving degraded xeric succulent thicket, based primarily on the findings of this study, are presented, together with the general conclusions on this work (Chapter 6).

STUDY SITE

All of the surveys were conducted at the 6493 ha Andries Vosloo Kudu Reserve (AVKR) of Cape Nature Conservation, situated 40 km north of Grahamstown in the Great Fish River Valley. The AVKR is located between $33^{\circ} 04'$ and $33^{\circ} 09'$ S, and between $26^{\circ} 37'$ and $26^{\circ} 49'$ E. The altitude ranges from 182 m to 548 m. The AVKR was established in 1973.

To the north and east the AVKR borders on the 16 500 ha Sam Knott Nature Reserve (SKNR), established in 1987 and also run by Cape Nature Conservation. The entire AVKR/SKNR complex was surveyed for possible study sites, but the most appropriate sites for study, as defined in the methods for Chapter 3, were located at the AVKR. The Great Fish River forms the boundary between the AVKR/SKNR complex and the approximately 20 000 ha Double Drift Game Reserve of the Ciskei (Figure 1.2).

Palmer (1982) conducted a detailed botanical survey of the AVKR, and from this study and that of Everard (1987) one notes that the vegetation of all three reserves is dominated

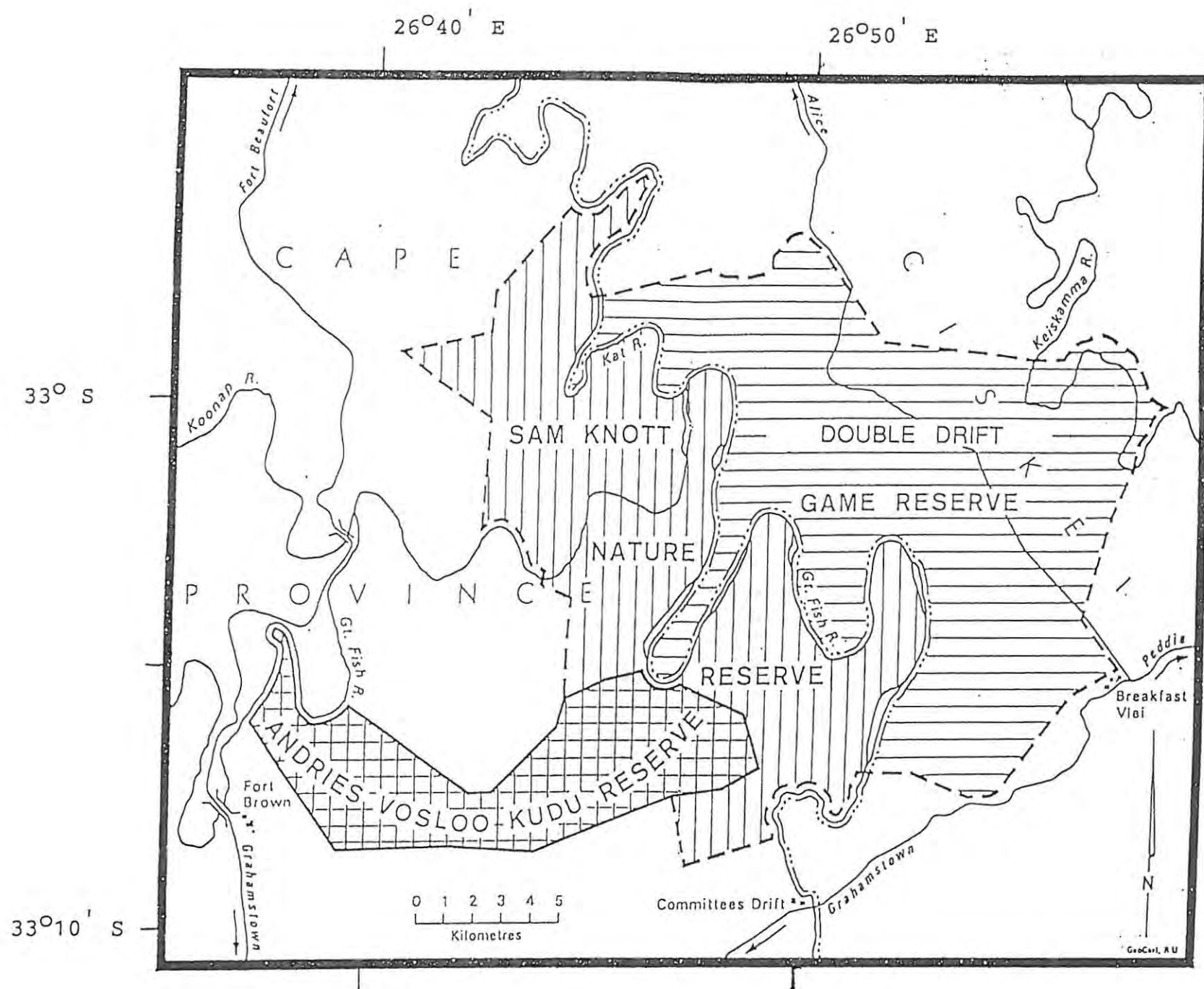


Figure 1.2. Map showing the boundaries of the three reserves.

by xeric succulent thicket, with some grasslands in the higher lying areas.

Prior to establishment the AVKR and SKNR were both utilised for domestic stock farming, and overutilisation of certain areas at both reserves is evident (pers obs). The AVKR was stocked with historically occurring game soon after establishment. Allen-Rowlandson (1980) considered the game numbers on the AVKR to be too high, and Palmer (1982) recommended that the reserve should not be heavily stocked. Introductions of game have started at the SKNR, and further introductions are planned for the immediate future.

Seed germination, seedling establishment and sapling survival may be affected by the presence of large browsers and grazers now common on the AVKR. These are warthog, African buffalo, greater kudu, eland, and red hartebeest. Black rhino have also been introduced. The AVKR is heavily utilised at present. Red hartebeest have been introduced to the SKNR, but their numbers are still low. Warthog have crossed the Great Fish River to the SKNR, and kudu occur there naturally.

The area is characterised by an unreliable, poorly distributed, relatively low rainfall of less than 500 mm, with a 25 % chance of receiving less than 80 % of the mean annual rainfall in a year (Aucamp & Tainton 1984). The mean annual rainfall at the AVKR is 434 mm, with peaks in March and October, and a winter trough (Palmer *et al.* 1988; Figure

1.3). Monthly rainfall for the year before and during the seedling survey (1989 & 1990) is expressed in Figure 1.4.

Mean monthly temperatures range between 16°C and 25°C , but summer maximum temperatures can reach 45°C , and winter minima can drop to -2°C (Palmer 1982). These high temperatures are favourable for germination and establishment of seedlings.

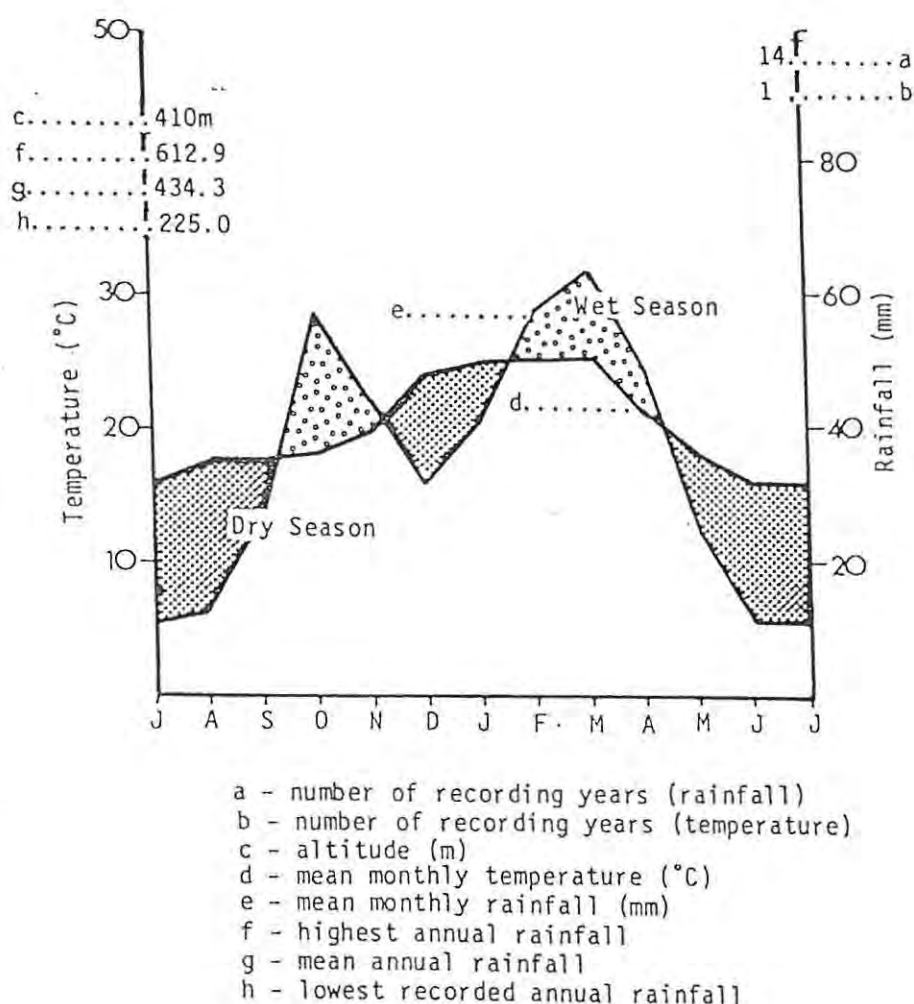


Figure 1.3. The climate diagram for the Andries Vosloo Kudu Reserve (from Palmer et al. 1988).

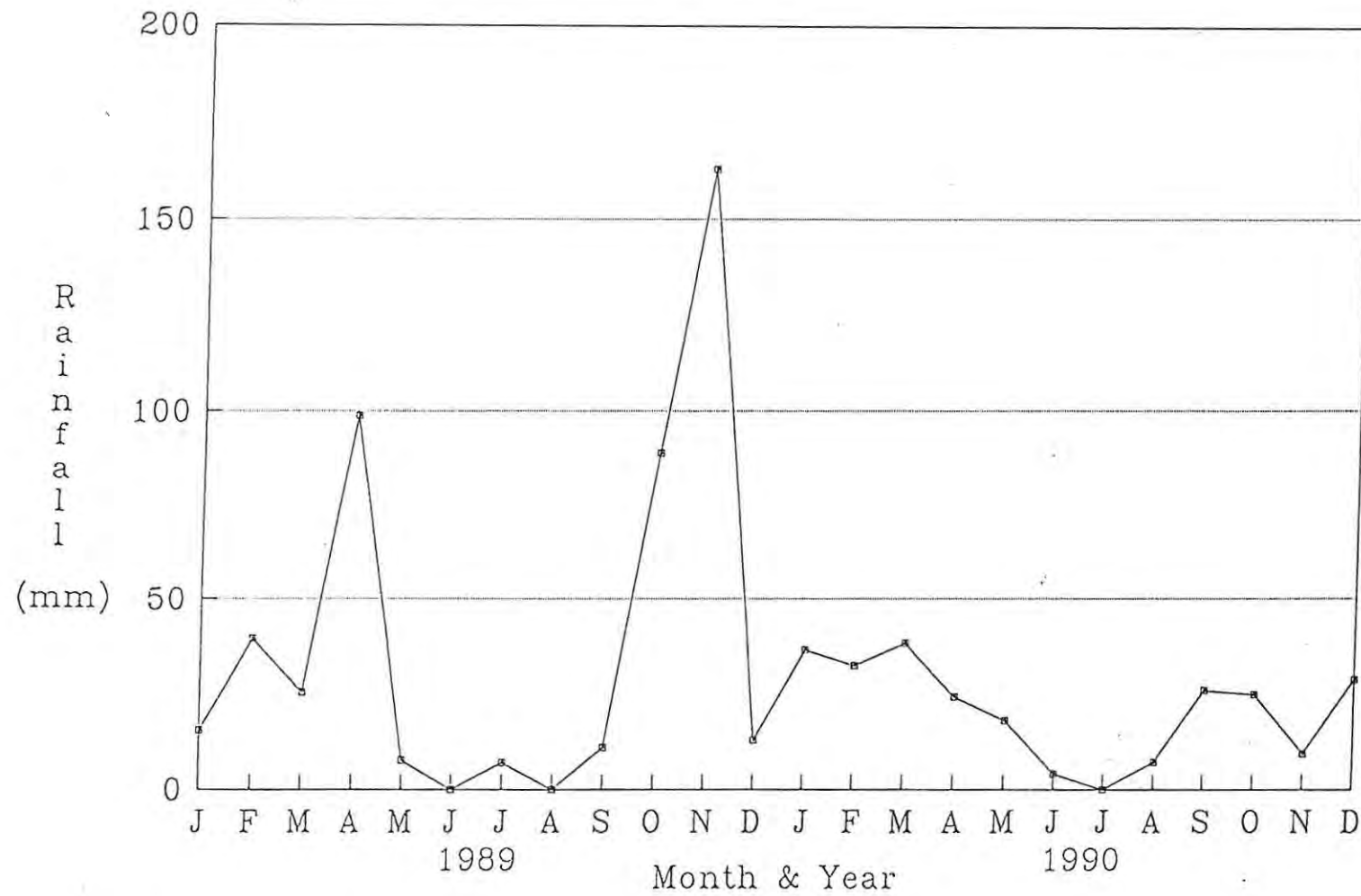


Figure 1.4. Monthly rainfall at the Andries Vosloo Kudu Reserve for January 1989 to December 1990.

The climate can be described according to the Koppen classification as *Cfa* (*C* = warm temperate climate - coldest month 18° C to -3° C; *f* = sufficient precipitation during all months; *a* = maximum temperature over 22° C) (Palmer et al. 1988).

Geologically the area comprises the Middleton formation, of the Adelaide subgroup of the Beaufort Group, and consists predominantly of grey and 'red' mudstone and sandstone (Johnson & Keyser 1976). The most abundant soil form on the AVKR is the Mispah form (MacVicar et al. 1977, Palmer 1981), in which the orthic A - horizon overlies parent rock. The soils are shallow, and associated with middle and upper pediment slopes (Palmer 1982).

CHAPTER 2

RE-ASSESSMENT OF THE AREA AND CONSERVATION STATUS OF SUBTROPICAL TRANSITIONAL THICKET IN THE EASTERN CAPE, SOUTHERN AFRICA.

INTRODUCTION

Valley bushveld (Acocks 1988), one of the most extensive vegetation types in the eastern Cape, southern Africa, is confined to the hot dry river valleys of the region (Lubke *et al.* 1988). Approximately 14028 km² of the eastern Cape, here defined as the area of southern Africa south of 32°S and east of 24°E (Figure 2.1), an area of 103 566 km²,



Figure 2.1. South African 1: 250 000 topographical sheets referred to in text.

comprised valley bushveld (Palmer 1990a). The vegetation is less than 5 m in height, dominated by spiny, woody shrubs, leaf, and stem succulents, and is possibly a recent (10 000BP) coloniser of the region as evidenced by strong

subtropical affinity, low endemism (Cowling 1984) and archaeological and palaeoclimatic evidence (Palmer 1990b). Valley bushveld, as well as portions of coastal forest and thornveld, spekboomveld, noorsveld and Alexandria forest, of the order subtropical transitional thicket (STT; Cowling 1984), have been classified into syntaxonomic and structural units (Everard 1987). Large tracts of STT are being cleared for crops (Hoffman & Everard 1987, Malan 1988). The boom in the mohair industry has also led to an increase in the grazing pressure on the STT.

Little is known about the dynamics of disturbed and undisturbed STT, and its post-disturbance recovery. STT has been considered to be stable, but with a low resilience (Cowling 1984). Hoffman & Everard (1987) considered the recruitment levels of shrubs within the STT to be low, and although adapted to a low disturbance regime, this vegetation will be slow to recover from high levels of disturbance, and unlikely to recover from severe disturbance. This poor recovery potential of the veld emphasises the need for its conservation.

Lubke et al. (1986) rated the subtropical thicket (=STT) as the vegetation type most in need of further investigation in the region, based on the number of threatened taxa, threat to and uniqueness of the vegetation, conservation status, and past study. The area of conserved valley bushveld in southern Africa has generally been considered to be less than 2 % (e.g. Edwards 1974, Scheepers

1983, Lubke et al. 1986, Palmer 1990a). The majority of these calculations were based on the area of the valley bushveld as mapped in 1950 (Acocks 1970). Subsequently, extensive debushing has taken place, and new conservation areas have been established.

Acocks (1970) produced his map following interpretation of monochromatic aerial photographs and extensive ground referencing. Since 1980, satellite-borne multi-spectral scanners (MSS) have provided another source of land-cover information in southern Africa. Recent mapping exercises in sub-tropical thicket of the eastern Cape (Palmer 1982, Everard 1985) investigated the possibility of mapping thicket from Landsat MSS data. The high aerial cover and greenness of thicket make it discernible in the infra-red spectral bands.

The aim of this study was to determine the total area and conserved area of STT in the eastern Cape; and the area which has been cultivated or developed and is of no further conservation value.

METHODS

Manual interpretation techniques (Harrington & Dunn 1980) were applied to Landsat imagery (1:1 000 000 edge-enhanced three band colour composites; Table 2.1) to map each suborder of the STT, and the area of transformed land. The 1:1 000 000 images were projected at a scale of 1:250 000 and registered with the relevant South Africa 1:250 000 Topo-cadastral sheets. Using Everard's (1985) map as ground

reference data, each image was manually classified into: the four suborders of STT; transformed land; and undifferentiated natural vegetation (non-STT) for each of the South Africa 1:250 000 Topo-cadastral sheets on which Everard (1987) had mapped STT (3226 King Williams Town, 3228 Kei Mouth, 3324 Port Elizabeth, and 3326 East London).

Table 2.1. Listing of the five Landsat images which cover the subtropical transitional thicket in the eastern Cape. Scene ID uniquely identifies a particular Landsat Scene. The form of the ID is SDDDDHHMMS, where S= spacecraft number, DDDD = days since launch for that spacecraft, HHMMS=Greenwich Mean Time (GMT) of scene centre in hours minutes and tens of seconds. WRS is the world wide reference system, track and frame.

SCENE ID	WRS	DATE	TIME	CENTRE
22314-07241	183-83	24/5/81	09H24	33°14'S 25°12'E
22169-07200	182-83/84	30/12/80	09H00	33°54'S 26°46'E
22169-07195	182-83	30/12/80	09H20	33°19'S 26°58'E
22456-07105	181-83	13/10/81	09H11	33°07'S 27°56'E
22456-07103	181-82	13/10/81	09H00	31°40'S 28°24'E

Everard's (1985) map of STT is at a scale of 1:2 500 000, and proved unsuitable for the calculation of areas of land. We enlarged this map to a scale of 1:250 000 and we accepted his boundaries between the suborders of STT for our maps. We considered the width of the coastal strip of xeric Kaffrarian thicket as depicted in Everard (1987) to be an over-representation of the actual width of this strip, which was seldom discernible on the imagery.

The polygons representing each suborder of STT and transformed land were cut out and their areas determined

using a calibrated AAC-400 Automatic Areameter. Calculations were based on the area of each South Africa 1:250 000 Topocadastral sheet (Palmer 1990a), with details of conserved areas extracted from Anonymous (1987), Van Wyk *et al.* (1988) and personal communications from conservation authorities.

RESULTS

The total land area is 61 645 km² (Palmer 1990a), of which 5436 km² (9 %) has been permanently transformed by debushing and is no longer of any conservation value. Acocks (1970) mapped 13 730 km² of the area as STT, whereas this survey recorded 9 179 km² (67 % of Acocks 1970; Table 2.2).

Table 2.2. Area of STT per 1:250000 Topographical map: Acocks (1970) vs this survey.

1:250000 map	1950	1981	% remaining
3226 King Williams Town	4251km ²	1309km ²	31
3228 Kei Mouth	1404	661	47
3324 Port Elizabeth	4304	3494	81
3326 East London	3771	3715	99
Total	13730	9179	67

Xeric succulent thicket comprised 51 % (4 657 km²) of STT (Table 2.3), and had the largest conserved area (531 km²; 11 %). Mesic succulent thicket had the highest percentage area under conservation (19 %; 283 km²). The mesic and xeric Kaffrarian thicket are both poorly conserved (2 % and 3 % respectively), in terms of the IUCN (1980) recommendation that 10 % of each vegetation type must be conserved. Ten

percent of the STT mapped in this exercise is conserved, and 6 % of Acocks (1970; Table 2.3).

Table 2.3. Conservation status of Subtropical Transitional Thicket in the eastern Cape.

Vegetation type	Area (km ²)	% of STT	Area cons. (km ²)	% cons.
order: Kaffrarian succulent thicket				
suborder: mesic succulent thicket	1488	16	283	19
suborder: xeric succulent thicket	4657	51	531	11
TOTAL: KAFFRARIAN SUCCULENT THICKET	6145	67	814	13
order: Kaffrarian thicket				
suborder: mesic Kaffrarian thicket	842	9	17	2
suborder: xeric Kaffrarian thicket	2192	24	63	3
TOTAL: KAFFRARIAN THICKET	3034	33	80	3
SUBTROPICAL TRANSITIONAL THICKET	9179	100	894	10

Subtropical transitional thicket occurs at thirty conservation sites, with the area of conserved STT at these sites ranging from 0,1 to 176,75 km² (Table 2.4). Six conservation sites contain mesic Kaffrarian thicket (Table 2.4), ranging in size from 10-691 ha. Xeric Kaffrarian thicket occurs in nine conservation sites, and ranges in extent from 67-4 259 ha, with eight sites under 550 ha. The six areas of conserved mesic succulent thicket range in size from 15-17 675 ha. including ding two of over 5 000 ha. The nine conserved areas of xeric succulent thicket range in size from 10-15 895 ha. Five of these are over 5 000 ha and two over 2 500 ha (Table 2.4).

Table 2.4. Area of STT in conservation areas in the eastern Cape.

	Size (km ²)
Mesic Succulent Thicket	
Uitenhage Nature Reserve	3,50
Yellowwoods Nature Reserve	,15
Loerie Nature Reserve	7,00
Groendal Wilderness Area	83,47
Alexandria State Forest	12,50
Formosa/Cockscomb/Kouga-	
Baviaanskloof Wilderness area	176,75
Total	283,37
Xeric Succulent Thicket	
Addo Elephant National Park	85,96
Andries Vosloo Kudu Reserve	56,76
Sam Knott Nature Reserve	158,95
Ecca Nature Reserve	1,28
Double Drift Game Reserve	100,00
Grahamstown Military Training Area	31,95
Adelaide Nature Conservation Station	,10
Zuurberg National Park/Boplaas	95,31
Total	530,27
Mesic Kaffrarian Thicket	
Bridle Drift Nature Reserve	1,50
Fort Pato Nature Reserve	6,91
King Williams Town Nature Reserve	,60
Umtiza Nature Reserve	5,55
Amalinda Nature Conservation Station	,10
Fort Gray Nature Reserve	1,97
Total	16,63
Xeric Kaffrarian Thicket	
Thomas Baines Nature Reserve	5,50
Waters Meeting Nature Reserve	42,59
Kowie Nature Reserve	2,60
Blaauwkrantz Nature Reserve	1,69
Cycad Nature Reserve	,89
T. Fitzgerald Private Nature Reserve	2,00
Ghio Wetland Reserve	,67
Kap River State Forest	2,86
Merville Private Nature Reserve	4,00
Total	62,80

DISCUSSION

A proportion of the difference between the area of STT in Acocks (1970) and this study (Table 2.3) could be attributable to Acocks (1988) recognising veld types as units of "farming potential" and not excluding areas where natural vegetation had been cleared (Moll & Bossi 1984). Acocks (1970) included areas which had been previously cleared such as Port Elizabeth and East London as valley bushveld. These urban areas as well as irrigation schemes have increased significantly in size since early mapping efforts.

It is evident that much of what was previously STT has been permanently transformed, especially the narrow strips along the fertile river valleys and in areas suitable for crops. A recent development has been the debushing of marginal areas for wheat in the Paterson district (Malan 1988). This attempted use of marginal ground has failed due to the rainfall patterns in the STT (Hoffman & Everard 1987).

Areas overutilised by livestock probably constitute a major source of transformed land in the STT. They could not be differentiated from healthy STT using the method applied because the dominant perennial shrubs are the last component to disappear and continue to provide good aerial cover and greenness. Aucamp & Tainton (1984) considered these over-utilised sites to be permanently transformed. Further

research effort should be made to differentiate between healthy and overutilised STT.

CONCLUSIONS

STT has changed from having one of the lowest percentage areas conserved to having one of the highest, however the conservation status of the order Kaffrarian thicket remains inadequate. The remaining areas of STT are almost exclusively used for farming, and the future conservation effort lies in educating the farmers not to overutilise the vegetation and not to debush marginal areas for crops. It is suggested that future conservation status calculations be based on these data.

CHAPTER 3

GERMINATION AND ESTABLISHMENT OF SELECTED SHRUBS IN THE XERIC SUCCULENT THICKET OF THE EASTERN CAPE.

INTRODUCTION

Subtropical transitional thicket has been considered to be stable with a low resilience (Cowling 1984, Hoffman & Cowling 1990), and post-disturbance recovery following heavy utilisation has been considered to be extremely slow to non-existent (e.g. Aucamp & Tainton 1984, Hoffman & Everard 1987, Stuart-Hill & Danckwerts 1988, Stuart-Hill 1989).

Lubke *et al.* (1986) rated the subtropical thicket as the most threatened vegetation type, and as the vegetation type most in need of research, in the eastern Cape. Until now, studies in the subtropical transitional thicket have predominantly been of a descriptive nature (e.g. Palmer 1982, Cowling 1982, 1984, Everard 1985, 1987, Hoffmann 1989a), therefore very little is known about the dynamics of subtropical transitional thicket. Stuart-Hill & Danckwerts (1988) and Stuart-Hill (1989) did, however, postulate that there is little or no recruitment of woody species through seeding in the xeric succulent thicket.

Seed production of woody shrubs has occurred in the subtropical transitional thicket (e.g. Palmer 1982, Pierce & Cowling 1984, Hoffman 1989a, b), and more specifically in the xeric succulent thicket (Palmer 1982, Hoffman 1989a, b). These seeds do germinate under nursery conditions, and will possibly germinate in the field. There are, however, no

published records of seedlings in the xeric succulent thicket, although they may have been observed by workers in the field. I myself am, however, unaware of observations of large numbers of seedlings by agriculturalists, academics, and conservationists working in the field. None of these people reported such occurrences to me during the planning phases of this project and during its execution, despite regular contact.

This study was conducted to determine whether a lack of germination and establishment was responsible for the failure of this vegetation to recover from disturbance. The key questions associated with this study were: 1) does seed germination and seedling establishment occur; and 2) if so, where and when does germination and establishment occur?

RESEARCH INTO THE DYNAMIC PROCESSES GOVERNING SIMILAR VEGETATION TYPES.

Many studies carried out in Chile, Australia, and North America in similar vegetation types are relevant to this study, and are briefly reviewed here under the following headings.

Maintenance of bushclumps through seeding.

In Chilean matorral bushclumps, Fuentes et al. (1984, 1986) showed that:

- 1) seed rain of bird dispersed species was important only around bird perches;
- 2) the seed shadow of mature matorral shrubs was small ;

- 3) nursing by shrubs, and not by rocks or fallen branches, was a requirement for survival of shrub seedlings ;
- 4) seedlings in bushclumps were more protected from herbivory and desiccation than seedlings would be in the open;
- 5) there were fewer seeds between bushclumps;
- 6) there were no seedlings of the major shrubs in open areas, with seedlings in the open being restricted to a ubiquitous "weedy" shrub;
- 7) the presence of seeds and seedlings of wind dispersed species was concentrated in bushclumps because of interception of seeds or reduced wind speed in clumps; and
- 8) the density of predators and risk of seedling predation may increase rapidly with increasing bushclump size, thereby restricting the maximum size of bushclumps.

Fuentes et al. (1986) further suggested that colonisation of clear areas occurred by a slow diffusion process by which the bushclumps increase in diameter, although they did not observe any changes in bushclump size over 26 years.

Role of nurse plants in seedling establishment.

In Chile bushclumps have been associated with a wide range of nurse plants (e.g. Fuentes et al. 1984, 1986). Similarly no single species could be identified as the main nurse in all bushclumps in the xeric succulent thicket (pers. obs). This matter does, however, require further investigation. In the more mesic xeric Kaffrarian thicket,

however, Acacia karroo and Rhus undulata fulfill the roles of pioneer species on cleared lands (Appendix 1). In matorral the ubiquitous composite Bacharris species and Acacia caven, a heavy-seeded legume, have invaded abandoned lands in certain areas (Fuentes et al. 1986), where they act as nurse plants. In certain coastal areas there has however been no invasion by shrubs of abandoned lands. Similar invasion of abandoned lands by A. karroo occurs in the Transkei (McKenzie 1989). In the Rio Grande Plains of Texas mesquite Prosopis glandulosa was the key species around which bushclumps formed, in the conversion of grasslands and savannah to closed-canopy woodlands (Archer et al. 1988).

Effect of exotic mammals on seedlings.

Exotic mammals have been implicated in the degeneration of veld. In Australia many arid zone trees and tall shrubs appear to be headed for extinction (cf Lange & Willcocks 1980), because of selective elimination of their seedlings by introduced sheep and rabbits (e.g. Crisp 1978, Fatchen 1978, Lange & Purdie 1976, Lange & Graham 1983).

In the Chilean matorral introduced European rabbits Oryctolagus cuniculus were capable of killing most shrub seedlings (e.g. Fuentes et al. 1983), as opposed to indigenous small mammals which only had an effect on seedlings concentrated around their refuge areas (Fuentes & Simonetti 1982, Fuentes et al. 1983). Fuentes et al. (1983) postulated that European rabbits may be halting the

secondary succession process, affecting the composition of matorral, and broadening the spacing between bushclumps.

European rabbits are indigenous to the Spanish maquis, and are confined to refuges by predatory pressure. These predatory pressures are released in the Chilean matorral, and the European rabbits occupy open areas they would not have normally inhabited in Spain (Jaksic & Soriguer 1981). Indigenous small mammals in Chile however remain confined to refuges by predatory pressure. European rabbits were introduced to Chile in the 1930's, and are now considered to be one of the most important components of the matorral (Jaksic *et al.* 1979).

Larger herbivores, both grazers and browsers, e.g. goats, sheep and cattle, have under incorrect management practices, had a detrimental effect on both the woody and herbaceous component of similar vegetation types similar to the subtropical transitional thicket, throughout the world (see Conrad & Oechel 1982). Goats had a more detrimental effect on Chilean matorral than indigenous herbivores (Fuentes & Simonetti 1982).

Maintenance of bare areas around bushclumps and effect of overutilisation on soil properties.

Fuentes *et al.* (1984) postulated that matorral bushclumps with open areas in between are a natural phenomenon, and not necessarily man-induced as previously proposed (see Mooney 1977). In Chilean matorral distinct bushclumps occur in more xeric areas, and only merge to form

a continuous vegetation matrix in more mesic areas (Fuentes et al. 1984, 1986). Similarly in southern Africa subtropical transitional thicket ranges from a bushclump mosaic in more xeric areas to a continuous vegetation matrix in mesic areas (Everard 1985, 1987).

Bare zones adjacent to and between bushclumps are a feature of the xeric succulent thicket (pers. obs). Similar bare zones are characteristic of the Californian chaparral (e.g. Bartholomew 1970) and the matorral (cf. Fuentes et al. 1983). Wells (1964) suggested that cattle grazing and trails were responsible for this zone in the chaparral, but allelopathic reactions between shrubs and herbs has been proposed as an alternative to cattle activity (e.g. Muller et al. 1964, McPherson & Muller 1969, Chou & Muller 1972). Muller et al. (1964) demonstrated that plant toxins from certain chaparral shrubs were capable of inhibiting seedling germination, but toxins do not occur at toxic levels under field conditions (Bartholomew 1970). Bartholomew (1970) demonstrated that a concentration of animal activity (rodents, rabbits, birds) in the bare zones was sufficient to maintain the bare zones. Similarly Jaksic & Fuentes (1980) demonstrated that grazing, probably by rabbits, was responsible for a scarcity of native herbs between bushclumps in the Chilean matorral. Allelopathy between shrubs and herbs has been discounted in the Chilean matorral (Montenegro et al. 1982). Keeley and Johnson (1977)

associated bare zones with heavy grazing by domestic stock or microclimatic factors, e.g. desiccation.

Soil properties of rangelands are negatively affected by grazing, especially heavy grazing. Features of soils on heavily utilised rangelands include: reduced water infiltration rates (e.g. Gifford & Hawkins 1978, Braunack & Walker 1985, Rostagno 1989); reduced water retention (e.g. Klemmenson 1956); lower organic content (e.g. Klemmenson 1956); nutrient loss (e.g. Charley & Cowling 1968); lower soil fertility than under trees (e.g. Belsky *et al.* 1989); increased surface soil hardness (e.g. Braunack & Walker 1985); and soil compaction (e.g. Knoll & Hopkins 1959, Webb & Wilshire 1980). In arid zones where vegetation and soils have been severely disturbed, vegetation recovery time may be in excess of 100 years (Webb & Wilshire 1980), and longer where soil compaction has occurred.

METHODS

A study of this nature is always prone to pseudoreplication (Hurlbert 1984). Although it is preferable to avoid pseudoreplication, this is sometimes impossible for practical reasons (e.g. Hawkins 1986). In this study sites were pseudoreplicated with reference to soil conditions, because there were no other soil types at the reserve. Similarly, the aim of the project was to determine if seeds germinated and seedlings became established in the xeric succulent thicket. This took one year of intensive surveys, and the climatic conditions during this year were not

anomolous (see Chapter 1). It would have been ideal to continue surveys for a few years to incorporate anomolous events, but the additional expense of keeping three people each in the field for an effective four months per year, until surveys were conducted during an episodic event, was clearly unacceptable.

Similarly if I was to avoid using the same quadrats for successive surveys, I would have had to lay out a new series of plots for each season. The laying out of the plots used in this survey took four people approximately two months. New plots for each season would be neccessary, because all plots for each season would have had to be surveyed before the start of the season to ensure that only newly germinated seedlings were recorded. This was obviously not feasible, therefore permanent plots were used. There would have also been increased variation between random plots, which could have affected germination patterns.

Selection of study species.

This germination study was conducted under the canopies of thirteen shrub and tree species (Table 3.1), as well as in open bare, karroid, and grassy areas (Figure 3.1). The criterion for selecting the shrub or tree species was that they were relatively common and widespread in the reserve, or, as in the case of Ptaeroxylon obliquum, had previously been fairly common (Moorcroft 1988). Earlier studies on the vegetation of the AVKR (Palmer 1982; Everard 1985, 1987) were consulted for a list of potential study species. The

Table 3.1. Tree and shrub species used in germination survey, their mean radius, the quadrat size used in sampling beneath them, and their primary dispersal mechanisms.

<u>Species</u>	<u>mean radius</u>	<u>quadrat size</u>	<u>primary dispersal mechanism</u>
<i>Azima tetracantha</i> Lam. (Salvadoraceae)	1.37	1 x 1m	birds
<i>Brachylaena ilicifolia</i> (Lam.) Phill. & Schweik (Asteraceae)	0.96	0.5 x 0.5m	wind
<i>Euclea undulata</i> Thunb. var <i>undulata</i> (Ebenaceae)	1.78	1 x 1m	birds, mammals
<i>Grewia robusta</i> Burch. (Tiliaceae)	1.46	1 x 1m	birds
<i>Jatropha capensis</i> (L.F.) Sond. (Euphorbiaceae)	0.57	0.5 x 0.5m	mechanical?
<i>Maytenus capitata</i> (E. Mey. Ex Sond.) Marais (Celastraceae)	1.33	1 x 1m	mechanical?
<i>Ozoroa mucronata</i> (Bernh. Ex Krauss) R. & A. Fernandes (Anacardiaceae)	2.09	1 x 1m	birds
<i>Portulacaria afra</i> Jacq. (Portulacaceae)	2.02	1 x 1m	wind
<i>Pappea capensis</i> Eckl. & Zeyh. (Sapindaceae)	2.47	1 x 1m	birds, mammals
<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk. (Ptaeroxylaceae)	1.13	0.5 x 0.5m	wind
<i>Phyllanthus verrucosus</i> Thunb. (Euphorbiaceae)	0.54	0.5 x 0.5m	mechanical
<i>Rhigozum obovatum</i> Burch. (Bignoniaceae)	0.91	0.5 x 0.5m	wind
<i>Schotia afra</i> (L.) Thunb. var. <i>angustifolia</i> (E. Mey.) Harv. (Fabaceae)	2.23	1 x 1m	mammals



(a)



(b)



(c)

Figure 3.1. Examples of the vegetation sampled in open habitats: a) bare area surrounded by bush dominated by Portulacaria afra; b) karroid area; c) grassy area

distribution of each of the study species throughout the four suborders of the subtropical transitional thicket of the eastern Cape appeared in Everard (1987). Everard (1987) also gave details of the biotic and abiotic conditions prevalent in each of the suborders.

Seeds of all the study species were collected from the reserves if available. Rhigozum obovatum seed was obtained from the Kirstenbosch Botanical Gardens, and Portulacaria afra seeds from the University of Port Elizabeth. Seeds of other tree and shrub species not included in the study were collected if encountered. Seeds were germinated, and seedlings were photographed and pressed, and made into field herbarium sheets to aid seedling identification in the field. During the survey, seedlings were often identifiable by the presence of cotyledons, distinctive first leaves, and thin fleshy stems. All seedlings were less than six weeks old when first encountered, because of the sampling interval. It was therefore usually possible to immediately identify the seedling as newly germinated. Excavations of seedlings from sites outside the permanent plots confirmed that seedlings in the veld were similar in appearance to those grown in the nursery. Suckers from roots of parent plants tended to have woodier stems. Further, seedlings were often recorded many metres away from a parent plant of the same species, thereby discounting vegetative reproduction. I am confident that the results reflect only newly germinated seedlings.

Site selection.

Sites were selected on north and south facing slopes across a gradient of vegetation condition, from poorly vegetated through moderately vegetated to well vegetated veld, with reference specifically to the aerial cover of the shrub component, and as determined from experience. This gradient has specific reference to the vegetation of the AVKR, and does not reflect veld condition of sites outside the reserve.

Vegetation cover was assessed from the most recent series of aerial photographs of the two reserves, in conjunction with an aerial survey in a fixed-wing aeroplane. Possible sites were plotted on a map of the reserves. These possible sites were then assessed by means of ground surveys. Sites had to meet the following criteria: 1) slope less than 1:10; 2) vegetation not dominated by tree euphorbias; 3) all or most of the thirteen study species present; 4) north and south facing slopes in each vegetation condition had to be as close to one another as possible.

Where all study species were not present in a selected site a nearby site of similar condition with the missing species present was selected. All species were present at the well vegetated sites; Azima tetracantha was not present at the moderately vegetated sites, and two alternative sites were used ; Jatropha capensis and Ptaeroxylon obliquum were not present at the poorly vegetated sites, and two

alternative sites were used. All the chosen sites were located at the AVKR (Figure 3.2). Examples of the vegetation at each site appear in Figure 3.3.

Plot selection.

Wind direction, shade, and the direction from which the prevailing rain falls could play an important role in the germination and establishment of seedlings, therefore it was decided to lay out the plots on the N, S, E and W side of a tree or shrub. The under canopy area surrounding the stem of the tree was avoided, because the surface area available for seedling establishment would vary according to the circumference of the tree trunk at ground level. The surveyed area had to be standard for comparative purposes.

Five specimens of each species, or the equivalent needed for five N, S, E and W combinations, were selected at each site. These trees had to be free of other trees, or where unavoidable had to have the dominant canopy in an entanglement of two trees. It was not always possible to fit the N, S, E, and W plot under the same tree, therefore the plots were often divided between two to four trees. The number of shrubs and trees under which plots were laid out was therefore not constant between species and sites, but the area sampled was standard for each species. The layout of plots around nurse species is presented in Figure 3.4.

In order to determine the quadrat size to be used for seedling survey plots under each species of nurse plant, the mean radius of large individuals of each species was

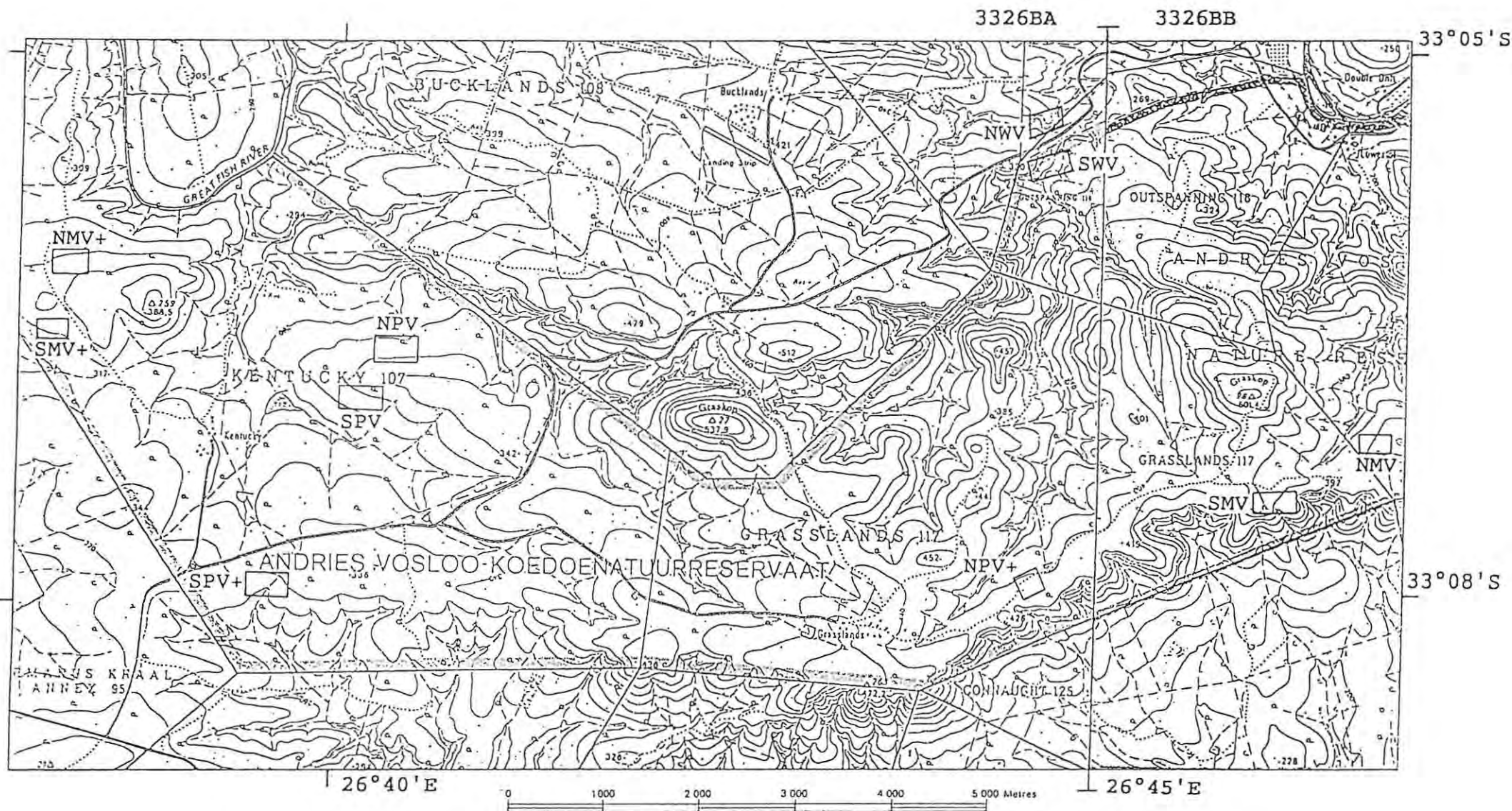


Figure 3.2. Map showing locality of survey sites at Andries Vosloo Kudu Reserve (from 1: 50 000 Topo sheets 3326BA, BB). Contour interval is 20 m. Abbreviations used on map: N = north; S = south; PV = poorly vegetated; MV = moderately vegetated; WV = well vegetated; + = additional sites used when all species not at main site.



south poorly
vegetated



north poorly
vegetated



south moderately
vegetated

Figure 3.3. Examples of the vegetation at the six survey sites.



north moderately
vegetated



south
well vegetated



north
well vegetated

Figure 3.3. Examples of the vegetation at the six survey sites.

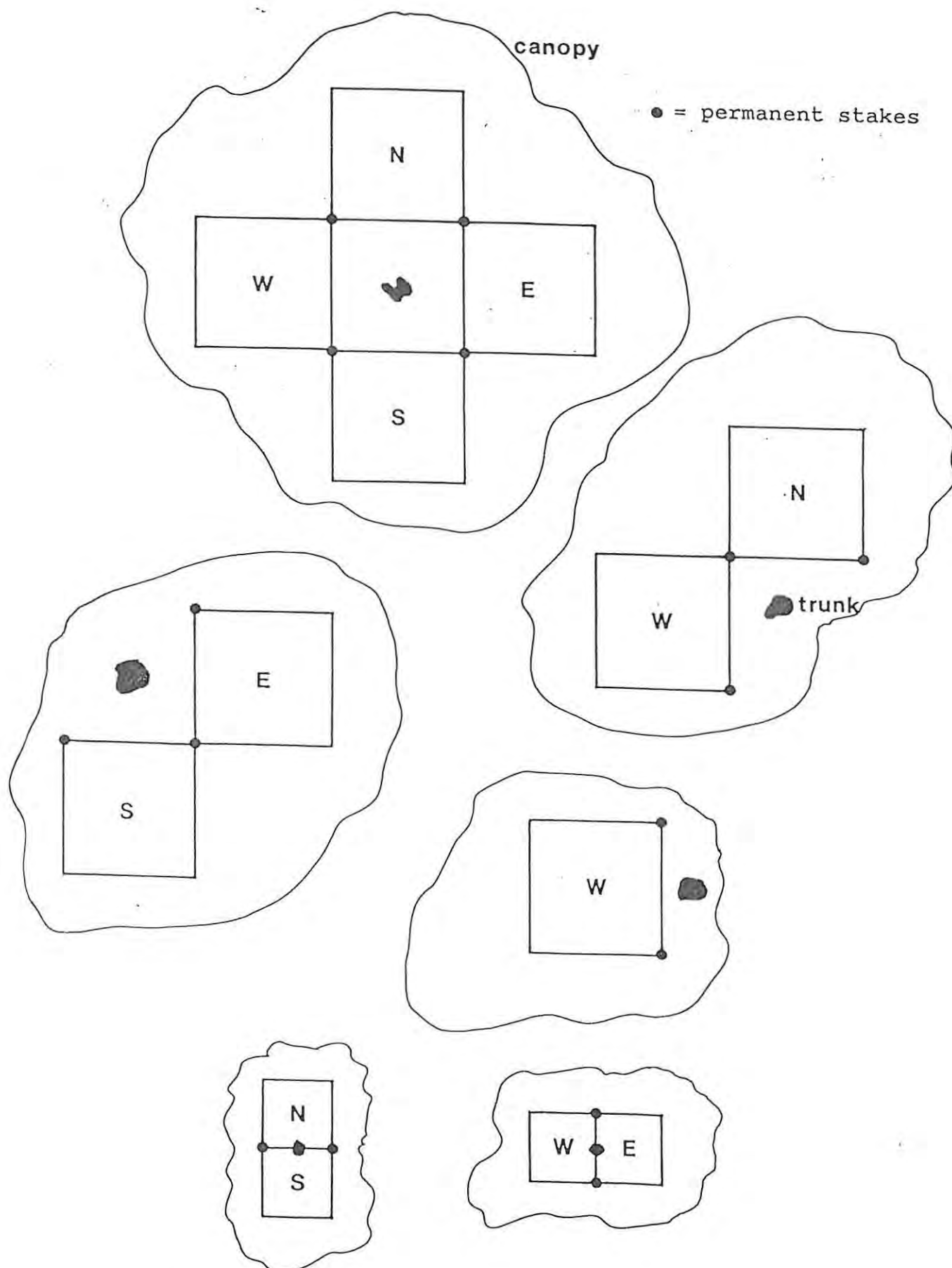


Figure 3.4. Examples of positioning of plots around tree.

determined. The diameter in two directions of ten large individuals of each species was measured at each site, and the mean radius calculated (Table 3.1). The quadrat size used for each species (Table 3.1) was based on these calculations. Species with a radius of under 1,2 m were allocated a 50 X 50 cm quadrat, and species with a mean radius of over 1,2 m a 1 X 1 m quadrat. At the start of the experiment it was not known which individuals would be selected as nurse plants, therefore we could not measure the nurse trees to decide on quadrat sizes.

Ten 1 X 1 m plots were also laid out in each of open bare, grassy and karroid areas at each site. No suitable grassy plots were available at the well vegetated sites. Any grass at these sites was under the canopies of trees. At all other sites the full complement of plots was surveyed. A total of 1 720 plots was searched for seedlings at each survey (Table 3.2).

There were no similar studies on which to base the number of plots, or quadrats, at each site. Each survey took three people surveying separate plots up to two weeks to complete, especially during periods of inclement weather. Due to other commitments the sample size chosen was logistically the maximum possible.

Survey method.

Plots were located randomly at each site, their distribution being decided by the location of suitable trees and shrubs under which plots could be laid out. A map used for

Table 3.2. Breakdown of number of plots surveyed, the starting date for each survey, and the surveys allocated to each season.

NUMBER OF SITES

Veld condition	3	Poorly, moderately and well vegetated
Aspect	x 2	North and South facing
Subtotal (No of sites)	<u>6</u>	

PERMANENT PLOTS ASSOCIATED WITH NURSE PLANTS

Nurse trees and shrubs	13	See Table
Replicates	x 5	
Side of tree	x 4	(N,S,E,W)
Subtotal	<u>260</u>	

Total plots under nurse plants $260 \times 6 = 1560$

QUADRATS IN OPEN HABITATS

(per site)	bare	10
	grassy	10
	karroid	10
		<u>30</u>

Total no. of quadrats in open habitats $30 \times 6 = 180$

Total all plots	1740
LESS no grassy plots at well vegetated sites	- 20
	<u>1720</u>

SAMPLING DATES

Spring: 7 November 1989^{*}; 12 December 1989.

Summer: 30 January 1990^{*}; 12 March 1990.

Autumn: 25 April 1990^{*}; 5 June 1990.

Winter: 17 July 1990^{*}; 23 August 1990; 1 October 1990^{*}.

^{*} Environmental variables recorded.

relocating plots in the field has been reproduced as an example of the randomness of the distribution of the plots (Figure 3.5). The surface area of sites varied from approximately one to two hectares. Each plot was permanently marked by two stakes at the two corners closest to the centre of the nurse plant (Figure 3.4). The quadrat was aligned with a mark on the left hand stake, and had to touch the second stake. This ensured that the quadrat was in exactly the same position for all surveys.

At each survey each plot was carefully searched for seedlings. The position of each seedling in a plot was recorded on a 5 X 5 cm grid system (Figure 3.6). This ensured the accurate relocation of seedlings in subsequent surveys, and allowed accurate monitoring of the survival of seedlings. The rainfall at the AVKR is unpredictable (e.g. Aucamp & Tainton 1984, *cf.* Figures 1.3 & 1.4), therefore there was no guarantee of receiving rain in a particular period. Most rain does however fall in spring (October, November) and late summer (February, March; Figure 1.3). Surveys were therefore conducted for each season, based on solstices and equinoxes, and started in spring 1989 (Table 3.2). Two surveys were conducted in each season, and three in winter. Each survey recorded the germination of the previous six weeks, therefore the last survey which started on 1 October 1990, although conducted in spring, was classed as a winter survey because it was for the previous six weeks, of which five occurred in winter. The required

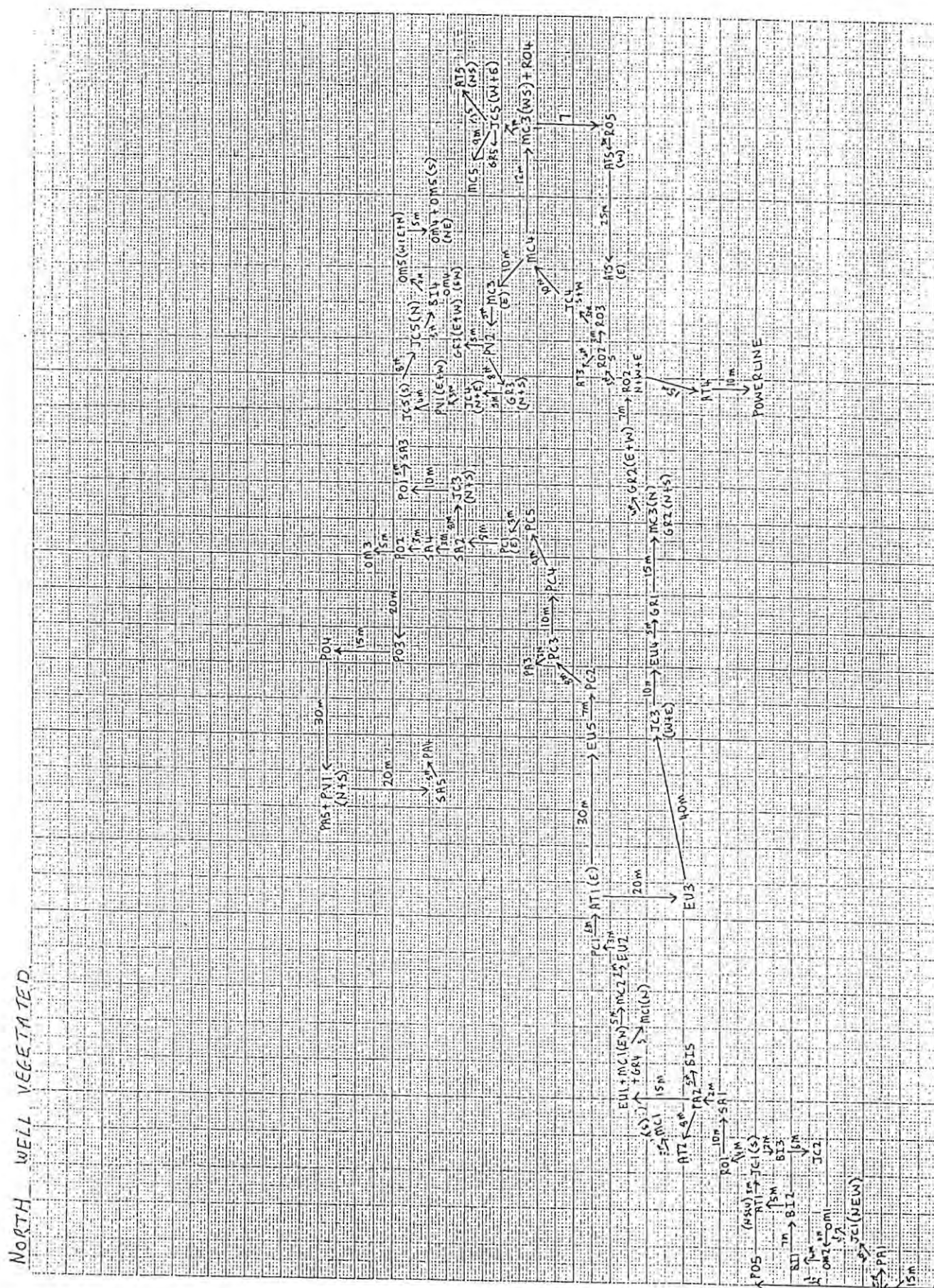


Figure 3.5. Field map of north well vegetated site, showing random plot distribution.

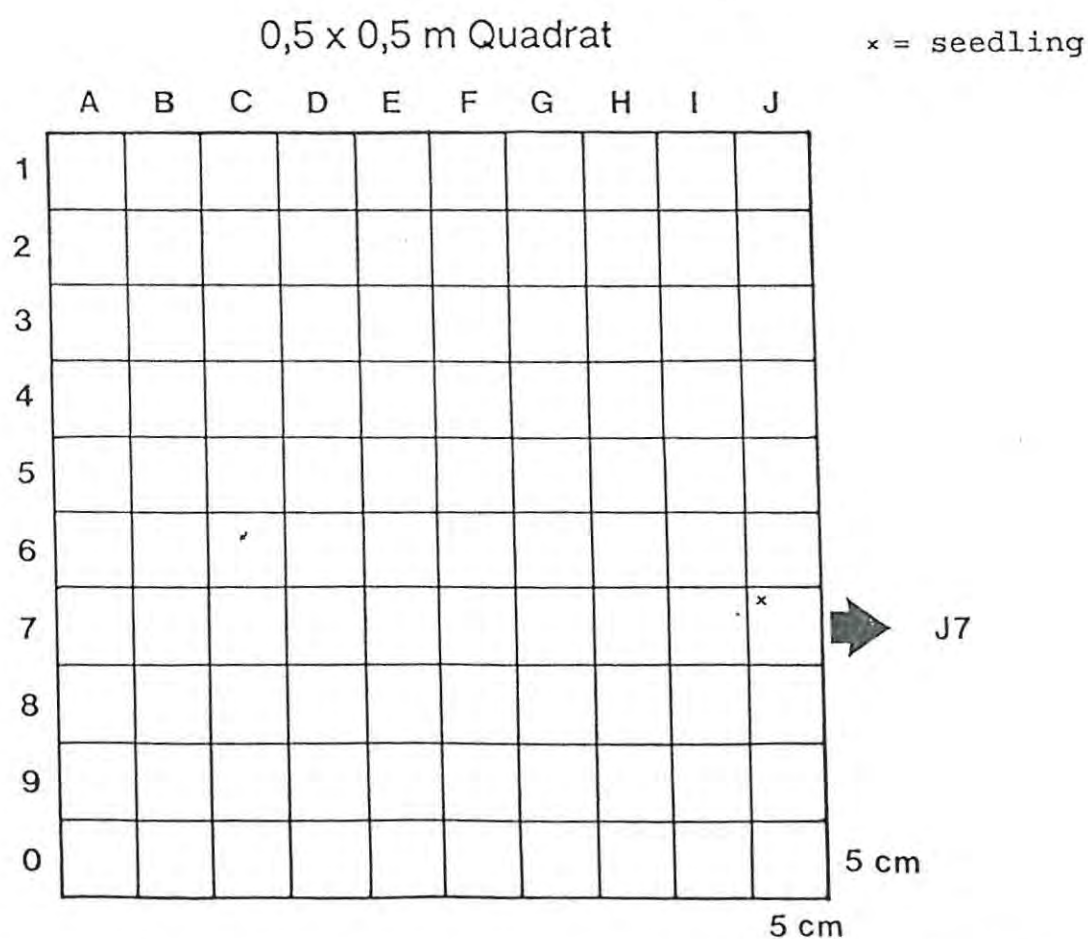
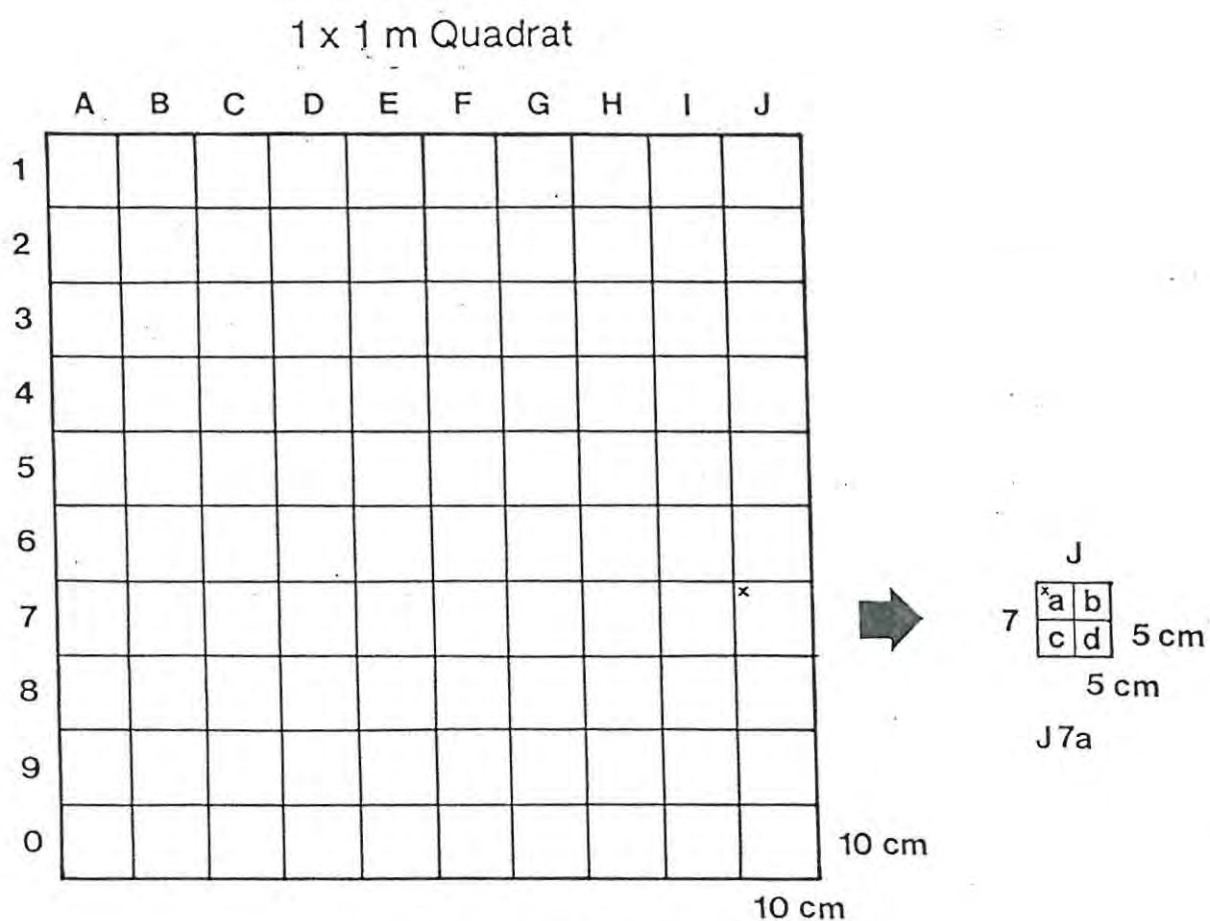


Figure 3.6. Examples of the quadrat sizes and the grid system annotation used in each.

information was germination per season. Surveys were conducted every six weeks to ensure that as many newly germinated seedlings were recorded for each season, therefore the data from the two surveys in a season were combined to obtain seasonal data.

A survey was conducted in August 1989 in order to allow the researchers to become accustomed to the techniques employed, and a second survey was conducted in September 1989 to determine which seedlings were already present in the plots at the start of the experiment. This was done to ensure that seedlings already present at the start of the experiment would not be recorded as newly germinated seedlings in ensuing surveys, thereby ensuring that all seedlings recorded from the 7 November 1989 survey onwards were definitely newly germinated. Data from these first two surveys were therefore not considered in the analysis of data. Data from all surveys from 7 November 1989 to 1 October 1990 were used in the analysis.

In summary the following data were recorded for each occurrence of a seedling: seedling species, date, site, plot (includes nurse plant and side of tree). The data were computerised, and sorted and arranged according to species of seedling, nurse plant species, and side of tree (Appendix 3).

Statistical analysis.

The data were analysed using a χ^2 method of investigating heterogeneity in a two-way contingency table (Greenacre

1988). This method considers chi-square decompositions of the Pearson chi-square statistic with respect to nodes of a hierarchical clustering of the rows and columns of the table. A cut-off point which indicates "significant clustering" is defined on the binary trees associated with the respective row and column analyses. This approach provides a simple graphical procedure which is useful in interpreting a significant chi-square statistic of a contingency table (Greenacre 1988). This is a clustering technique, but it points to significance on the basis of χ^2 between the clustering of rows and columns of a frequency data matrix. An advantage of this method is that it provides a compact visualisation of the Pearson chi-square statistic, and it serves as a guide to which subsets of rows or columns are significantly different from one another.

This method is often applied in conjunction with correspondence analysis. Correspondence analysis accounts for the chi-square using continuous constructs, the principal axes, to which all rows and columns make a contribution, whereas the cluster analyses decompose the chi-square using discrete constructs, namely the nodes where specific subsets of rows or columns are merged or split. In certain situations the two methods reinforce one another, whereas in other situations one or the other of the techniques may be more enlightening (Greenacre 1988). It is feasible that significant clusters of rows or columns can be identified by the χ^2 contingency table, which do not

coincide with significant principal axes of the correspondence analysis.

In this study the results which could be obtained from the chi-square contingency table in which the nodes where specific subsets of rows or columns are merged or split, was considered more important than the correspondence analysis, to which all rows and columns make a contribution, therefore the χ^2 method of investigating heterogeneity in a two-way contingency table was used. Further in the correspondence analysis each set of profiles can be compared descriptively in the display, but no statistical inferences may be drawn, whereas statistical inferences can be drawn in the two-way contingency table.

The two-way contingency table is best described with reference to Figure 3.7, and will be more fully described under the section dealing with Figure 3.7 under the results.

Soils

Soil samples were collected from under bushclumps and in clear unvegetated areas at each survey site, and from under bushclumps at locations throughout the AVKR. This was done to determine whether there were differences in the soil properties between sites, and whether the soil properties at the sites differed from those areas not surveyed. Open bare areas were sampled to determine whether soil properties could partially explain why these areas were unvegetated. Twenty-four 100 cm³ samples were collected from the surface

to 300 mm using a bucket-type soil auger. Litter was removed from the surface before collection.

The soil samples were analysed at the Plant Nutrition Research Unit at Rhodes University. Techniques of the Soil Society of South Africa (1990) were used to determine the following soil properties: pH in KCl; P (mg/kg); K (ppm); Ca (ppm); Mg (ppm); and Na (ppm). The following properties were determined according to a handout to science students of the University of Transkei (G. Lewis, pers. comm.): Al (ppm); exchangeable acidity (meq); organic content (%); and soil texture (% sand, silt and clay).

A Principal Component Analysis (PCA) programme (Anonymous 1989), as used by Palmer *et al.* (1988) and Palmer (in press) was used to ordinate the samples on the basis of the soil properties.

Environmental variables

On every second survey (1 per season; Table 3.2) the following variables were measured for each quadrat: percentage grass, herb, litter, and worm cast cover; presence or absence of spoor, dung, and cracks. The data for the season with the highest germination were used to determine if germination could be related to any of these environmental variables. There were very few records of spoor, dung and cracks, therefore these variables were excluded from the final analysis. Grass, herb, litter and worm cast cover are interrelated variables, therefore a multiple regression was applied to the data (BMDP 1990). The

quadrats were scored for either the presence or absence of seedlings for correlation with the environmental variables.

RESULTS

Occurrence of newly germinated seedlings.

Three hundred and eleven (311) newly germinated seedlings occurred under the canopies of trees (Table 3.3) at a mean density of $0,28 \text{ m}^{-2}$ (Table 3.4). No seedlings were recorded in the open bare, grassy and karroid sites. Despite the high sampling intensity the number of seedlings was low, with newly germinated seedlings only occurring in 197 (12,6 %) of the 1 560 plots located under nurse plants, or 11,5 % of all 1720 plots.

Species of seedlings.

Seedlings of nineteen shrub and tree species were recorded during the study (Table 3.3). The species were ranked and categorised as having a high (> 40 seedlings), moderate (10 to 40), or low (< 10) incidence of occurrence of newly germinated seedlings (Table 3.3). The three species with a high incidence of occurrence were Portulacaria afra (88; 28,3 % of all seedlings), Pappea capensis (51; 16,4 %), and Euclea undulata (46; 14,8 %).

Survival

One hundred and thirty-seven (44,1 %) of seedlings survived to the end of the survey. The survival rates for each season were as follows: spring (35,1 %); summer (41,7 %); autumn (51,4 %); winter (78,9 %). These data probably reflect the age of the seedling since germination, with many of the

Table 3.3. Number of seedlings of each species at each site.

Species of seedling	poorly veg.		moderately veg.		well veg.		TOTAL	
	S facing	N facing	S facing	N facing	S facing	N facing		
<i>Portulacaria afra</i>	34	13	8	19	10	4	88	HIGH
<i>Pappea capensis</i>	11	0	17	0	18	5	51	
<i>Euclea undulata</i>	18	6	10	2	5	5	46	
<i>Grewia robusta</i>	4	0	3	6	6	5	24	MODERATE
<i>Ozoroa mucronata</i>	0	15	0	3	5	1	24	
<i>Maytenus capitata</i>	2	2	8	1	3	1	17	
<i>Phyllanthus verrucosus</i>	5	1	7	3	0	0	16	
<i>Azima tetraacantha</i>	0	1	2	0	6	6	15	
<i>Ptaeroxylon obliquum</i>	0	0	0	2	9	1	12	
<i>Jatropha capensis</i>	0	1	3	0	0	0	4	LOW
<i>Ehretia rigida</i>	0	0	1	1	1	0	3	
<i>Capparis sepiaria</i> var. <i>citrifolia</i>	0	0	1	0	0	1	2	
<i>Jasminum multipartitum</i>	0	0	0	0	2	0	2	
<i>Rhus</i> sp	0	0	2	0	0	0	2	
<i>Brachylaena ilicifolia</i>	0	0	0	0	0	1	1	
<i>Cussonia spicata</i>	0	0	1	0	0	0	1	
<i>Diospyros scabrida</i>	0	0	1	0	0	0	1	
<i>Grewia occidentalis</i>	1	0	0	0	0	0	1	
<i>Olea europaea</i> subsp. <i>africana</i>	0	1	0	0	0	0	1	
TOTAL	75	40	64	37	65	30	311	

Table 3.4. Number of newly germinated seedlings under each nurse species at each site, the total seedling density (seedlings m⁻²) under each species, and the mean seedling density under nurse species.

Nurse plant species	Poorly veg.		Moderately veg.		Well veg.		TOTAL ¹	Density Seedlings m ⁻²
	S. facing	N. facing	S. facing	N. facing	S. facing	N. facing		
<i>Azima tetracantha</i>	1	1	4	14	7	1	28	0.23
<i>Brachylaena ilicifolia</i> ²	4	3	2	3	0	1	13	0.43
<i>Euclea undulata</i>	18	0	2	2	2	5	29	0.24
<i>Grewia robusta</i>	12	0	2	5	6	2	27	0.23
<i>Jatropha capensis</i> ²	2	0	1	2	0	4	9	0.3
<i>Maytenus capitata</i>	6	8	5	2	5	3	29	0.24
<i>Ozoroa mucronata</i>	8	4	5	3	3	0	23	0.19
<i>Portulacaria afra</i>	3	6	8	1	5	2	25	0.21
<i>Pappea capensis</i>	7	13	17	1	22	9	69	0.58
<i>Ptaeroxylon obliquum</i> ²	3	1	11	1	3	0	19	0.63
<i>Phyllanthus verrucosus</i> ²	3	2	2	3	3	0	13	0.43
<i>Rhigozum obovatum</i> ²	2	0	1	0	3	1	7	0.23
<i>Schotia afra</i>	6	2	4	0	6	2	20	0.17
open : bare	0	0	0	0	0	0	0	
grassy	0	0	0	0	0	0	0	
karroid	0	0	0	0	0	0	0	
Subtotal	75	40	64	37	65	30	311	mean density = 0,28 seedlings m ⁻²
TOTAL	115		101		95			
% OF TOTAL	37.0		32.5		30.5		100	

¹ Quadrat size varies therefore totals are not directly comparable.

² 50 x 50cm quadrats. All others 1 x 1m quadrats.

seedlings recorded in the winter surveys having germinated in the preceding two months. Alternatively seedlings which germinated in spring have had to survive a full year. A higher mortality rate would therefore be expected in these seedlings.

Of the three most common species of seedlings, 53,4 % (n = 88) of Portulacaria afra, 39,2 % (n = 51) of Pappea capensis, and 41,3 % (n = 46) of Euclea undulata survived.
Nurse plants.

Germination occurred under the canopies of all the study species (Table 3.4), the highest densities of newly germinated seedlings being under Ptaeroxylon obliquum (0,63 m⁻²) and Pappea capensis (0,58 m⁻²). The other densities ranged between 0,17 and 0,43 m⁻².

Seedling species - nurse plant relationships.

There were insufficient numbers of seedlings to perform meaningful statistics on any seedling species - nurse plant relationships (P. van der Watt, pers. comm.). These relationships will be discussed qualitatively for the three most commonly occurring seedlings: Portulacaria afra (88); Pappea capensis (51); and Euclea undulata (46).

Portuacaria afra.

Wind dispersed P. afra germinated under all the nurse plants, with the highest densities being under the small shrubs: Brachylaena ilicifolia (0,27 seedlings m⁻²);

Jatropha capensis (0,17); Phyllanthus verrucosus (0,17); and Rhigozum obovatum (0,13). Lowest P. afra seedling densities were recorded under P. afra itself (no seedlings) and the tall canopy trees: Pappea capensis (0,01); Schotia afra (0,03); and Ozoroa mucronata (0,03).

Pappea capensis.

Bird dispersed P. capensis seedlings occurred almost exclusively under P. capensis trees, having the highest density of seedlings of the same species as the nurse plant in the study (0,33 seedlings m^{-2}). The tall canopy trees Ptaeroxylon obliquum (0,07 m^{-2}) and S. afra (0,04 m^{-2}) were the only other nurse plants to have a Pappea capensis seedling density greater than 0,02 m^{-2} . Six species of nurse plant had no P. capensis seedlings, and three species one only.

Euclea undulata.

Bird dispersed E. undulata seedlings occurred primarily under tall canopy trees (Ptaeroxylon obliquum, Portulacaria afra, Schotia afra, Maytenus capitata) and trees with bird dispersed seed (Euclea undulata, Grewia robusta, Pappea capensis). Only one E. undulata seedling was recorded under the four small shrub species.

Aspects affecting germination

Season of germination.

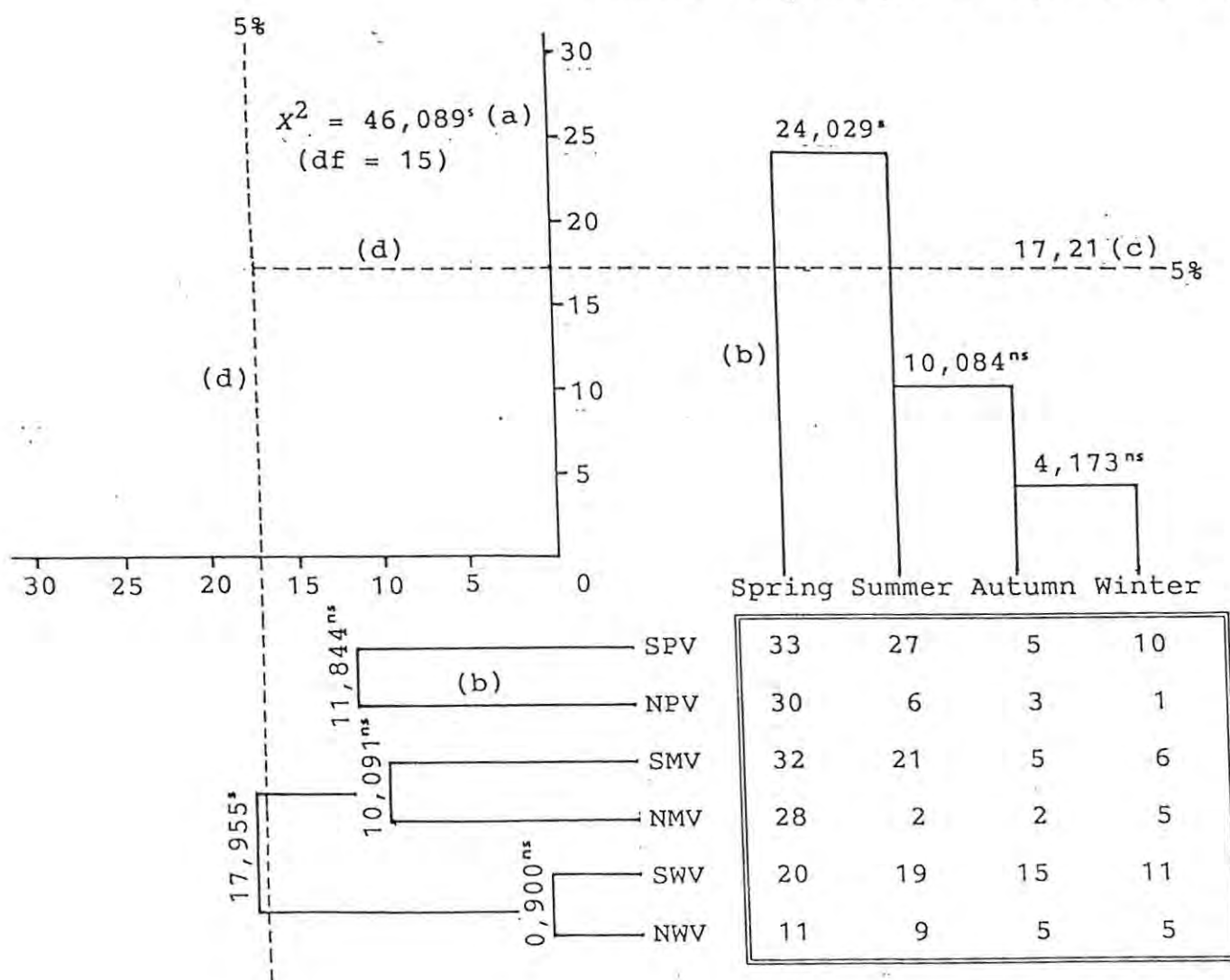
Most newly germinated seedlings occurred in spring and summer (Table 3.5). The germination in spring was

Table 3.5. Number of newly germinated seedlings at each site for each season.

<u>Site</u>	<u>Slope</u>	<u>Season</u>				<u>TOTAL</u>	<u>% OF TOTAL</u>
		<u>Spring</u>	<u>Summer</u>	<u>Autumn</u>	<u>Winter</u>		
Poorly vegetated	S. facing	33	27	5	10	75	
	N. facing	30	6	3	1	40	
	Subtotal	63	33	8	11	115	37
Moderately vegetated	S. facing	32	21	5	6	64	
	N. facing	28	2	2	5	37	
	Subtotal	60	23	7	11	101	32.5
Well vegetated	S. facing	20	19	15	11	65	
	N. facing	11	9	5	5	30	
	Subtotal	31	28	20	16	95	30.5
TOTAL		154	84	35	38	311	
% OF TOTAL		49.5	27.0	11.3	12.2	100	100
TOTAL S. FACING						204	65.6
TOTAL N. FACING						107	34.4
						311	100

significantly higher than in summer and autumn, but there were insufficient data to reveal significance between spring and winter, despite there being approximately four times more germination in spring than in winter (Figure 3.7).

The overall chi-square statistic ($df = 15$) is 46,089 (a in Figure 3.7), and is significant ($p < 0,001$). This indicates that there is a significant heterogeneity between two or more of the rows or columns. The nodes are indicated by the coupling lines (b in Figure 3.7), and the chi-square components associated with each node are indicated by *s* (significant) or *ns* (not significant) at the top of each coupling. The cut-off point for significant clustering is found from the largest eigenvalue of a Wishart matrix variate. In Figure 3.7. we are dealing with a 6×4 contingency table, therefore the largest eigenvalue of the Wishart matrix variate $W_3(5)$ is applicable. The 5 % critical point of distribution in Figure 3.7 is 17,21 (c in Figure 3.7). This cut-off point is indicated by a line across both binary trees (d in Figure 3.7). Chi-square values to the left of this line (in the case of rows) or above this line (in the case of columns) are significant at the 95 % level. The diagram is restricted by the order in which rows and columns are arranged. The diagram in Figure 3.7 does not imply that other couplings of season, e.g. spring - autumn are not significantly heterogeneous. Other couplings were tested by re-ordering the rows and columns. Results obtained

Wishart variate $W_3(5) = 17,21$ at 5 % (c)

Other χ^2 values for couplings of season of germination.
 Autumn - Spring 21,236^s
 Spring - Winter 12,903^{ns}
 Summer - Winter 5,079^{ns}

Figure 3.7. Joint cluster analysis of site and season of germination, showing decompositions of the chi-square at the two sets of nodes, and the cut-off point for significant clustering at the 95 % level. (row abbreviations: PV = poorly vegetated; MV = moderately vegetated; WV = well vegetated; S = south facing slope; N = north facing slope). ^s = significant, ^{ns} = not significant. For detailed explanation of the diagram and (a), (b), (c), and (d) refer to text under "season of germination" in results section.

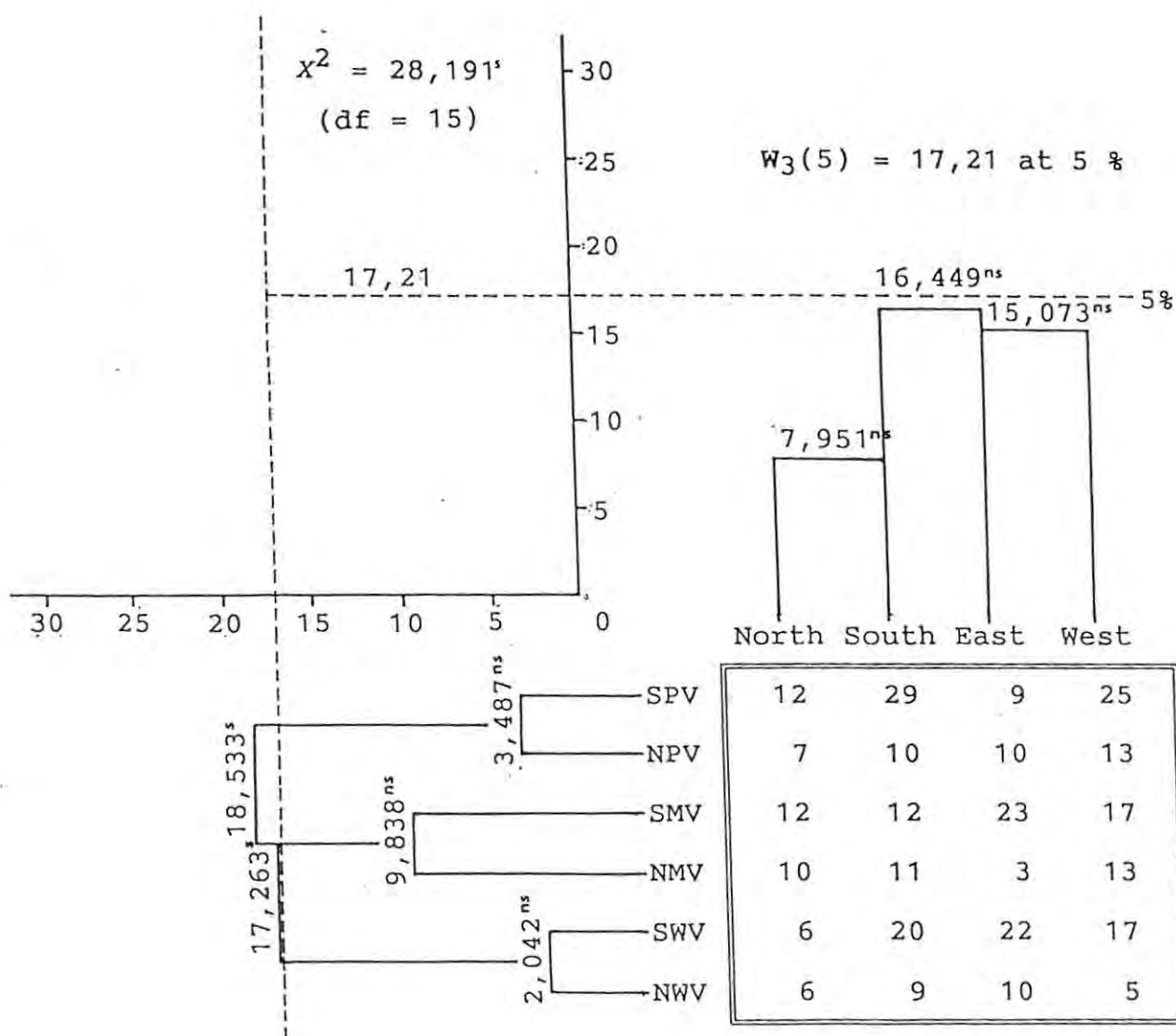
by these additional calculations are presented underneath the contingency table.

Veld condition.

There was little difference in the number of seedlings at the different sites on the vegetation gradient (37 % of all seedlings in poorly vegetated, 32,5 % in moderately vegetated, and 30,5 % in well vegetated veld; Table 3.4). Despite these small differences in number of seedlings across the gradient, when season of germination (Figure 3.7) and side of tree (Figure 3.8; Table 3.6) are taken into account the method of statistical analysis employed revealed significant differences in germination across the gradient. For the purposes of this study seeds germinating in different seasons and on different sides of trees were considered to have equal chances of survival, therefore these two parameters should not be key issues here. Instead a χ^2 analysis was done on the total number of seedlings germinating in each vegetation condition. There was no significant difference in the number of new seedlings across the vegetation gradient ($\chi^2 = 2,031$; $df = 2$; $p > 0,05$).

Aspect.

Germination on the S facing slope comprised approximately 65 % of total germination compared with the N facing sites (Table 3.3; 3.4; 3.5; & 3.6). There was significantly more germination at the S poorly vegetated site than at the N poorly vegetated site, and at the S moderately vegetated site than at the N, but there was insufficient data to show



Other χ^2 values for couplings of side of tree.
 North - East 12,835^{ns}
 North - West 3,245^{ns}

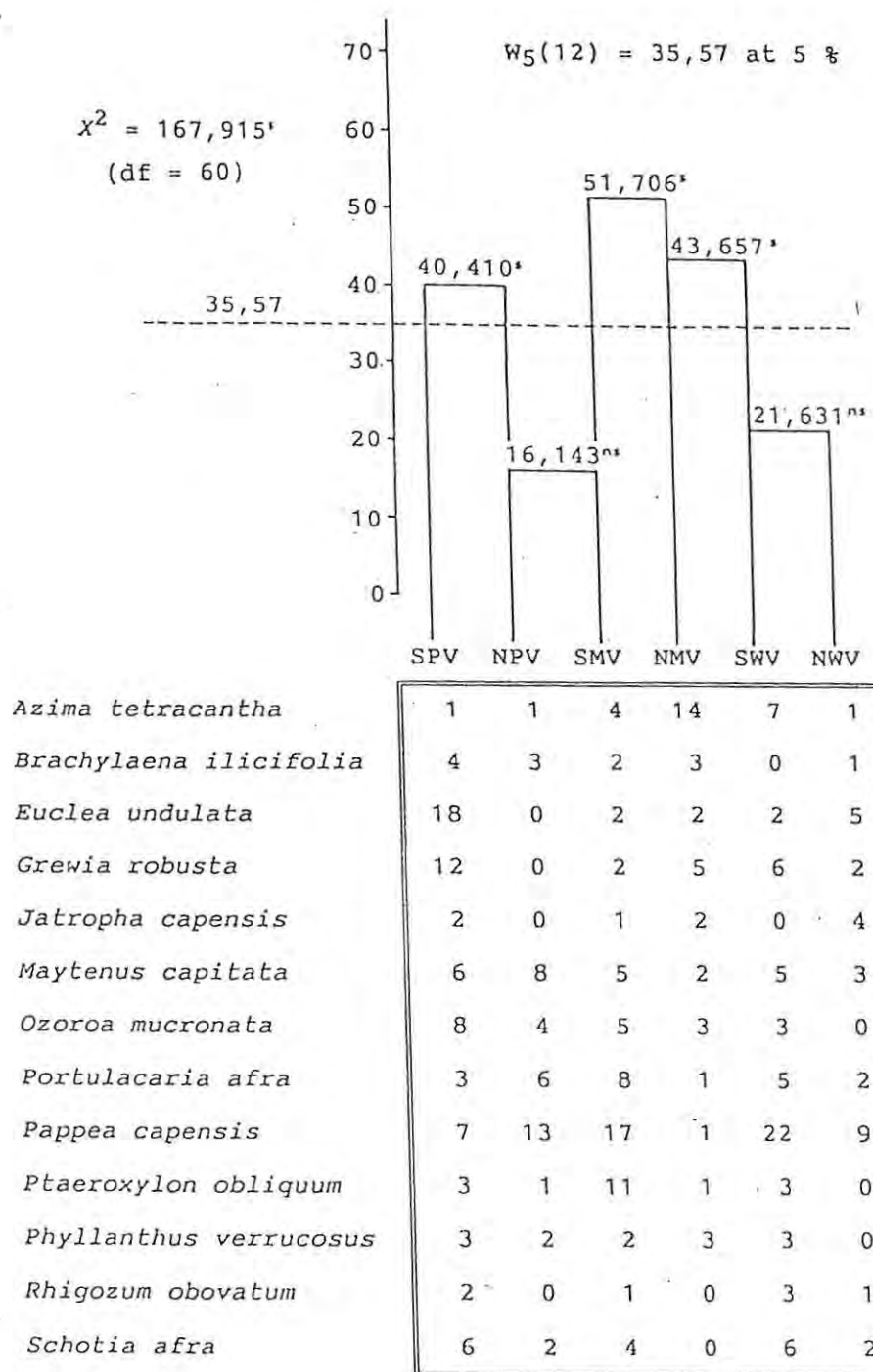
Figure 3.8. Joint cluster analysis of side of tree and site of germination, showing decompositions of the chi-square at the two sets of nodes, and the cut-off point for significant clustering at the 95 % level. (row abbreviations: PV = poorly vegetated; MV = moderately vegetated; WV = well vegetated; S = south facing slope; N = north facing slope).
^s = significant, ^{ns} = not significant.

Table 3.6. Number of newly germinated seedlings at each side of tree at each site.

<u>Site</u>	<u>Slope</u>	<u>Side of tree</u>				<u>TOTAL</u>
		<u>North</u>	<u>South</u>	<u>East</u>	<u>West</u>	
Poorly vegetated	S. facing	12	29	9	25	75
	N. facing	7	10	10	13	40
	Subtotal	19	39	19	38	115
Moderately vegetated	S. facing	12	12	23	17	64
	N. facing	10	11	3	13	37
	Subtotal	22	23	26	30	101
Well vegetated	S. facing	6	20	22	17	65
	N. facing	6	9	10	5	30
	Subtotal	12	29	32	22	95
TOTAL		53	91	77	90	311
% OF TOTAL		17.0	29.3	24.8	28.9	100

a significant difference between the S well vegetated and N well vegetated site, despite there being twice as many seedlings at S than at N (Figure 3.9). The overall χ^2 value of 167,915 (df = 60, $p < 0,01$) indicates significant heterogeneity between sites of germination.

The number of seedlings under the different species of nurse plants could not be analysed by this method, because of the different quadrat sizes used. Instead the seedling



Other χ^2 values for couplings of site of germination.

SWV - SMV 15,582 ^{ns}	SWV - SPV 37,327 [*]
NPV - NWV 25,048 ^{ns}	SPV - SMV 42,558 [*]
NPV - NMV 50,247 [*]	NMV - NWV 42,060 [*]

Figure 3.9. Cluster analysis of site of germination versus nurse species, showing decompositions of the chi-square for the site of germination, and the cut-off point for significant clustering at the 95 % level. (column abbreviations: PV = poorly vegetated; MV = moderately vegetated; WV = well vegetated; S = south facing slope; N = north facing slope). ^{*} = significant, ^{ns} = not significant.

densities under the nurse species were compared qualitatively.

Side of tree.

Slightly more germination occurred on the south and west sides of trees than on the east and north (Table 3.6), but there was no significant difference between sides (Figure 3.8). The overall χ^2 value of 28,191 (df = 15, $p < 0,05$) indicates significant heterogeneity, but in this situation it is restricted to heterogeneity between sites (i.e. rows). All χ^2 values associated with sides of tree were below the critical 5 % level.

Soils.

The soils from under the bushclumps were all similar with respect to their soil properties, but the soil samples from the open bare sites differed from those under the bushclumps. There were no distinct differences between soil properties of samples taken from bushclumps at the survey sites and from bushclumps outside the survey sites. Details of the soil properties for each soil sample are given in Table 3.7.

In the principal components analysis of the soil properties the first and second principal components accounted for 44,3 % and 17,8 % of the total variance respectively. The first principal component corresponded most strongly to a gradient of decreasing Al and exchangeable acidity, and increasing pH, Ca and organic

SAMPLE	%SAND	%SILT	%CLAY	LOSS ON IGNITION (%Organic Matter)	pH		P mg/kg	K ppm	Ca ppm	Mg ppm	Na ppm	Al		Exchangeable acidity			
					I KCl	I H2O						ppm	ppm	ppm	ppm	meq	meq
1	70.3	14.4	15.7	5.7	13.36	4.54	66.4	84	430	88	96	203.3	2.35				
2	72.7	20.3	6.3	9.6	16.26	6.87	25.5	398	2475	843	154	2.7	0.03				
3	51.5	23.1	25.4	8.9	15.08	5.60	21.4	214	1695	200	122	0.0	0.06				
4	68.0	12.7	21.4	5.6	14.06	5.50	17.6	93	970	156	89	31.0	0.45				
5	54.0	26.3	19.8	9.3	16.62	7.30	11.3	686	1980	767	128	0.0	0.04				
6	55.2	22.7	22.2	14.0	17.71	8.70	8.3	2033	4250	1375	327	0.0	0.02				
7	54.6	21.7	23.6	8.3	17.11	7.86	9.8	292	4050	454	96	2.0	0.04				
8	53.9	24.6	21.6	9.6	17.03	7.63	187.5	298	3425	448	126	0.0	0.06				
9	57.8	20.7	21.5	5.9	13.74	4.90	32.6	108	600	104	95	98.0	1.32				
10	56.7	26.6	16.7	10.4	17.08	7.56	15.0	219	3700	404	133	0.0	0.02				
11	60.7	18.9	20.4	4.4	13.62	4.88	18.0	75	450	59	86	121.0	1.59				
12	55.8	21.9	22.3	9.6	15.71	6.54	15.0	290	2025	390	111	0.0	0.02				
13	56.9	26.0	17.1	10.5	16.65	7.32	21.4	393	3025	274	120	0.0	0.03				
14	48.0	25.8	26.2	6.8	16.67	7.80	4.1	335	1765	755	296	0.0	0.02				
15	54.2	27.9	17.9	8.9	15.94	6.68	48.0	2412	910	399	191	3.0	0.04				
16	63.1	18.6	18.3	5.6	13.49	4.90	13.5	83	335	100	82	168.0	1.90				
17	48.8	34.2	21.0	11.5	15.78	6.66	11.3	147	3575	264	116	0.0	0.03				
18	52.5	21.5	26.0	9.6	14.44	5.39	26.3	183	1225	154	110	15.0	0.35				
19	32.6	21.2	46.2	12.4	14.97	5.91	31.1	363	3050	305	125	0.0	0.06				
20	37.2	18.5	44.3	8.3	14.73	5.91	37.5	230	2250	163	87	3.0	0.12				
21	60.8	24.1	15.1	7.7	15.05	6.01	6.0	142	1145	184	97	0.0	0.05				
22	52.6	27.0	20.4	11.8	17.16	7.75	26.3	435	5100	373	104	0.0	0.04				
23	45.1	34.6	20.3	10.3	15.41	6.34	9.0	182	1640	367	138	1.0	0.10				
24	57.1	18.4	24.5	6.7	17.94	8.68	18.0	788	605	277	172	3.0	0.02				

Table 3.7. Soil properties of the soil samples from open bare sites (sample 1, 4, 9, 11, 16, 20), from under bushclumps at the study sites (sample 2, 3, 5, 8, 10, 12, 13, 14, 17, 18, 19, 21), and from under bushclumps at sites not in the survey area (sample 6, 7, 15, 22, 23, 24).

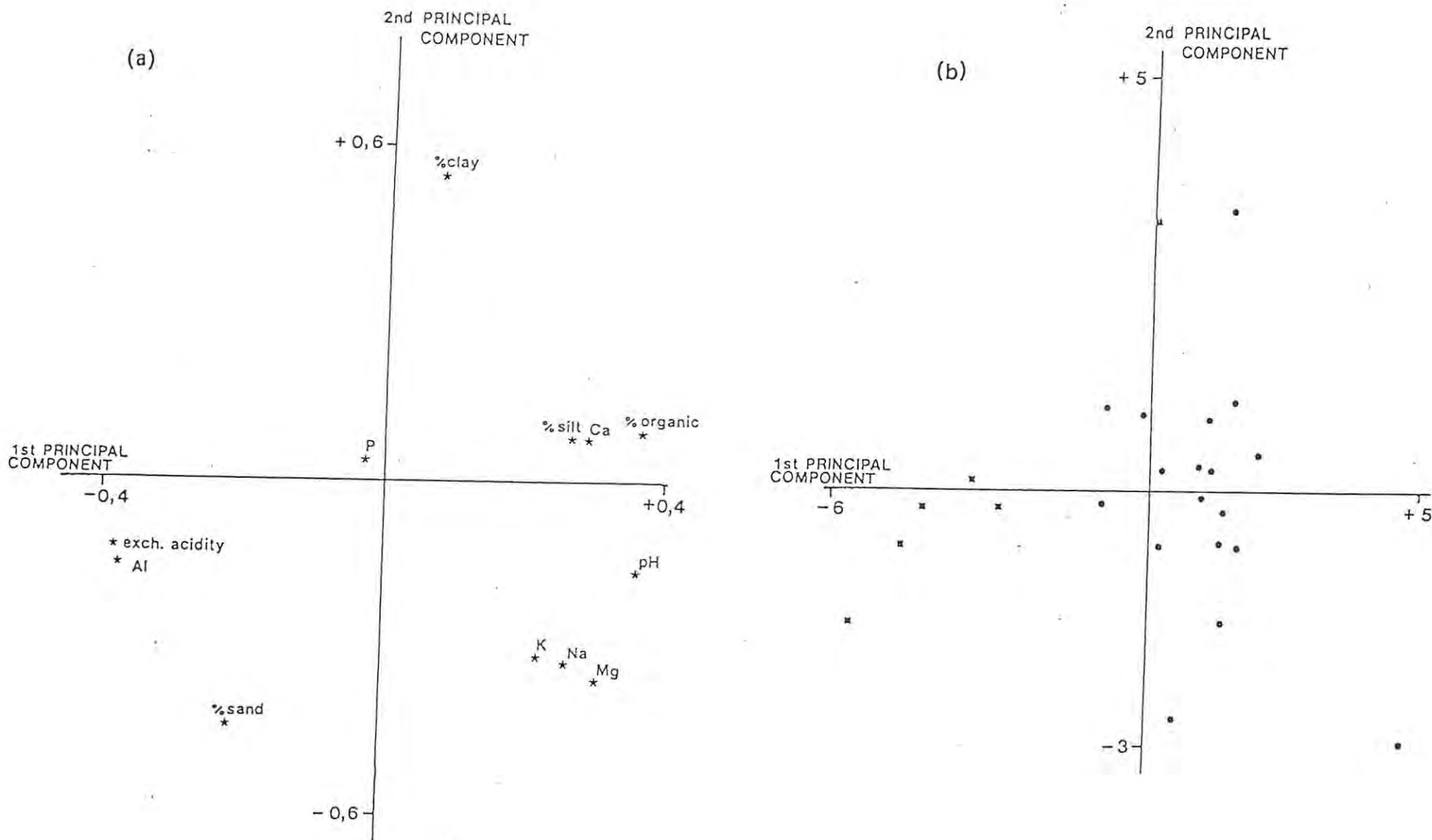


Figure 3.10. Plot of the first and second principal components for the twelve soil variables (a), and for the twenty-four soil samples (b). Soil samples were randomly collected from throughout AVKR, therefore are not numbered. (■ = open bare samples; ● = bushclump samples).

content (Figure 3.10a). The second principal component corresponded to a gradient of increasing clay and decreasing sand content.

In the plot of the soil samples (Figure 3.10b) five of the six open bare samples were grouped to the left of the first principal component. A comparison between Figure 3.10a and Figure 3.10b (plotted on separate axes because of differences in the values associated with the axes) indicates that these five samples were all characterised by high Al and exchangeable acidity, and low pH, Ca and organic content. Most of the samples from under bushclumps were grouped towards the middle of the plot of the first two principal components (Figure 3.10b). Three samples from under bushclumps fell outside the central grouping, however other samples from the same sites fell within the grouping in each instance. It can therefore be assumed that on a broad scale there were only small differences in soil properties between bushclump sites. This similarity of soils throughout the reserve prevented replication of this survey on other soil types, within the reserve.

Environmental variables

The environmental variables measured, i.e. percentage grass, herb, litter, and worm cast cover, all had values ranging from nought to one hundred percent, and none of them exhibited any distinct pattern. The mean percentage cover ($\pm$ SD; $n = 1720$ throughout) of each variable was as follows: grass ($15,91 \pm 23,56$); herb ($14,77 \pm 19,29$); worm casts

(10,32 $\pm$ 19,19); litter (49,02 $\pm$ 35,94). Seedlings occurred in sites ranging from bare ground under the nurse plant to sites totally covered in grass, herbs, litter or worm casts, and no pattern was observed. The multiple regression on the environmental variables revealed no repeatable pattern capable of relating the presence of seedlings to any specific conditions.

DISCUSSION

It is evident from this study that germination and establishment of the shrub component of xeric succulent thicket does take place through seeding, contrary to ideas expressed by certain authors (Stuart-Hill & Danckwerts 1988, Stuart-Hill 1989). This study has however shown that the pattern of distribution of seedlings is responsible for the failure of the shrub component of xeric succulent thicket to recolonise poorly vegetated areas, as opposed to a lack of germination and establishment. All seedlings occurred under the canopies of trees, with none in the clear, grassy and karroid areas (Table 3.4). Unfortunately recolonisation of large clearings typical of poorly vegetated areas by shrubs and trees is essential if a rapid recovery of overutilised veld is desired.

Seedlings of a large range of shrubs and trees, representative of the established shrub and tree component of xeric succulent thicket, became established, therefore it is unlikely that the vegetation will become dominated by one or a few species, as is currently the situation at the Addo

Elephant Park (pers. obs). This large range of seedlings is also indicative of sufficient seed production in the system.

Portulacaria afra is the dominant shrub in the xeric succulent thicket (Stuart-Hill 1989). As expected P. afra is also dominant in the xeric succulent of the AVKR (pers. obs, Chapter 5). The poorly vegetated sites have the lowest proportion of P. afra in their canopy (Chapter 5), but have the highest number of P. afra seedlings, when compared to the moderately and well vegetated sites. P. afra is one of the first species to disappear when subjected to heavy utilisation (Aucamp & Tainton 1984, Stuart-Hill 1989), so therefore may possibly have been more common in the poorly vegetated areas in historical times. The high seedling densities suggest that P. afra has the potential to become more common in the poorly vegetated areas under correct management. There was a higher density of seedlings under the canopy at the poorly vegetated sites than at the moderately and well vegetated sites, but the total canopy cover of trees here is lower than at the moderately vegetated site, and both have a lower canopy cover than at the well vegetated site (pers. obs; see Chapter 5). The overall seedling density per unit area of veld, including open areas, would therefore be more similar throughout the vegetation condition gradient than these data suggest.

Seedlings were associated with a wide range of nurse plants, with seedling - nurse plant relationships being dependent on dispersal methods to a certain degree, as

shown by the associations of the three most common seedlings with nurse plants, as discussed in the results. Bird dispersed seedlings tended to be associated with tall canopy trees, or other bird dispersed species, whereas wind dispersed species were normally associated with smaller shrubs. This broad spectrum of nurse plants illustrates the important role played by the whole range of trees and shrubs in the dynamic functioning of the xeric succulent thicket. It is therefore important to manage the xeric succulent thicket so that no species are lost from the system.

One species which has been lost to the system is sneezewood Ptaeroxylon obliquum. Sneezewoods are now rare in the xeric succulent thicket, because of uncontrolled collecting due to their suitability as fence poles and as fuel for firing furnaces and boilers (e.g. Acocks 1988, Moorcroft 1988). P. obliquum is the tallest tree in the veld (pers. obs), and was the nurse plant supporting the highest seedling density during this study. Sneezewood saplings are common in groves where sneezewoods still occur (Chapter 5). As in the Chilean matorral (Fuentes et al. 1984, 1986) no specific species could be identified as being pivotal to bushclump formation in xeric succulent thicket (pers obs.). P. obliquum may possibly have filled this essential role in the xeric succulent thicket, just as Prosopis glandulosa does in the transformation of grasslands to woodlands in Texas (Archer et al. 1988). Sneezewoods may well therefore have played a major role in

the dynamic functioning and shaping of xeric succulent thicket. Most seedlings occurred on the cooler south facing slopes. At the AVKR the prevailing rains are from the south-west. This prevailing rain could possibly explain the higher number of seedlings on the south and west side of individual trees, the north and east sides being in the rain shadow. This phenomenon has been observed in Acacia karroo (Stuart-Hill et al. 1987, Stuart-Hill 1988).

Despite the restricted nature of this study several similar factors to those maintaining Chilean matorral bushclumps (Fuentes et al. 1984, 1986) were observed in this study: 1) seedlings of bird dispersed species (e.g. Pappea capensis, Euclea undulata, Grewia robusta, Ozoroa mucronata) occurred most commonly under the canopies of tall trees; 2) seedlings of wind dispersed species (e.g. Portulacaria afra) occurred most commonly under smaller shrubs; 3) no seedlings were observed between bushclumps; 4) although not specifically measured, seeds of bird dispersed species were observed almost exclusively within bushclumps, with very few observed in the open (pers. obs); 5) no seedlings were observed to be associated with rocks and fallen branches, and all were nursed by shrubs and trees.

Indigenous hares and rabbits are present in the xeric succulent thicket, but these do not appear to pose a threat to seedlings. No browsed seedlings were observed, but one seedling disappeared after a hare or rabbit burrowed at the

exact location of the seedling, as recorded during earlier surveys. This is in contrast to the effect of introduced European rabbits on seedlings of the Chilean matorral. Stuart-Hill (1989) has, however, speculated on the increase in rodent and rock hyrax Procavia capensis populations with removal of avian and mammalian predators, and the effect this could have on the veld. The effect of predator removal on small mammal populations and distribution in the xeric succulent thicket, and the effect on the veld, needs further investigation. The black-backed jackal population at the AVKR is high, and may be keeping rabbit and hare populations under control.

Large and small domestic stock, especially Angora goats, have however significantly altered the vegetation (e.g. Aucamp & Tainton 1984, Hoffman & Cowling 1990, Hoffmann & Everard 1987, La Cock et al. 1990, Stuart-Hill 1989, Stuart-Hill & Danckwerts 1988). No studies have been conducted on the influence of domestic stock on shrub seedlings in the xeric succulent thicket, but by implication destruction of shrubs will result in destruction of suitable germination habitat, thereby reducing recruitment of shrubs through seedling establishment.

The restriction of shrub seedlings to bushclumps, and the soil properties within these bushclumps (Palmer 1982, Palmer et al. 1988, this study) indicate that these bushclumps will be able to maintain themselves. There are distinct differences in soils between bushclumps and

adjacent karroid and grassland areas at the AVKR (Palmer 1982, Palmer *et al.* 1988), and between bushclumps and adjacent bare areas (this study). Palmer (1982) found that grassland soils had low organic content and mineral richness, indicating young soil still undergoing pedogenesis, whereas bushclump soils were "old" by comparison. Palmer (1982) concluded that the grasslands had probably developed subsequent to the bushclumps.

Palmer (1990b) postulated that a subtropical thicket became established in the Graaff-Reinet region during a moist phase about 10 000 BP. This moist period was followed by a dryer phase, during which thicket vegetation would not have been able to colonise an area. Palmer (*pers. comm.*) postulates that bushclump dynamics ensure that the climate within bushclumps is hospitable, and that these bushclumps are not rainfall dependent. He further postulates that there will be low seedling survival in dry areas outside bushclumps, and higher survival within bushclumps. My results fit this pattern. There is however the possibility that seed dispersal is concentrated around bushclumps, and this may be a reason for the lack of seedlings in open areas. Further, if lack of moisture is a problem, one would expect germination to take place in years of anomalously high rainfall, as do occur periodically at the AVKR (see Chapter 4). There is no evidence of same-aged saplings in open areas at the AVKR, as could be expected (see Chapter 5). Palmer's model of low moisture between bushclumps

retarding germination should be further tested in sites where there is sufficient moisture outside of bushclumps, e.g. in the moister valley bushveld of Umfolozi. The increasing shrub and tree cover with increasing moisture in the subtropical transitional thicket (Everard 1987) is possible support for Palmer's model.

Palmer (1982) suggested that high ungulate densities at the AVKR (Allen-Rowlandson 1980) were retarding pedogenesis between bushclumps, thereby retarding recovery from previously heavy utilisation by domestic stock. This study has identified another possible reason for the maintenance of bare zones adjacent to bushclumps, namely aluminium toxicity.

Soil samples from five similar bare zones throughout the AVKR had a mean Al concentration of $124,3 \pm 66,3$ ppm (range 31 - 203,3ppm), and low pH's. At high concentrations Al is toxic to plants (e.g. Clarkson 1969, Grime & Hodgson 1969, Le Roux 1985). Al toxicity is prevalent in acid soils, and is one of the most widespread and drastic effects reducing fertility of acid soils (Grime & Hodgson 1969). Al has inhibitory effects on plant growth, especially the growth of roots (cf. Bennet & Breen 1991).

It is unlikely that Al toxicity is solely responsible for the lack of seedlings in these bare areas (R.J. Bennet in litt.). Instead it is probably a combination of Al toxicity, heavy utilisation by domestic stock in the past and game at present, microclimatic effects (Keeley & Johnson

1977), dispersal patterns of seed (Fuentes et al. 1984), and soil properties which are not conducive to germination of seeds and establishment of seedlings (see Introduction).

CONCLUSIONS.

This study has shown that xeric succulent thicket can and probably will regenerate through seeding under conditions of utilisation by wild herbivores, but that this regeneration is confined to within bushclumps. This implies that the revegetation of clear areas, which are a feature of the poorly vegetated sites, will not take place through the dynamic processes currently functioning in the xeric succulent thicket.

The wide range of trees serving as nurse plants has emphasised the need to maintain individual trees, and not to lose species from the system. The loss of Ptaeroxylon obliquum through mismanagement from the system may well have altered the regeneration pattern in xeric succulent thicket.

The buildup of aluminium in clear areas between bushclumps to levels toxic to plants, and current heavy utilisation by game, further retard the possible natural recovery of this veld.

The results of this study suggest that badly degraded areas of xeric succulent thicket at the AVKR will not regenerate under current management practices, and with the public demands for highly visible animals for sightseeing and tourism, there is no chance of this veld receiving the

long rest that it needs. It appears that active interference on the part of managers may be the only solution.

CHAPTER 4

AN AD HOC STUDY OF A BLACK RHINOCEROS DUNG MIDDEN AS A GERMINATION SITE FOR PAPPEA CAPENSIS SEEDS IN THE XERIC SUCCULENT THICKET.

INTRODUCTION

It has been postulated that megaherbivores play a vital role in the dynamics of subtropical transitional thicket (e.g. J.J. Midgely, in litt.; Fabricius et al. 1990; Stuart-Hill 1991) in the eastern Cape. Megaherbivores occurred in the eastern Cape until the beginning of the twentieth century, but from then until 1986 the only megaherbivores present were at the Addo Elephant National Park.

Black Rhinoceros Diceros bicornis minor once frequented the Great Fish River Valley (Skead 1987), but by 1843 severe hunting pressure by the early settlers and explorers resulted in their local extinction in the area (cf. Skead 1987). They were reintroduced to the Great Fish River Valley at the AVKR in 1987, as part of the national conservation plan for black rhinoceros (Brooks 1988). A population of fifty to seventy is envisaged for the AVKR (Brooks 1988, Brooks & Goodman 1989), as well as twenty for the adjacent Double Drift Nature Reserve (Ciskei Wildlife Resources Board 1989).

If, as postulated, megaherbivores play a major role in the dynamics of subtropical transitional thicket, they will

have to be of some benefit to the vegetation, either by providing germination habitats or by seed dispersal. From the results of Chapter 3 it does not appear as if gap formation is a prerequisite for germination in the xeric succulent thicket. Dung, however, has a high moisture content and is rich in humus, which contains high levels of nitrogen (Theron 1957, van Vuren 1957). These conditions favour the germination of seeds. Higher germination rates could therefore be expected in a rhino dung midden.

This chapter is a report on an *ad hoc* experiment conducted on a rhino dung midden under the canopy of a Pappea capensis tree, at a time when the tree was fruiting profusely. P. capensis is one of one of the dominant canopy trees in both xeric and mesic succulent thicket (Everard 1987), is one of the most important nurse plants, and is one of the species with the highest number of seedlings, at the AVKR (Chapter 3).

It was not possible to replicate the experiment at other rhino middens situated under P. capensis trees, because this was the only incidence of such a combination of events observed at the reeserve. This chapter should therefore be seen as a once-off study which, although limited, will provide some knowledge and ideas on the role of black rhinoceros in the xeric succulent thicket, an area about which we have very limited knowledge at present. This is important when the future large populations of black rhinoceros in the area are taken into account.

The aim of this study was therefore to determine what role a black rhinoceros midden under a P. capensis tree would play in the germination of P. capensis seed and the survival of the seedlings.

STUDY SITE

P. capensis seedlings were observed in a black rhinoceros midden under a P. capensis tree in early February 1989. A survey of rhinoceros middens has not been undertaken at the AVKR, but this is the only known incidence of a midden under a P. capensis tree at the reserve. This tree was approximately 5m high, with a canopy diameter of 6m, and 2m between the ground and the lowest branches. The minimum seed density under the tree was determined by counting the number of seeds in four 50 X 50cm samples of litter collected at the start of the experiment. The minimum P. capensis seed density in the midden was 628 m^{-2} . Investigation of individual dung balls revealed no evidence of ingestion of P. capensis seeds by the black rhinoceros, but P. capensis was one of the preferred dietary items of three black rhinoceros during a boma feeding trial at the AVKR (Maddock et al. in prep.). Most seeds would have been above the browse-line of the rhinoceros, and therefore would not have been present in the diet. The ingestion of some seed by the rhinoceros was a possibility, but based on the shape of the tree and location of the seeds on the tree most seeds in the dung midden could be attributed to seedfall from the tree, with limited bird dispersal.

METHOD

Six 1 x 1 m plots were laid out within the rhinoceros midden under the tree, and four control plots on the other side of the tree where there was no rhinoceros dung. All living *P. capensis* seedlings were counted in the plots approximately every two weeks from mid-February to September 1989. Seedlings were not individually marked, but in instances where dead seedlings had not disappeared reasons for their death were noted.

RESULTS

The density of seedlings in the dung midden increased rapidly from 37 m⁻² on 15 Feb to a peak of 290 m⁻² on 30 March (Figure 4.1). The seedling density then decreased rapidly to 43 m⁻² on 20 June, whereafter it decreased gradually until none were present by 9 November. The seedling density in the control also increased rapidly to a peak of 54 m⁻² on 30 March, whereafter it decreased gradually until no seedlings remained on 9 November.

Disturbance from the rhinoceros scraping the dung in the midden only affected 40 % of one plot in the midden. This occurred in May, during which time the density of seedlings was declining rapidly, and this activity was not considered important in influencing the overall trend.

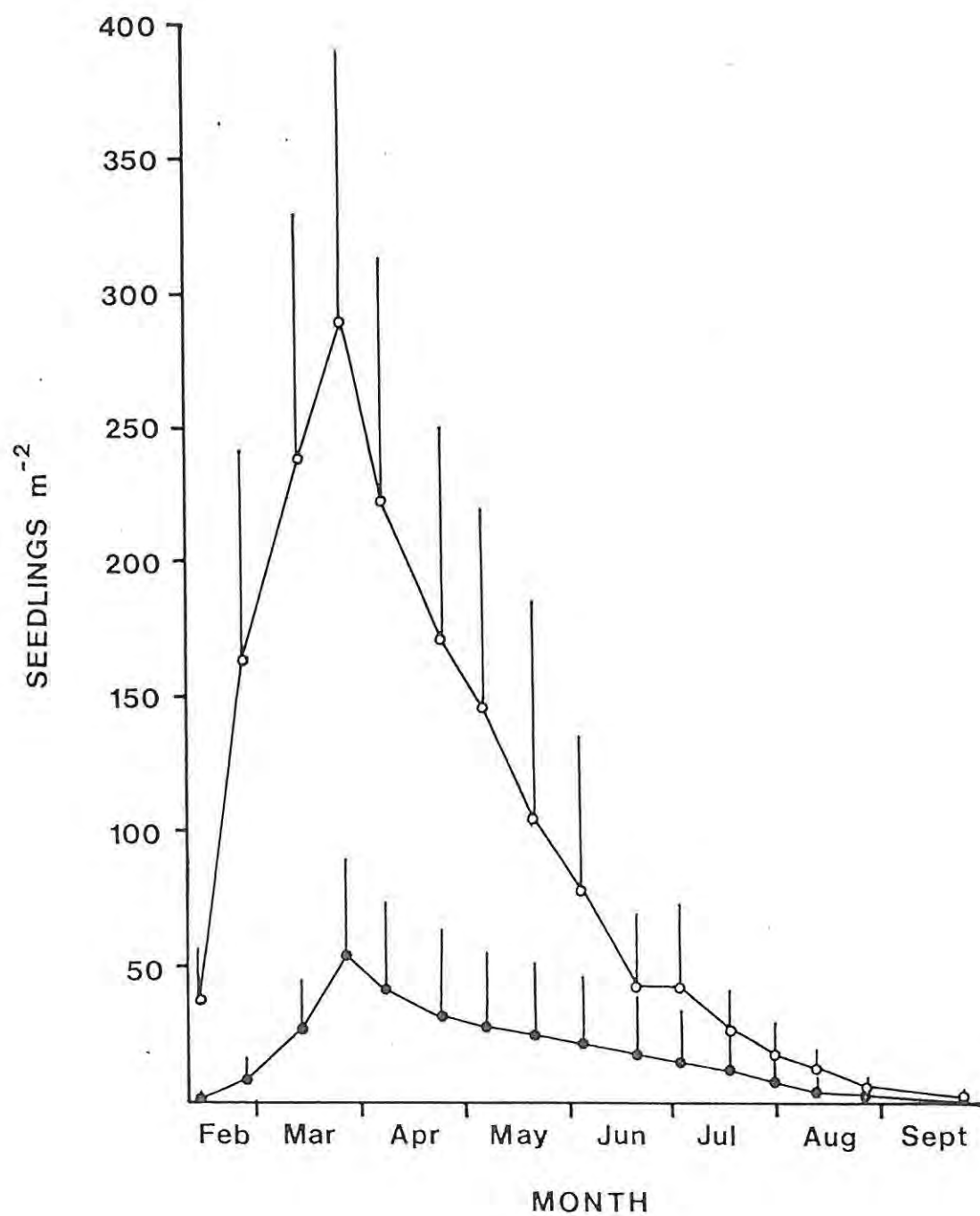


Figure 4.1. Mean density (+ 1 SD) of *Pappia capensis* seedlings in black rhinoceros midden (○—○) and in control (●—●) under canopy of *P. capensis* tree in 1989.

There were significantly more seedlings on the rhinoceros dung midden than below the tree in the control area where there was no rhinoceros dung (for 30 March 1989: $U = 0$; $p < 0,05$; Mann-Whitney U Test. also $t = 4,07$; $p < 0,05$).

Dehydrated seedlings were first noted in mid-March, whereafter they were common. Where the layer of dung was more than 10 cm thick dehydrated seedlings were not rooted in the ground, but instead the roots were confined to the dung. Some resprouting of seedlings occurred following browsing. These browsed seedlings were less frequent than dehydrated seedlings. Dehydration during the dry winter appeared to be responsible for greater mortality of seedlings than browsing.

Several additional species were represented by individual seedlings in the dung midden, i.e. Azima tetracantha, Ptaeroxylon obliquum, Jasminum multipartitum, and Rhus sp. Seedlings of tree and shrub species recorded in the control area were P. obliquum, J. multipartitum and Hippobromus pauciflorus.

DISCUSSION

The density of germinated seeds in the rhinoceros dung was an order of magnitude higher than any density recorded during the seedling survey (Chapter 3), suggesting that the presence of a midden in a sheltered environment greatly enhances the chances of seed germination. The density of

seedlings in the control area was also higher than recorded in the seedling survey (Chapter 3). This could possibly have been as a result of a high litter cover and dung of other herbivores being present. This season of germination also followed one of the best years of P. capensis seed production in the subtropical transitional thicket of the eastern Cape for eleven years, according to B. Fike, the reserve manager at the nearby Thomas Baines Nature Reserve. At the time of this report he had been a conservator in the region for twelve years. The seedling survey (Chapter 3) was conducted a year later, when seed production was not prolific (pers. obs). The period of highest germination of P. capensis seeds in this study corresponded to the period of P. capensis seed production at the AVKR, which is in summer (Palmer 1982). The low production of P. capensis seed in the year of the seedling survey may have influenced the season of highest germination in the seedling survey. High seed production, as in the year of this experiment, is uncommon. The year of the seedling survey could probably be considered as being more representative of prevailing conditions than the year of abnormally high seed production.

Few viable seeds would have been available for germination after the initial spate of germination from late February to early April, because of the presence of the sucking bug Leptocoris hexophthalma, which suck oil from the fallen Pappea capensis seeds (Palmer & Pitman 1972) thereby destroying them. The bugs became more abundant under the

tree with increasing time (pers. obs). The number of seeds available for germination in autumn and winter would therefore have been greatly reduced. At the beginning of the experiment the bug numbers were low, and I was unaware of the influence these bugs would have. I therefore did not quantify their numbers in any way, and did not compare their effect on seedlings within the rhino dung midden and outside it. I aim to conduct experiments on the effect of these bugs on P. capensis seed when next there is a large crop of seeds. There has not been another prolific year of P. capensis seed production since this experiment.

The rainfall pattern for 1989 was similar to the annual trend, with a winter trough. From May to September the monthly rainfall ranged from 0 mm (August) to 7,8 mm (September), insufficient for germination and survival of seedlings.

No seedlings became established in the midden, one of the possible reasons being the usual low winter rains following germination. The subtropical transitional thicket is characterised by an unreliable annual rainfall, and there is a 25 % chance that a region will receive less than 80 % of its mean annual rainfall (Aucamp & Tainton 1984). Episodic events, e.g. unseasonally high rainfall, may therefore be an important factor in subtropical transitional thicket dynamics (Midgely, in litt.; Fabricius et al. 1990). In Australia anomalously high rainfall events are needed for the survival of certain bushveld seedlings (Lange & Purdie,

1976). Similarly anomalously high winter rainfall in the xeric succulent thicket could prevent dehydration, ultimately resulting in the establishment of P. capensis seedlings.

If rainfall of 30 mm in each of two months from May to August in a year is considered sufficient to prevent or reduce dehydration, establishment of seedlings could have occurred in three years from 1974 to 1989 (1974, 1979, 1981). In 1979 the annual rainfall was 910 mm, with 335 mm falling in July and August. This was more than double the mean annual rainfall for the AVKR (cf. Palmer 1982, Everard 1987, Chapter 1).

CONCLUSIONS

The density of germinated seeds in the rhinoceros midden was an order of magnitude higher than any density recorded during the seedling survey (Chapter 3), suggesting that the presence of a midden in a sheltered environment greatly enhances the chances of seed germination. Under certain climatic conditions germinated seeds may become established.

At the time of this study an event such as this was probably unique, since only four black rhinoceros were present. The frequency of such events could be expected to increase when the black rhinoceros once again becomes an integral part of xeric succulent thicket, following more reintroductions to the AVKR. These observations, although of a limited nature, support the speculative view that

megaherbivores once played a part in subtropical transitional thicket dynamics. Full surveys will however need to be conducted once the black rhinoceros population has increased to approximately fifty, in order to determine whether this enhanced germination in a dung midden is a common occurrence, or whether this was an unusual incident.

CHAPTER 5

OCCURRENCE OF SAPLINGS IN THE XERIC SUCCULENT THICKET OF THE EASTERN CAPE.

INTRODUCTION

Many authors have postulated that recruitment of new shrubs into the xeric succulent thicket occurs very slowly, if at all (e.g. Aucamp & Tainton 1984, Hoffman & Everard 1987, Stuart-Hill & Danckwerts 1988, Stuart-Hill 1989). Chapter 3 showed that a lack of germination and establishment is not responsible for this failure to regenerate.

The aim of this study was to determine whether seedlings survive to enter the system as saplings, and if saplings do occur, where do they occur. The study was conducted in an attempt to gain insight into what could be expected with regard to saplings in a naturally occurring cross section of xeric succulent thicket, taking into account the natural dominance of certain woody species. Emphasis was not placed on specific nurse plant - sapling relationships, as opposed to Chapter 3 where the effect of nurse plants on germination was studied. Sampling was done by transects, and there was no guarantee that any or all of the transects would pass through each species of nurse plant used in the seedling survey. This method therefore precluded any quantitative comparisons between nurse plants and nurse plant - sapling relationships. Similarly, although it would be useful to obtain information on possible dispersal

distances by assuming that a sapling was the offspring of the nearest adult of the same species, it was not the intention of this survey to provide this information. This would be speculation in an environment dominated by bird- and wind-dispersed species. Details of unexpected occurrences, such as saplings far from a parent plant, were merely noted.

METHODS

Survey method

Sapling surveys were conducted at each of the six sites used in the seedling survey. At each site two 50m X 2m belt transects were surveyed; i.e. a surface area of 200 m² per site. This is comparable with the 215 m² surveyed for seedlings at each site. The surveys were conducted at the end of winter in late August, the period of lowest germination of seeds under veld conditions (Chapter 3). An area of characteristic homogeneous vegetation of each site was chosen, and the direction of the transect randomly decided by an assistant unfamiliar with the terrain. A 50 m tape measure was laid out, and all saplings within one metre on either side recorded. Two researchers each searched both sides of the tape for saplings.

Sapling identification

Most shrubs in the xeric succulent thicket can reproduce vegetatively (pers.obs), either from branches touching the ground and taking root as in the case of the succulent Portulacaria afra (Stuart-Hill 1989, 1991), or from suckers

from exposed or unexposed roots in the case of most woody species (pers. obs). It was therefore difficult to differentiate between saplings produced from seed and saplings from vegetative growth. To ensure that only saplings from seed were recorded, all saplings within one metre of a large individual of the same species were excavated to ensure that they were not attached to the roots of a parent plant.

Tree and shrub sizes differ between species, therefore for this study different size classifications were used as criteria for qualification as saplings for the different species. Saplings of trees were defined as being non-reproductive individuals up to 1,5 m in height, with a basal stem diameter of <40 mm. On rare occasions when in heavy shade saplings taller than 1,5 m were included, provided the basal stem diameter was <40 mm. When saplings were two- or three-stemmed the stem with the largest basal diameter was measured (e.g. Ward & Parker 1989). For smaller trees and shrubs, including *P. afra*, saplings up to 50 cm in height were included, and up to 30 cm in height in the case of *Phyllanthus verrucosus* and *Jatropha capensis*.

Researchers have, in the past, used diameter as opposed to height as an indication of relative age of saplings of unknown age (e.g. Ward & Parker 1989, Weldon *et al.* 1991). The primary growth of stems is elongation, whereas secondary growth is responsible for increase in diameter, or girth, of stems (Raven *et al.* 1976). Plants exhibit internodal

elongation in response to light detection and intensity, i.e. effect of shading. Light of longer wave lengths (red to far-red) filters through in shaded conditions, and stems respond to this light by stem elongation (Raven et al. 1976, Weier et al. 1970). Light does not have the same effect on stem girth growth, therefore stem diameter is a more accurate measure of age, because it isn't influenced by light to the same extent as stem height. The irregular distribution of shade and canopy height in this survey would therefore result in different growth rates, especially in height, of same aged saplings, therefore basal diameter size classes were used as an indication of age.

Sapling data

For each sapling the following were measured or recorded: height; basal diameter; distance to edge of bushclump or nearest open space; dominant nurse plant; and protection from herbivores. The protection of saplings from herbivores was subjectively scored. Saplings were rated as being poorly protected, partially protected, and well protected. This subjective rating was based on the exposure of the sapling to herbivory. Saplings which were easily accessible, and did not have any protection from surrounding stems or branches, were scored as being poorly protected. Saplings located amongst stems and branches which restricted access to them by herbivores, were scored as being well protected. These saplings were often at the centre of a bushclump. The rating for each sapling was decided on by

consultation between both researchers. This joint decision reduced the bias which could have been experienced if researchers took the decision on protection individually. The danger of bias of this subjective technique also influenced the decision to only use three categories of protection. Protected saplings should have a greater chance of ultimately being recruited to the system.

Contribution of saplings to bushclump expansion

Bushclumps in the xeric succulent thicket probably increase in size through expansion, or creep, of the perimeter of the bushclump (Chapter 3), similar to the Chilean matorral (Fuentes *et al.* 1986). To contribute to this expansion saplings should have the potential to extend beyond the perimeter of the bushclump and overhang previously open areas when fully grown. This will ultimately provide suitable germination and establishment sites.

To determine the potential contribution of saplings to the expansion of the bushclump the average size of common tree and shrub species was determined, and used as an indication of the size the saplings could attain. The diameter in two directions of ten large individuals of each shrub and tree species used in the seedling survey were measured at each site if present in sufficient numbers, and the mean radius calculated for each species at each site. For each sapling the distance to the edge of the canopy was compared to the mean radius of that species at that site, and if greater than the mean radius it was considered to

have the potential to contribute to the expansion of the bushclump. For uncommon trees and shrubs, or for shrubs which are always tangled in a bushclump, and for which the mean radius could not be determined, the following radii were arbitrarily assigned, based on measurements of other similar-sized species: large trees - 125 cm; small shrubs - 50 cm. Ehretia rigida is a scrambling shrub which is always tangled in the canopy. All E. rigida saplings were therefore assumed to have no potential to contribute to the expansion of bushclumps.

Aerial cover

In order to estimate the proportion of open space and aerial canopy cover at each site, a line intercept survey, i.e. the distance on the tape intercepted by total canopy cover and individual species canopy cover (Cox 1985), was conducted along the line of each belt transect. The data for the two lines at each site were pooled for each site, and results expressed as percentages. The dominance of open veld at each site was calculated according to the following formula (Cox 1985):

$$\text{dominance of open veld} = \frac{\text{total intercept of open areas}}{\text{total transect length}} \times 100$$

The relative dominance of each species at each site was calculated according to the following formula (Cox 1985):

$$\text{relative dominance} = \frac{\text{total intercept lengths of a species}}{\text{total intercept lengths of all species}} \times 100$$

RESULTS

Occurrence of saplings

Two-hundred and ninety-four saplings representing 25 shrub and tree species were recorded, at a density of 0,25 m⁻² (Table 5.1). Overall the four most common saplings were Ptaeroxylon obliquum (56; 19 %), Portulacaria afra (52; 17,7 %), Pappea capensis (34; 11,6 %), and Ehretia rigida (24; 8,2 %). A sapling of a further species, Olea eoropea subsp. africana, was observed outside a transect.

Size distribution of selected saplings

The size distributions of saplings of the three most common saplings (Ptaeroxylon obliquum, Portulacaria afra, Pappea capensis) showed the expected trend of higher numbers of smaller, and therefore probably younger, saplings, with numbers decreasing with increasing size (Figure 5.1). This age distribution indicates continual establishment and probable recruitment of saplings temporally. Comparisons of height class would have been biased by high numbers of small plants, as in the case of Portulacaria afra, or by high numbers of tall plants, as in the case of Ptaeroxylon obliquum. This supports the decision to use basal diameter for size comparisons.

Nurse plants

The majority of the saplings (288; 98 %) occurred within bushclumps. Four saplings (1,4 %) occurred in the open, but all were closely associated with the edge of the bushclump. Three (2 Ptaeroxylon obliquum, 1 Brachylaena

Table 5.1. Number of saplings of each species occurring at each site.

SPECIES	POORLY VEGETATED			MODERATELY VEGETATED			WELL VEGETATED	
	S. FACING	N. FACING	TOTAL	S. FACING	N. FACING	TOTAL	S. FACING	N. FACING
<i>Azima tetracantha</i>	2	0	2	0	2	2	1	4
<i>Boscia oleoides</i>	0	0	0	0	0	0	0	1
<i>Brachylaena ilicifolia</i>	1	1	2	1	1	2	2	1
<i>Capparis sepiaria</i> var. <i>citrifolia</i>	0	0	0	10	3	13	0	0
<i>Carissa haematocarpa</i>	0	0	0	0	0	0	0	1
<i>Cassine crocea</i>	0	0	0	5	4	9	0	0
<i>Coddia rudis</i>	0	0	0	1	0	1	0	0
<i>Cussonia spicata</i>	0	0	0	3	2	5	0	1
<i>Diospyros scabrida</i>	0	0	0	6	0	6	0	0
<i>Ehretia rigida</i>	0	1	1	0	10	10	5	8
<i>Euclea undulata</i>	1	1	2	3	1	4	2	5
<i>Grewia robusta</i>	3	1	4	3	2	5	1	2
<i>Hippobromus pauciflorus</i>	0	0	0	0	1	1	0	0
<i>Jasminum multipartitum</i>	0	0	0	0	1	1	0	0
<i>Jatropha capensis</i>	4	3	7	1	0	1	3	2
<i>Maytenus capitata</i>	1	0	1	1	1	2	3	2
<i>Ozoroa mucronata</i>	0	0	0	2	2	4	0	0
<i>Pappea capensis</i>	0	1	1	2	13	15	4	14
<i>Pavetta</i> sp.	0	0	0	1	0	1	0	0
<i>Phyllanthus verrucosus</i>	3	3	6	6	0	6	1	0
<i>Portulacaria afra</i>	31	19	50	1	0	1	1	0
<i>Ptaeroxylon obliquum</i>	0	0	0	24	25	49	7	0
<i>Rhus longispina</i>	0	0	0	0	1	1	0	0
<i>Rhus</i> sp.	0	0	0	5	1	6	0	1
<i>Rhigozum obovatum</i>	0	0	0	0	0	0	0	1
TOTAL	46	30	76	75	70	145	30	43

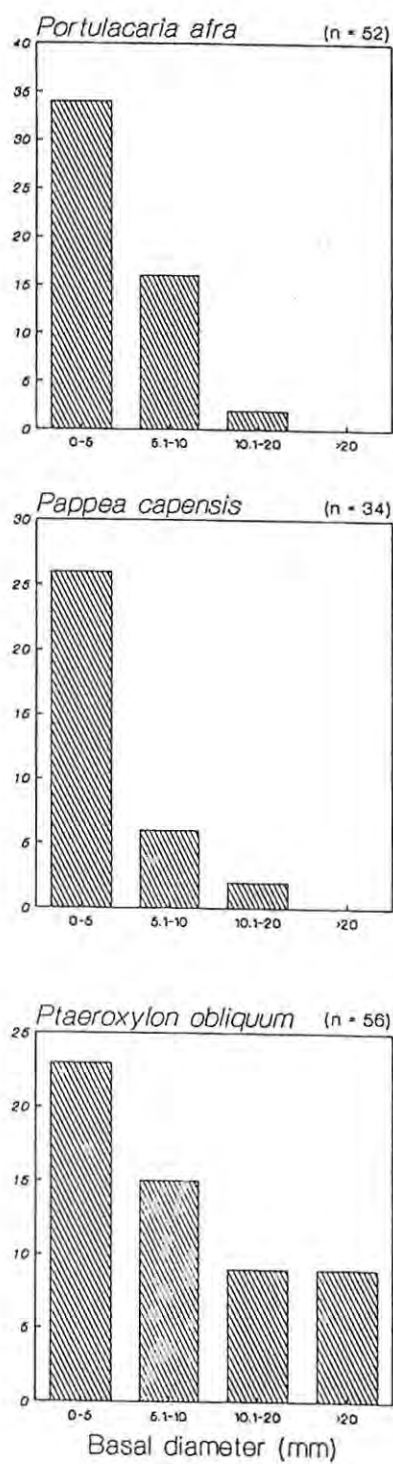


Figure 5.1. Basal diameter size class distribution for saplings of the three most commonly occurring species of saplings.

ilicifolia) were within 20 cm of the edge of bushclumps, and the other, a Grewia robusta, was 50 cm from the edge. Two saplings, both of mechanically dispersed Phyllanthus verrucosus, occurred under small karroid shrubs and herbs. One occurred under a Pentzia incana, the other under a Helichrysum sp.

Saplings occurred under 20 shrub and tree species (Table 5.2). Saplings most commonly occurred under Portulacaria afra (101; 34,4 %), Maytenus capitata (34; 11,6 %), Schotia afra (32; 10,9%), Pappea capensis and Ozoroa mucronata (20; 6,8 % each). The high contribution by Portulacaria afra to the canopy cover would have been responsible for the high proportion of saplings occurring under P. afra, as opposed to P. afra being more suitable as a nurse plant than other species.

Nurse plant - sapling relationships

For reasons discussed earlier nurse plant - sapling relationships cannot be discussed quantitatively. It was evident however that no Portulacaria afra saplings occurred under P. afra nurse plants (Table 5.3), despite having the second highest number of saplings and serving as a nurse plant to the highest number of saplings.

The high proportion of Pappea capensis saplings under Portulacaria afra (Table 5.3) was probably influenced by seed fall from adult Pappea capensis trees adjacent to Portulacaria afra shrubs, which served as nurse plants to many small Pappea capensis saplings. Similarly the high

Table 5.2. Nurse plants under which saplings occurred for each site.

NURSE PLANTS	POORLY VEGETATED			MODERATELY VEGETATED			WELL VEGETATED			TOTAL
	S. FACING	N. FACING	TOTAL	S. FACING	N. FACING	TOTAL	S. FACING	N. FACING	TOTAL	
<i>Azima tetracantha</i>			0			0	1		1	1
<i>Brachylaena ilicifolia</i>	4	5	9	4	1	5		1	1	15
<i>Cassine crocea</i>			0	1	6	7			0	7
<i>Coddia rudis</i>			0	1		1			0	1
<i>Cussonia spicata</i>			0		1	1			0	1
<i>Ehretia rigida</i>			0	2	1	3		1	1	4
<i>Euclea undulata</i>	2		2		4	4	3	1	4	10
<i>Euphorbia bothae</i>	6	2	8			0			0	8
<i>Grewia robusta</i>		1	1	3		3	1	1	2	6
<i>Jatropha capensis</i>			0	2		2			0	2
<i>Maytenus capitata</i>	17	3	20	3	9	12	2		2	34
<i>Ozoroa mucronata</i>			0	2	18	20			0	20
<i>Portulacaria afra</i>	3	2	5	44	10	54	14	28	42	101
<i>Pappea capensis</i>	3		3		16	16	1		1	20
<i>Phyllanthus verrucosus</i>	3	2	5	6	2	8			0	13
<i>Rhigozum obovatum</i>		1	1			0	6	2	8	9
<i>Rhus</i> sp.			0		1	1			0	1
<i>Rhus longispina</i>			0			0	2		2	2
<i>Schotia afra</i>	6	14	20	3		3		9	9	32
<i>Sideroxylon inerme</i>			0	1		1			0	1
Open			0	3	1	4			0	4
Herbs	2		2			0			0	2
TOTAL	46	30	76	75	70	145	30	43	73	294

Table 5.3. Nurse plant - sapling relationships for the most commonly occurring nurse plants and saplings.:

SAPLINGS	NURSE PLANTS					OTHER	TOTAL
	<i>Portulacaria afra</i>	<i>Maytenus capitata</i>	<i>Schotia afra</i>	<i>Pappea capensis</i>	<i>Ozoroa mucronata</i>		
<i>Portulacaria afra</i>	0	18	16	0	0	18	52
<i>Pappea capensis</i>	25	1	1	3	0	4	34
<i>Ptaeroxylon obliquum</i>	17	6	0	3	12	18	56
<i>Ehretia rigida</i>	7	1	4	8	3	1	24
OTHER	52	8	11	6	5	46	128
TOTAL	101	34	32	20	20	87	294

proportion of Ptaeroxylon obliquum saplings under Ozoroa mucronata (Table 5.3) could be explained by a similar set of circumstances.

The occurrence of saplings of certain species appeared to depend on the proximity of the transect to parent plants of the same species. This was especially evident in the case of certain wind-dispersed species (e.g. Ptaeroxylon obliquum) and mechanically-dispersed species (e.g. Phyllanthus verrucosus).

Effect of environmental variables on sapling distribution

There were occasional large differences in the number of saplings occurring in the two transects within a site, but the trends between aspect and vegetation gradient were consistent. There were no significant differences between the number of saplings occurring on north and south facing slopes at any of the three vegetation gradient categories (poorly vegetated: $\chi^2 = 3,368$; moderately vegetated: $\chi^2 = 0,172$; well vegetated: $\chi^2 = 2,328$; $df = 1$ and $p > 0,05$ for all three). Similarly significantly more saplings occurred at the moderately vegetated sites than at the poorly and well vegetated sites on both north and south facing slopes (N: $\chi^2 = 17,468$; S: $\chi^2 = 20,677$; $df = 2$ and $p < 0,001$ for both). This consistency in trends permitted statistical analysis between aspects and vegetation gradients.

1. Vegetation gradient

There were significantly more saplings at the moderately vegetated sites than at the poorly and well vegetated sites ($\chi^2 = 33,858$, $df = 2$, $p < 0,001$).

The proportion of open area was highest at the poorly vegetated sites, and lowest at the well vegetated sites (Table 5.4). Conversely well vegetated sites had the highest canopy cover, and poorly vegetated sites the lowest. Portulacaria afra contributed the most to canopy cover, in some well vegetated and moderately vegetated areas contributing over 40 %. P. afra is the dominant species in xeric succulent thicket (Stuart-Hill 1989), therefore this dominance would be expected. Virtually all of the Portulacaria afra saplings occurred at the two poorly vegetated sites (50; 96,2 %; Table 5.1). Similarly most P. afra seedlings occurred at the two poorly vegetated sites (see Chapter 3). There is less P. afra at the poorly vegetated sites than at other sites (Table 5.4), and P. afra seedlings do not occur under P. afra (Chapter 3), therefore these results reflect the expected trend.

Excavations revealed that small P. afra plants around the skirt of parent plants were all the product of vegetative reproduction, as a result of rooted side branches (Stuart-Hill 1991).

Ptaeroxylon obliquum occur at the moderately and well vegetated sites, but in very low numbers. P. obliquum saplings most commonly occurred in transects located close

Table 5.4. Percentage open area and canopy cover for each site, and the relative dominance of each species.

SPECIES	POORLY VEGETATED		MODERATELY VEGETATED		WELL VEGETATED	
	S. FACING	N. FACING	S. FACING	N. FACING	S. FACING	N. FACING
OPEN	45.7	52.2	34.6	33.3	22.5	14.7
CANOPY	54.3	47.8	65.4	66.7	77.5	85.3
<i>Azima tetracantha</i>	2.7	2.3	0.0	0.0	4.2	2.8
<i>Brachylaena ilicifolia</i>	7.7	3.5	7.7	1.1	3.6	4.8
<i>Capparis sepiaria</i> var. <i>citrifolia</i>	1.5	0.0	1.1	0.3	0.0	0.3
<i>Carissa haematocarpa</i>	0.0	0.0	0.0	0.0	0.0	0.4
<i>Cassine crocea</i>	0.0	0.0	3.0	3.8	0.0	0.0
<i>Coddia rudis</i>	0.0	0.0	1.4	0.0	0.0	0.0
<i>Crassula</i> sp.	0.0	0.5	0.0	0.0	0.0	0.0
<i>Diospyros scabrida</i>	0.0	0.0	1.1	0.0	0.0	0.0
<i>Ehretia rigida</i>	2.9	0.7	0.0	1.8	0.2	1.3
<i>Euclea undulata</i>	4.7	1.1	1.2	2.4	6.9	1.5
<i>Euphorbia bothae</i>	21.5	18.9	0.0	0.0	0.0	0.0
<i>Grewia robusta</i>	11.2	10.4	6.6	6.0	18.0	11.9
<i>Jasminum multipartitum</i>	0.0	0.0	0.0	1.4	0.0	0.0
<i>Jatropha capensis</i>	0.5	0.5	2.4	3.9	0.0	0.7
<i>Maytenus capitata</i>	12.3	8.1	8.7	15.0	2.3	3.9
<i>Olea europea</i> subsp. <i>africana</i>	0.0	2.6	0.0	0.0	0.0	0.0
<i>Ozoroa mucronata</i>	3.5	0.0	4.8	5.5	2.7	0.9
<i>Pappea capensis</i>	3.0	2.5	0.0	17.0	2.4	0.7
<i>Phyllanthus verrucosus</i>	2.4	2.5	11.3	3.8	0.0	0.0
<i>Portulacaria afra</i>	17.3	29.3	44.4	26.5	44.7	52.1
<i>Ptaeroxylon obliquum</i>	0.0	0.0	0.3	0.0	0.0	0.0
<i>Rhigozum obovatum</i>	0.0	1.9	0.3	0.0	10.0	4.7
<i>Rhus longispina</i>	0.0	0.0	0.0	0.0	3.7	0.0
<i>Rhus</i> sp.	0.0	0.0	0.0	4.9	0.8	0.0
<i>Rhus undulata</i>	0.0	0.0	0.8	0.0	0.0	0.0
<i>Scolopia zeyheri</i>	0.0	0.0	1.0	0.0	0.0	0.0
<i>Schotia afra</i>	8.8	15.3	3.7	7.0	0.0	14.2

to parent plants. One *P. obliquum* sapling was observed outside a transect at the poorly vegetated sites. This was unexpected, because there are no large adult plants left at these sites, and saplings from coppice growth are rare.

2. Aspect

There was no significant difference in the number of saplings occurring on north and south facing slopes ($\chi^2 = 0,218$; $df = 1$; $p > 0,05$).

Potential contribution to bushclump expansion

The majority of saplings were close enough to the edge of the canopy to contribute potentially to bushclump expansion (192; 65,3 %).

Most of the saplings were either well protected (146; 49,7 %; Table 5.5) or partially protected (91; 31,3 %) from large herbivores. Approximately half (95; 49,5 %) of the saplings which could contribute to bushclump expansion were well protected, and a further 53 (27,6 %) were partially protected. Overall 32,3 % of all saplings were well protected and had the potential to contribute to bushclump expansion. A further 18 % which could contribute were partially protected.

Table 5.5. Level of protection from herbivory by large herbivores of saplings at each site.

		PROTECTED	PARTIALLY PROTECTED	UNPROTECTED	TOTAL
POORLY VEGETATED	S. Facing	7	13	26	46
	N. facing	10	18	2	30
MODERATELY VEGETATED	S. Facing	52	15	8	75
	N. Facing	38	19	13	70
WELL VEGETATED	S. Facing	17	8	5	30
	N. Facing	22	13	8	43
TOTAL		146	86	62	294

DISCUSSION

This study has demonstrated that a wide range of saplings occur in xeric succulent thicket at the AVKR. Similarly newly germinated seedlings were also represented by a wide range of species (Chapter 3). It has been postulated that there is little or no recruitment of woody species through seeding in the xeric succulent thicket (Stuart-Hill 1989, Stuart-Hill & Danckwerts 1988). The high density of saplings recorded in this survey indicates that recruitment of woody species through seeding does take place in xeric succulent thicket.

A wide range of tree and shrub species fulfilled roles as nurse plants to the saplings. Similarly a wide range of species served as nurse plants to the newly germinated seedlings (Chapter 3). The results of this and the germination survey indicate that the survival of trees is not only important for biomass production, but that they also serve as nurse plants by providing protection for saplings and suitable germination habitat (Chapter 3). Without mature trees there is probably no chance of degraded areas of xeric succulent thicket ever recovering. The survival of individual trees is therefore essential to the continued functioning of this system, and management strategies must take this into account.

The best method of maintaining this veld is to allow browsed areas to recover to their pre-browsing biomass

(Stuart-Hill 1989), therefore the survival of individual trees is vitally important.

There was no significant difference in the number of saplings on north and south facing slopes, whereas there were significantly more seedlings on south facing slopes (Chapter 3). This could indicate a greater survival of seedlings and ultimately the occurrence of saplings on north facing slopes.

Similarly there were significantly more saplings at the moderately vegetated sites, whereas there was no significant difference in the number of newly germinated seedlings across the vegetation gradient. The number of saplings at the poorly vegetated sites could be influenced by the absence of mature Ptaeroxylon obliquum trees at these sites, and the resultant absence of a seed supply. P. obliquum was the most common sapling in the survey, but saplings only occurred where there were adult trees to act as a seed source. The absence of these trees from the poorly vegetated sites is possibly the reason for there being no P. obliquum saplings at these sites.

The difference in survey techniques between the seedling and sapling surveys would also influence the number of saplings negatively. In the seedling survey equal areas of under-canopy habitat were surveyed across the vegetation gradient, whereas in the sapling survey the area of under-canopy habitat differed according to the vegetation present. Seedlings and saplings were always associated with the

canopy, with no seedlings and virtually no saplings occurring in clear areas. The poorly vegetated sites had the highest proportion of clear area, and therefore the lowest proportion of suitable germination habitat. This lower proportion of suitable germination habitat would influence the number of saplings present.

The well vegetated sites had the highest proportion of suitable germination habitat, and therefore potentially the highest number of saplings. The dense vegetation at these sites may not provide the most suitable habitat for survival of saplings, with limited sunlight penetrating the canopy and high competition for resources.

The moderately vegetated sites, where significantly more saplings occurred, may have more suitable habitat for survival of saplings. The vegetation canopy is more open, allowing greater infiltration of sunlight, and there is less competition for resources. There is also sufficient canopy cover to provide suitable germination habitats, so that there is a potential regular input of newly germinated seedlings into the system. A combination of these two factors may be responsible for the significantly higher number of saplings at the moderately vegetated sites.

The distribution of seeds probably plays a major role in relationships between saplings and nurse plants. Saplings often occurred in the immediate vicinity of mature plants of the same species, probably the parent plant. This was especially evident with wind and mechanically dispersed

species, and to a lesser extent with trees which have large seed which are often dispersed through seedfall. The presence of a seed source was probably a more important factor than the presence of a suitable nurse plant in deciding sapling distribution. The wide range of nurse plant species which support saplings supports this idea of seed distribution being more important than nurse plant in determining sapling distribution.

As with the seedling survey, many of the dynamic processes governing similar vegetation types elsewhere in the world (see Chapter 3 for review) have been illustrated by this survey:

- 1) nursing by shrubs, and not by rocks or fallen branches, is a requirement for survival of shrub seedlings (Fuentes et al. 1986);
- 2) seedlings in bushclumps appear to be more protected from herbivory and desiccation than seedlings in the open (Fuentes et al. 1986);
- 3) there are no seedlings of the major shrubs in open areas (Fuentes et al. 1984);
- 4) the presence of seedlings and saplings of wind dispersed species is concentrated in bushclumps, possibly as a result of interception or reduced wind speed in clumps (Fuentes et al. 1984);
- 5) the potential of many of the saplings in this study to contribute to the expansion of the bushclumps supports the suggestion of Fuentes et al. (1986) that colonisation of

clear areas occurs by a slow diffusion process by which the bushclumps increase in diameter;

6) bushclumps are associated with a wide range of nurse plants (Fuentes et al. 1984, 1986);

7) clear bare zones adjacent to bushclumps are not colonised by saplings, possibly because of the degeneration of soil quality (see Chapter 3), which is not conducive to germination and establishment.

Fuentes et al. (1983) further postulated that in Chilean matorral European rabbits may be halting the secondary succession process, affecting the composition of the matorral, and broadening the spacing between bushclumps.

In the xeric succulent thicket there are no introduced rabbits, but the mohair boom has resulted in many farmers in the eastern Cape farming with Angora goats. Goats tend to eat the shrubs and trees from below, creating a clear browse line at about 1,5 m above the ground (Stuart-Hill 1991, in prep.). Poor management results in little or no plant material below this height. In this survey most of the canopies, especially that of Portulacaria afra, reached to the ground, thereby offering protection to the saplings and seedlings. On poorly managed farmlands this protection would be missing, and the provision of suitable germination and establishment sites by nurse plants would be retarded. Goats may therefore be exerting the same pressures as European rabbits exert in Chilean matorral, by halting the secondary succession process in the xeric succulent thicket.

The correct management of this vegetation is therefore essential for its continued existence.

Portulacaria afra is the dominant shrub in the xeric succulent thicket (e.g. Aucamp 1979, Aucamp & Tainton 1984, Stuart-Hill 1989), and also the dominant shrub at the AVKR (this study). P. afra does not support a high density of newly germinated seedlings compared to other species (Chapter 3), but by being the dominant shrub it will probably support the highest number of seedlings. P. afra does support the highest number of saplings, solely because of its dominance.

P. afra is one of the first species to disappear when xeric succulent thicket is overutilised (Aucamp & Tainton 1984). The high number of P. afra seedlings and saplings in the poorly vegetated areas, where P. afra is less dominant than in moderately and well vegetated areas, indicates that P. afra has the potential to become dominant in these poorly vegetated areas. P. afra seedlings are very slow growing under veld conditions (pers. obs), therefore this veld would have to be rested for several years. This cannot be expected of a farmer, and conservation agencies are being forced by public pressure to stock areas to the detriment of the veld, therefore there is no possibility of degraded areas being allowed to recover through rest.

Ptaeroxylon obliquum saplings were the most common, despite there being no mature trees to act as a seed source at the poorly vegetated sites. P. obliquum trees have been

removed from the subtropical transitional thicket in large numbers (Moorcroft 1988), and large trees are now uncommon in the xeric succulent thicket (pers. obs). Alternatively Portulacaria afra and Pappea capensis, both common trees, each had high numbers of saplings as well as seedlings. This suggests that the removal of most mature trees has resulted in a low input of Ptaeroxylon obliquum seed into the system. The importance of P. obliquum in the system is further illustrated by it being the nurse plant which supported the highest density of seedlings (Chapter 3).

Bushclumps in the xeric succulent thicket do not appear to be associated with one specific species (pers. obs). Similarly bushclumps in the Chilean matorral do not appear to form around one specific species (Fuentes et al. 1986). However in arid lands in North America bushclumps tend to form around one specific species (Archer et al. 1988). P. obliquum may well have fulfilled a similar role in xeric succulent thicket.

CONCLUSIONS

This study has proven that many seedlings, representative of a wide range of species, survive the early stages of their life cycle to enter the system as saplings, and it is probable that many of these saplings will survive to recruit ultimately to the system as reproductive trees and shrubs. This survey, together with the seedling survey (Chapter 3), has proven beyond doubt that recruitment of the shrub and tree component of xeric succulent thicket does take place

through seeding. A wide range of mature trees fulfill a vital function as nurse plants in the dynamic functioning of this system, which further highlights the importance of maintaining individual trees.

Many of the saplings were well protected by bushclumps from herbivory by large herbivores, and were close enough to the edge of the bushclumps to aid ultimately in the spread of the bushclump by creep. Unfortunately, as with the seedlings (Chapter 3), no saplings were dissociated from bushclumps, so there is no possibility of bushclumps establishing naturally in clear and degraded areas.

Sneezewood Ptaeroxylon obliquum was the most common sapling in this study, despite the scarcity of adult trees remaining in the system as a seed source. Sneezewood was also one of the most important nurse plants to seedlings (Chapter 3). This recurring importance of sneezewood suggests that there may now be one of the most vital links in xeric succulent thicket dynamics missing from the system. The role of P. obliquum in the functioning of xeric succulent thicket needs further investigation.

CHAPTER 6.

CONCLUSIONS AND MANAGEMENT PROPOSALS.

CONSERVATION STATUS AND LARGE-SCALE DEGRADATION.

The subtropical transitional thicket is now comparatively well conserved, with 10 % of remaining subtropical transitional thicket being conserved. There is however a bias in conservation status between the order Kaffrarian succulent thicket, with 13 % of 6145 km² conserved, and Kaffrarian thicket, with 3 % of 3034 km² conserved. The Kaffrarian thicket is more mesic than the Kaffrarian succulent thicket, and is therefore extensively cleared for the planting of crops such as pineapples and chicory, or for natural or planted grazing. Improved technology and periods of hardship for farmers have resulted in marginal areas in Kaffrarian thicket being cleared recently, and this practice will continue in the future.

Further, the rate of disappearance of STT through debushing and as a result of overutilisation is cause for concern (e.g. Hoffman & Everard 1987). In xeric areas the farmers will not survive if poor management is practised, therefore correct stocking rates and management are essential for the continued existence of farmers and of the STT. Bushclearing regulations of the Department of Agriculture concerning the clearing of STT need to be strictly applied, to prevent marginal lands being cleared for a quick profit, and then being allowed to lie fallow. Abandoned lands are common throughout the Kaffrarian thicket

(pers obs). These should be utilised before large-scale clearing is allowed to continue.

The Kaffrarian thicket is the most species rich in the STT (Everard 1987). Because of large-scale bushclearing and its poor conservation status, the identification and establishment of suitable conservation areas in the Kaffrarian thicket, especially the mesic Kaffrarian thicket, should be a conservation priority in the eastern Cape.

REGENERATION OF STT THROUGH SEEDING.

The seedling and sapling surveys revealed that germination of seeds and the establishment of seedlings and saplings representing a large range of woody species does take place in the xeric succulent thicket. Further, it is probable that recruitment to the system will occur. These findings contradict the current ideas that regeneration of the woody component of xeric succulent thicket through seeding does not take place (e.g. Stuart-Hill 1989, Stuart-Hill & Danckwerts 1988).

The confinement of all newly germinated seedlings and virtually all of the saplings to the area under the canopies of a wide range of shrubs and trees is however a problem, because mismanagement often results in the loss of individual trees which are essential as nurse plants. No newly germinated seedlings occurred in the open bare, karroid and grassy areas, and all saplings were associated with bushclumps, therefore open areas which were previously xeric succulent thicket will not recolonise naturally. The

association of all saplings with bushclumps further indicates that episodic events have had no long-term effect on the establishment of saplings at sites not associated with bushclumps. Episodic events may however promote seed germination and establishment of saplings in bushclumps, ultimately enhancing the chances of a bushclump increasing in size.

The degradation of the soil surrounding bushclumps through heavy utilisation may well render these sites unsuitable for germination, particularly because of the high Al concentrations in soils of these clear areas. The suitability of these soils for germination of seeds of woody species, and their effect on Portulacaria afra truncheons (Anonymous 1990), must be tested by means of an ecological bioassay technique (Kinako 1982).

If these soils prove unsuitable for seed germination and for P. afra truncheon growth (Anonymous 1990), the only solution to recovery of these areas may be long rest, possibly several decades, as suggested by Palmer (1982). Bushclumps may increase in area by gradual centrifugal growth, ultimately coalescing with each other. Approximately one-third of saplings recorded in the sapling survey have the potential to contribute ultimately towards the expansion of bushclumps. Climatic constraints may however restrict the size of bushclumps. Kudu-proof exclosures must be erected at the SKNR to determine whether rest does in fact play a role in the expansion of bushclumps and ultimate

recovery of the vegetation. Rest is a long-term option, and it is apparent that any rapid recovery of the veld will require active management on the part of the land managers.

Long rest is impractical for farmers, and recently proclaimed reserves such as the Sam Knott Nature Reserve will not be allowed to recover because of the importance placed on animals above their habitats by conservation and preservation agencies and the public. The general public's perception that animals are the primary aim of conservation will need to be seriously addressed by environmental educationalists if newly acquired areas are to serve a function in ecosystem conservation for which they are proclaimed.

Sneezewood Ptaeroxylon obliquum was identified as one of the key species in this survey. Sneezewoods were the nurse plant with the highest density of newly germinated seedlings, and had the highest number of saplings, despite no longer being present in certain areas surveyed. In the past sneezewoods were removed as fencepoles, and for firing bunkers of ships. They are now rare in accessible areas in the xeric succulent thicket. Sneezewoods are slow growing, so there is no chance of their fulfilling a role as nurse plants around which bushclumps develop, a role they once possibly fulfilled. It is therefore obvious that active management practices will have to be introduced in an attempt to speed up the process of recovery of degraded xeric succulent thicket.

One possibility is the planting of Portulacaria afra truncheons in small areas of degraded land (Anonymous 1990). This has been applied to an old fence line at the AVKR. The truncheons have survived, but they are heavily browsed, and will therefore have little chance of reaching a suitable size to attract seed-dispersing birds, thereby acting as nurse plants around which a bushclump could develop. Where possible reclamations of this kind and the establishment of these truncheons should be completed before historically occurring animals are reintroduced. The Department of Agriculture is currently conducting experiments near Kirkwood to determine the best method of planting these truncheons (Anonymous 1990). P. afra is the dominant shrub species throughout the xeric succulent thicket, therefore there will be no shortage of truncheons.

Another possibility is the establishment of Acacia karroo as a pioneer, to serve as a nurse plant. A. karroo is common along river courses and around dams in the xeric succulent thicket, but it is uncommon in the veld (pers. obs). It does however serve as a pioneer in the more mesic xeric Kaffrarian thicket (Appendix 1), and bushclumps form around it in the false thornveld of the eastern Cape (Acocks (1988) veld type 21). The false thornveld occurs adjacent to the xeric succulent thicket (*cf.* Acocks 1988) and has a mean annual rainfall of 400 - 650 mm. The mean annual rainfall for the AVKR of 434 mm is close to the lower limit of 400 mm for the false thornveld of the eastern Cape, but may be

sufficient to support A karroo trees. Branches containing seed can be cut and packed on degraded areas. Seed of a large range of other shrub and tree species can be broadcast in these brushpacked areas. This brushpacking should be carried out in early spring to coincide with the rainy season as well as with the season of highest germination. This method needs to be tested.

In Chilean matorral seed dispersal is concentrated around bushclumps (e.g. Fuentes et al. 1984, 1986). If similar dispersal patterns are present in the xeric succulent thicket, then a lack of seed in the open areas may be a problem. Seed could be broadcast in open karroid and grassy areas in an attempt at re-establishing shrubs and trees in these areas. This technique, if successful, will be the cheapest, least labour intensive, and will not be hampered by inaccessibility of sites, and should therefore be tested.

Stuart-Hill (1989) has emphasised the importance of not allowing individual trees to die as a result of mismanagement. This study has confirmed the importance of individual trees in the functioning of xeric succulent thicket. All shrubs and trees studied in the seedling survey (Chapter 3) proved important for the provision of microhabitats suitable for germination of seeds and establishment of seedlings of a wide range of species. The protection of individuals is also important to ensure a regular seed supply. The current practice of clearing bush

to aid in game capture operations at the AVKR must be stopped, and alternative capture methods investigated.

The current practice on farms and nature reserves in xeric succulent thicket is to base management practices on years of adequate rainfall. The rainfall in this area is unpredictable, and years of below average rainfall occur often. These years of low rainfall are classed as "droughts", whereas they should be expected. Maintaining animal populations, especially on reserves, at artificially high numbers by feeding them during normal dry periods will ultimately result in overutilisation of the veld, because the veld will never have a chance to recover from previous heavy utilisation. Stocking rates should therefore be based on the carrying capacity during dry periods.

The management plan of the Andries Vosloo/Sam Knott Nature Reserve complex is currently under review and still in a draft stage, but if the most recent primary goal "to provide a benchmark against which the nature and rate of change of alternative land uses can be measured" is to be met, no reintroductions of historically occurring animals must take place at the Sam Knott Nature Reserve. Game farms and well stocked nature reserves are now common in the xeric succulent thicket. The Sam Knott Nature Reserve must serve as a benchmark against which the veld on these game farms and reserves can be compared. The Andries Vosloo Kudu Reserve is well stocked with game, and so is unable to meet the primary goal for the complex.

Another problem at the Sam Knott Nature Reserve is the large number of roads, dams and drainage channels (Burdett 1988) built in the mid-1980's. The dams are close together, therefore mammals will be able to concentrate around a waterhole without ever having to migrate over a distance of a few kilometres. This will ultimately place stress on the surrounding vegetation. There is already an erosion hazard in a few areas because of previous utilisation patterns. The introduction of large herbivores such as buffalo will compound these erosion problems. It is essential that the groundcover be allowed to recover, and that some dams are closed up so that mammals will have to disperse. The effect of current populations of naturally occurring kudu, duiker and steenbok on the shrubs and trees should also be assessed to ensure sound management decisions.

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APPENDIX 1.

BRIERS, J. H. & LA COCK, G. D. *submitted*. Tree successional dynamics of xeric Kaffrarian thicket in an old land on the Thomas Baines Nature Reserve. *Journal of the Grassland Society of southern Africa*.

The manuscript which appears here is the version which was submitted for publication by my co-author, J. H. Briers. I did not see the final version before he submitted it, and have not edited it.

TREE SUCCESSIONAL DYNAMICS OF XERIC KAFFRARIAN THICKET IN AN OLD LAND
ON THE THOMAS BAINES NATURE RESERVE

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Abstract. The spatial pattern of regeneration in Xeric Kaffrarian Thicket was studied and described on an old land of approximately 25 years old. Little is known about the dynamics and post disturbance recovery of Xeric Kaffrarian Thicket, but it is considered to be stable, with a low resilience. The effect of the canopy cover of the two key pioneer tree species of this veld type namely, *Acacia karroo* a microphyllous, deciduous and deep-rooted tree and *Rhus undulata* a broadleaved, evergreen and shallow-rooted tree on the establishment pattern of tree saplings, was examined to develop an understanding of the succession in this veld type. The results of the study explained the contribution seed dispersal, under-canopy environment and competition made in shaping the observed pattern. *Acacia karroo* seems to play a key role in the enhancement of succession, the direction of the process and the diversity of the resulting thicket.

Die spasiële regenerasie patroon van bome in die "Xeric Kaffrarian Thicket" in 'n ou land, ongeveer 25 jaar oud is ondersoek en beskryf

met die doel om 'n begrip van die suksessieproses in hierdie veldtipe te vorm. Min is bekend oor die dinamika en veldherstel na versteuring in hierdie veldtipe, maar dit word aanvaar dat die veld stabiel is met 'n lae herstelvermoeë. Die effek van kruinbedekking van die twee sleutel pionier boomspesies in hierdie streek naamlik, *Acacia karroo* 'n mikrofile, bladwisselende diep gewortelde boom en *Rhus undulata* 'n breëblaar, immergroen en vlak gewortelde boom op die vestigings patroon van boom saailinge is ondersoek. Die resultate is gebruik om die bydrae van saadverspreiding, onder-kruin omgewing en kompetensie maak tot die waargenome patroon te probeer verklaar. Dit blyk of *Acacia karroo* 'n sleutel rol speel om die proses te bespoedig, die rigting van die proses en ook die diversiteit van die bos wat uiteindelik vestig bepaal.

INTRODUCTION

Xeric Kaffrarian Thicket is a sub-order of the Subtropical Transitional Thicket. The taxonomic Class Subtropical Transitional Thicket (Cowling 1984) formerly Valley Bushveld (Acocks 1975), was divided into four sub-orders based on structure by Everard (1987). This study was conducted on the Thomas Baines nature reserve in Xeric Kaffrarian Thicket in the eastern Cape, South Africa.

Large tracts of Xeric Kaffrarian Thicket have been cleared for grazing and crops such as chicory, pineapples and wheat (La Cock, Palmer & Everard 1990 and Malan 1988). Old lands are commonly abandoned and used for grazing. Little is known about the dynamics of Subtropical Transitional Thicket and its post disturbance recovery. Subtropical Transitional Thicket is considered to be stable, but with a low resilience (Cowling 1984 and Hoffman & Cowling 1990). Aucamp & Tainton (1984) and Hoffman & Cowling (1990) consider badly overutilized areas to be permanently transformed through the replacement of the shrub component by karroid dwarf shrubs. The concern for conservation of this veld type stems from the low resilience and the extensive bush clearing coupled with the abandonment of old lands. Only 2% of this sub-order is formally conserved (La Cock *et al.* 1990).

Contrary to the view that this veld type has a low resilience Mc-Kenzie (1989) found that land clearance and field abandonment in Mesic Kaffrarian thicket in the Transkei caused an increase in

woodland area. Mc-Kenzie (1989) did not discriminate between the quality of the resulting woodland on the basis of diversity and structure. *Acacia karroo* is dominant in old fields and is the most important pioneer tree species in the Transkei (Mc-Kenzie 1989). Most old lands in the more mesic parts of the valley bushveld became dominated by *A. karroo* and/or *Rhus undulata* to create veld with a savanna-like physiognomy (pers. obs.). These two species were considered to be the most important pioneer species, and thus chosen as the key species for this study.

Models developed for the understanding of savanna structure were used to help explain this process. Huntley & Walker (1982) and Bourliere (1983) predict that low , seasonally variable water availability and low soil fertility are contributing factors to the determination of the physiognomic structure of savannas. The role of water availability is in part supported by the physiognomic gradient of increasing tree density with increasing rainfall (Smith & Goodman 1986). The control of savanna physiognomic structure has been focused on the potential competition for limited soil moisture between herbaceous and woody components of the vegetation. Walter (1971) developed a simple model, later used by Walker (1980) to describe the relationship between grass and trees based on competition for water in two functional soil layers by the tree and grass components of the veld. Competition between woody plants could play a important role in determining the structure and dynamics of savanna communities (Smith & Walker 1983, Smith & Goodman 1986 and Knoop & Walker 1985).

A study of the spatial pattern of sapling establishment was conducted in order to develop an understanding of the process of succession from a savanna type physiognomic structure to a diverse, closed canopy thicket similar to the Xeric Kaffrarian Thicket. The aims of the study were:

- * To describe the pattern of succession of the tree component relative to established pioneer trees, namely *Acacia karroo* and *Rhus undulata*, and in the open.
- * To determine whether the vital attributes of the two pioneer canopy species and the open grassveld influence the pattern of re-establishment of tree species.
- * To try to explain the factors controlling the successional process by fitting the observed pattern to different hypotheses that could explain the pattern.

By answering these questions we hope to obtain a better understanding of the successional process, which would facilitate better advice on the management options for old lands and disturbed areas in the Xeric Kaffrarian Thicket.

STUDY SITE

The study was conducted in Thomas Baines nature reserve 33° 23'S, 26° 30'E and altitude 400 m) on a plain with a 2° to 4° north facing slope.

The reserve is located in the summer rainfall region, with an average annual rainfall of 756 mm measured on the reserve over the last 10 years. The wet season lasts from September to April with the highest rainfall occurring in October and March. The mean daily maximum summer temperature is 26,6 °C and mean daily minimum summer temperature is 14,6 °C. The absolute maximum summer temperature is 41,9 °C. Winters are mild with a mean daily maximum temperature of 18,9 °C and a mean daily minimum temperature of 4,8 °C.

The ± 7 ha old land was chosen as an experimental site from a number of old lands of differing successional stages. A stage was chosen where such that only *Acacia karroo* and *Rhus undulata* were dominant. These two species were considered to be the most important pioneer species of this veld type and made up more than 95% of the total tree cover on the study site.

From a series of aerial photographs it was determined that the site had not been interfered with since abandonment approximately 25 years ago.

The soil in the study site is grayish to red alluvial soils, more than 1 meter deep and has a sandy-clay-loam texture. These soils are fairly common throughout the region.

The study site was included into the reserve in 1970 and since then it was managed to provide grazing for several species of game.

METHODS

The structure of the woody vegetation in the study site was determined in six 400 m² plots by counting the number of individuals in five subjectively chosen height classes. The percentage crown cover of each species in the plot was estimated separately and an average percentage crown cover determined for the study site. The number of tree saplings indicated in Figure 1 were calculated from the survey data and based on a 10% *A. karroo*, and 10% *R. undulata* crown cover and 80% open area.

Forty solitary individual *A. karroo* and *R. undulata* trees with a height and diameter of at least 3 m and 2 m, respectively, were randomly selected for the transect surveys. A 2 m wide transect was surveyed from the stem of the tree up to 5 m from the outer edge of the canopy of each tree. The transects were directed away from the stem of the tree and positioned randomly with respect to compass direction, avoiding other established trees by at least 5 m. All seedlings and saplings under the canopy were identified and counted. Within the transect the distance to the stem, and the height of saplings were measured. The relative position of each sapling with respect to canopy cover was calculated by dividing the distance from the stem by the distance to the canopy edge. Values thus range from 0 at the base of the tree to 1,0 at the outer edge of the canopy. Saplings were divided into two groups, namely, those beneath the tree canopy (values $\leq 1,0$) and those with no canopy cover (values $> 1,0$).

The under-canopy observations were subdivided into five distance classes (0,0-0,2; 0,2-0,4; 0,4-0,6; 0,6-0,8; 0,8-1,0) to examine position relative to canopy cover, which may reflect gradients of light or moisture from the bole of the tree to the outer edge of the canopy. The number of individual saplings of each species within each class was expressed as a percentage of the total observations for that species. Percentages were corrected for the differences in open and under-canopy areas sampled by the transects so that each of the groups represents sampling from an equal area.

Only species with 15 or more observations were included in the pattern descriptions. The data collected for saplings found in the under-canopy area of the selected trees outside the transect were used to substantiate the results of the transects. This larger survey area pushed the number of observations of the species used in the pattern descriptions up to ≥ 40 individuals for any particular species used. The uncommon species all seems to establish in a similar pattern, therefore these species were lumped together for *A. karroo* (17 species and 71 observations) and for *R. undulata* (9 species and 16 observations) and used in Figures 2 & 3 describing the establishment pattern.

The Fisher-Williams diversity statistic (α) was used to describe diversity since it is relatively unrelated to sample size and independent of the underlying model (Taylor *et al.* 1976).

$$S_i = \alpha \log(1 + N_i/\alpha)$$

Data for the determination of the diversity index and in Table 1 includes the number of all individuals found under a tree or in the open.

RESULTS

From aerial photographs it was determined that the land was still cultivated in 1965 and succession progressed from at least 1973 until 1990. The age of the veld in the old land is thus not more than 25 years. The mean estimated crown cover of both *A. karroo* and *R. undulata* is 10%, with ranges of 8% to 12% and 3% to 25% respectively. The area of open veld was therefore 80%.

The size class distribution of established trees consists of a distinct height class for bigger trees of > 2 m and $> 1,5$ m height of *A. karroo* and *R. undulata* respectively and a peak in sapling size class of individuals $< 0,5$ m (Figure 1).

The contribution of the *A. karroo* patches to the diversity of the developing veld is more than twice that of the *R. undulata* and more than four times that found in the open (Table 1). Saplings of up to ten tree species could be found in the canopy area of a single *A. karroo* tree. More than half the tree species occurred in the canopy area of *A. karroo* trees only. Excluding saplings of *A. karroo* and *R. undulata*, sapling density in the canopy area of *A. karroo* is more than five times that found in the canopy area of *R. undulata* and more than ten times that found in the open (Table 1).

The distribution of saplings relative to the overstory canopy for *A. karroo* and *R. undulata* are presented in Figures 2 and 3 respectively. Six species occur in sufficient numbers to be presented for *A. karroo* and three for *R. undulata* plus a rest-of-the-species-graph was included. The saplings of all species except *A. karroo* seem to be associated with the canopy cover of *A. karroo* (Table 1, Figures 2 & 3). These species include *Rhus undulata*, *Coddia rudis*, *Grewia occidentalis*, *Burchellia bubalina*, *Scutia myrtina*, plus 15 other species which occur less frequently. Only *R. undulata* saplings were more abundant under established *R. undulata* trees than in the canopy area of *A. karroo* or in the open. *A. karroo*, *Rhus undulata* and *Coddia rudis* are the only species that also occur commonly in the open. *A. karroo* is the only species that occurs in lower numbers under the canopy of trees than in the open. *A. karroo* does occur under the canopy of established *A. karroo* and *R. undulata* trees, but in declining numbers nearer to the bole of the tree (Figures 2 & 3).

More than 90% of *A. karroo* and *C. rudis* saplings in all cover conditions and *R. undulata* saplings under *R. undulata* are less than 0,4 m in height (Figure 4). *R. undulata* saplings in the canopy area of *A. karroo* or in the open have a distinctly greater proportion of saplings in the greater height classes (Figure 4) compared to those found in the canopy area of *R. undulata* itself.

DISCUSSION

The total dominance of the two pioneer tree species indicate that the veld is in an early successional stage (Figure 1). *A. karroo* is a

microphyllous, deciduous, deep-rooted tree and *R. undulata* a broadleaved, evergreen, relative-shallow rooted tree.

From the results in Table 1 it is clear that *A. karroo* plays an important role in the process of succession in the Xeric Kaffrarian Thicket. The number of tree species which established under the canopy area of *A. karroo* was more than 3 times that in the open areas and double that found under the canopy of *R. undulata*. *A. karroo* is also the only species with saplings occurring commonly in the open.

Endemic and rare plant species in the Subtropical Transitional Thicket are not tree species but rather succulent species from families such as Euphorbiaceae, Mesembryanthemaceae and Crassulaceae (Cowling 1984, Everard 1987 and Hoffman & Cowling 1991). It is therefore necessary that a follow-up study should include such species.

From the results (Figures 2 & 3) the following sapling establishment pattern can be identified:

- * Broadleaf-evergreen species namely, *R. undulata*, *C. rudis*, *G. occidentalis*, *B. bubalina*, *S. myrtina*, plus 15 other species which occur less frequently, are all closely associated and clumped under the canopy of established *A. karroo* trees.
- * Saplings do not seem to be associated with *R. undulata* canopy cover. Only *R. undulata* saplings were more abundant in the canopy area of *R. undulata* than in the open, or under *A. karroo*.

- * Some species namely, *R. undulata* and *C. rudis*, did establish in the between-canopy areas.
- * *A. karroo* is the only species that occurs in lower numbers with in the canopy area of trees than in the open.

This different response, between saplings of different species, to the sphere of resource (water and nutrients) depletion and physical properties around an established tree needs to be explained. What causes this difference and what can we deduce from the pattern concerning successional dynamics? The observed pattern (Figures 2 & 3) was fitted to different hypotheses that could explain the pattern. The components of the observed pattern that could be explained by, or contradict each hypotheses is discussed separately.

Three possible hypotheses that could explain the clumped pattern of tree seedling establishment that was used were:

1. The patchy seedling pattern reflects the different seed dispersal patterns;
2. Some resource, other than water associated with the under canopy sites (such as nutrient status, organic matter, water infiltration and/or shade and resulting in lower temperatures and less evapotranspiration) enhances or limits the distribution of different species in the thicket;
3. Although water is limiting to all seedlings in the canopy area of a tree, the partitioning of available water through interspecific differences in rooting strategies leads to competitive avoidance of competition.

1. Pattern reflects seed dispersal pattern.

Seeds of all the species occurring clumped in the under canopy area of *A. karroo* trees in the study are primarily dispersed by birds. Seeds of most trees encountered in the study, except *A. karroo* are primarily dispersed by birds. Mammals, especially monkeys and baboons, also utilize the fruit of *S. myrtina*, *C. rudis*, *R. undulata*, *G. occidentalis* etc. (Palmer & Pitman 1972) and (pers. obs.). *A. karroo* are primarily distributed by ungulates (Du Toit 1966 and Pratt 1967). Seedfall directly under the canopy of both *A. karroo* and *R. undulata* was evident. The establishment pattern in the study reflects the expected clumped distribution of seedlings of bird distributed plants around *A. karroo* trees (Figures 2 & 3). *A. karroo* which is primarily distributed by ungulates has a random distribution over the study site. Tester, Paton, Reid & Lange (1987) hypothesises that clumped distribution of saplings reflects the pattern of seed dissemination, shrub densities under trees, and seed dispersal by birds in Australia. They concluded that seed dispersal by birds was responsible for high seedfall under tree canopies and is involved in the eventual plant distribution pattern, but that seed germination and seedling survival also play a role. Seed dispersal is a possible contributing factor explaining clumped distribution of plants in Natal (Smith & Goodman 1986, 1987).

The hypothesis namely, that establishment pattern reflected dispersal pattern is partially explain the observed clumped establishment pattern, but the following still needs to be explained:

- * Sapling numbers under the canopy of *R. undulata*, which in addition to shelter also has edible fruit to draw birds, are much lower than those found under *A. karroo* and similar to that in the open. The greater height of *A. karroo* could result in more bird visitation and a higher seed store underneath these trees, but sapling numbers underneath *R. undulata* similar to that in the open, could not be explained (Figures 2 & 3). Both trees will presumably be used by birds for protection and roosting and the *R. undulata* also for fruit.
- * The extremely low sapling numbers in the open, although the seeds of most species are also mammal dispersed and birds also defecate whilst flying.
- * Seedfall underneath both *A. karroo* and *R. undulata* is high and only seedling establishment of *R. undulata* shows a peak underneath its canopy.

2. Resource associated with canopy responsible for pattern.

Recent studies describe the effect that an individual tree has on the physical and chemical environments around it (Stuart-Hill Tainton & Barnard 1987, Stuart-Hill & Tainton 1989 and Belsky Amundson Duxbury Riha Ali & Mwonga 1989). It was found that:

- * Significantly less rain fell in the rain shadow of the tree canopy, resulting in less soil water being available.

- * Shade and lower light intensities result in lower soil temperatures.
- * There is more leaf litter.
- * There is a greater soil fertility around trees.
- * Higher rates of water infiltration.
- * A better soil water holding capacity.
- * Stemflow occurs but the contribution to soil water is difficult to quantify.
- * Trees suppressed grass growth up to 9 m away from the tree.
- * Despite less water reaching the ground (Stuart-Hill *et al.* 1987) and the competition for this resource immediately under the canopy of trees (Knoop & Walker 1985), the grass production was up to 25% higher under individual trees than in the open (Stuart-Hill *et al.* 1987, 1988 and Belsky *et al.* 1989). This higher production is attributed to measured, shade and leaf litter and water holding capacity and lower temperatures and greater soil fertility around a tree.

The picture is completed by including the competition effect that this different herbaceous plant cover might have on the survival and growth of tree saplings.

The observed establishment patterns described in this study (Figures 2 & 3) were similar to that of Smith & Walker (1983) and Smith & Goodman (1986, 1987) working in *Acacia* savanna in Natal with saplings of a great number of tree species clumped in the ameliorated environment in the canopy area of trees. These authors also explain the difference in the establishment pattern of microphyllous,

deciduous trees (*A. tortilis*, *A. nilotica* and *D. cinerea* and *A. karroo*) and that of broadleaved-evergreen trees. Broadleaf evergreen species could make use of the ameliorate environment in the canopy area of trees and are all closely associated and clumped under the canopy of established trees despite the rainfall interception and greater competition. While *A. karroo* saplings, which is shade intolerant, could not occur in the under canopy environment. Smith & Goodman (1987) single out seedling mortality and not germination, under tree canopy as the most important factor controlling seedling numbers. Smith & Walker (1983) and Smith & Goodman (1987) suggest that irradiance under both tree and grass canopies could limit seedling establishment of *Acacia*'s, either as a sole factor or in combination with others. Contrary to the findings of these authors *Acacia* seedlings were not absent from under the canopy of established trees although sapling numbers are lower and decline nearer to the stem of the tree (Figures 2 & 3). The lower numbers of *A. karroo* in the under canopy area in the observed pattern which is still unexplained by the seed dispersal hypotheses can thus be explained by this hypothesis.

Light does not seem to have any effect on the germination of *Acacia* species (Briers Theron Van Rooyen & Bredenkamp 1991) and can not influence distribution. *Acacia* seeds germinate well in the accumulated organic matter under trees (Smith & Walker 1983). Broadleaved species related to those associated with the under canopy environment in this study all need a relatively long damp period (> 14 days) before the seeds germinate, while seeds of all *Acacia*'s respond quickly (within 4 days) once seed hardedness is lifted (Briers

1988). The prolonged period of wet conditions needed for germination could be associated with the more humid and organically rich top layer under the canopy of trees, which make it difficult for these species to establish in open areas where the top layer (on which the seeds are dependant for germination) dries out quickly. The germination requirements of these broadleaved species thus make it difficult for them to establish in the open. Germination requirements could thus play a role in determining the pattern preventing these species from establishing in the open explaining the extremely low sapling numbers in the open.

Still unexplained by this hypothesis are:

- * the low number of broadleaved, evergreen, shade tolerant saplings in the canopy area of *R. undulata*.
- * More *A. karroo* saplings, which are supposed to be more shade intolerant, occurred in the canopy area of *R. undulata* than under the canopy of *A. karroo*, even though the shade of *R. undulata* is deeper than that of *A. karroo*.

3. Competitive avoidance.

The third hypothesis used to try and explain the observed pattern is partitioning through differentiation of rooting strategies and resultant competition avoidance (Yeaton *et al.* 1977). This hypothesis could explain the lower number of saplings of *A. karroo* and high number of broadleaved tree saplings under *A. karroo* plus the lower

numbers of broadleaved tree saplings in the under canopy area of *R. undulata*.

This hypothesis can best be illustrated by the simple model developed by Walter (1971) and later used by Walker (1980) to describe the relationship between grass and trees based on competition for water in two functional soil layers by the tree and grass components of the veld. Grass, the dominant competitor for water in the top functional soil layer, and trees with exclusive axes to water in the deeper functional soil layer. This model could be applied here since a preliminary study indicates that the saplings of broadleaved, canopy tolerant species have shallower root systems or are less dependent on a tap root, and water from the deeper soil layers but rather make use of water in the top functional layer. *A. karroo* saplings seems to be very dependant on its tap root and thus water from the deeper soil layer for survival. *Acacia* seedlings develop tap roots of longer than 1 meter in less than 30 days after germination (Briers 1988).

Broadleaved tree species can thus make use of the ameliorated micro-environment in the top soil layer under the deep rooted *Acacia* trees without competing with the *Acacia* tree. The deep-rooted *A. karroo* seedlings compete directly with *A. karroo* and shallow-rooted *R. undulata* compete directly with the seedlings of the shallow rooted broadleaved species. The similar sapling numbers of *A. karroo* under both *A. karroo* and *R. undulata* further suggests that light is not the most important factor controlling the survival and distribution of *A. karroo* as suggested by Smith & Goodman (1987).

The predicted establishment pattern based on this hypothesis can explain the unexplained part of the observed pattern, namely:

- * the lower numbers of *A. karroo* saplings and higher numbers of shallower rooted, broadleaved tree saplings under the canopy of *A. karroo* trees
- * plus the lower numbers of broadleaved saplings in the canopy area of the shallower rooted *R. undulata* trees.

The size class distribution of saplings (Figure 4) of *A. karroo* and *C. rudis* under all cover treatments and *R. undulata* saplings in the canopy area of *R. undulata* indicate the expected high mortality of small seedlings. The prepositional high number of sapling survivors of *R. undulata* in the open and in the under-canopy area of *A. karroo* even though the total number of saplings established are low, support the competitive avoidance hypothesis. A high percentage of *Rhus* saplings survive and grow into bigger plants in this condition.

The greater number of saplings of *R. undulata* under its own canopy area (Figure 3) are mostly saplings in the height class smaller than 400 mm (Figure 4). The number of *R. undulata* saplings higher than 400 mm are in fact similar to the number found in the open and much less than the number found in the under canopy area of *A. karroo*. The high number of small saplings underneath *R. undulata* can therefore most probably be attributed to high seedfall in the under canopy area and a die-off of these saplings due to interspecific competition.

The higher grass production under tree canopies reported by Stuart-Hill *et al.* (1987, 1989) Stuart-Hill (1988) and Belsky *et al.* (1989), despite the reported lower rainfall and the presumed higher competition under trees could also be explained by the competitive avoidance hypothesis. This help to confirm the importance and validity of the competitive avoidance hypothesis. Knoop (1982) and Belsky *et al.* (1989) report lateral roots extending from *A. tortilis* at a depth of between 200 mm to 300 mm below the surface, depending on the soil texture while more than 80% of grass roots are found in the top 150 to 200 mm of the soil profile (Opperman 1975 and Knoop & Walker 1985).

It seems, therefore that seed dispersal play a role in determining the succession process. Germination and microhabitat in the under-canopy area determine establishment pattern but competition and survival ultimately determines the observed pattern found in the veld as shown in Figures 2 & 3.

In a period of 25 to 30 years the veld developed from a ploughed land with a seedbank, probably with little or no seeds of indigenous plant species, to a open savanna with *A. karroo* dominant and *R. undulata* and *C. rudis* also common. In the canopy area of a *A. karroo* tree, numerous saplings, representing up to ten tree species common in the Xeric Kaffrarian Thicket could occur. This state can therefor be described as an transition state between a grassveld and a diverse closed canopy thicket. The degree of dominance of *A. karroo* will increase the diversity of this resulting state, and reduce the transitional period. If *R. undulata* and *C. rudis* (these species

resprout more readily but grow slower than *A. karroo*) dominate this transitional stage the diversity and primary productivity of the resulting closed canopy thicket will be much lower, and the transitional period will be much longer. Eliminating all pioneer trees from the early stages of this process will result in grassveld. The eliminating of pioneer trees with the exception of scattered, bigger *A. karroo* trees will result in a diverse bushclump thicket-grassveld mosaic. Because most of the tree species that establish in the canopy area of *A. karroo* will resprout after fire this can probably be attained by a infrequent burning frequency of fifteen years or more.

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Table 1. Numbers of established saplings in the under-canopy area of *A. karroo*, *R. undulata* and in the Open.

Sapling species	COVER		
	A. karroo	R. undulata	Open
<i>Acacia karroo</i>	377	182	670
<i>Rhus undulata</i>	197	111	27
<i>Coddia rudis</i>	320	34	92
<i>Scutia myrtina</i>	213	3	1
<i>Burchellia bubalina</i>	51		
<i>Grewia occidentalis</i>	31	2	6
<i>Diospyros dichrophylla</i>	19	2	1
<i>Euclea undulata</i>	12	1	
<i>Maytenus</i> sp	9	2	
<i>Maytenus heterophylla</i>	6		
<i>Trimeria trinervis</i>	5	1	
<i>Rhus crenata</i>	4		
<i>Rhus chirindensis</i>	3		
<i>Ehretia rigida</i>	2		
<i>Hippobromus pauciflorus</i>	2		
<i>Apodytes dimidiata</i>	2		
<i>Cassine</i> sp	2		
<i>Canthium ciliatum</i>	1		
<i>Xanthoxylon capensis</i>	1		
<i>Cussonia spicata</i>	1		
<i>Vepris undulata</i>	1		
<i>Clausena anisata</i>	1		
<i>Scolopia</i> sp	1		
<i>Phyllanthus verrucosus</i>			1
<i>Olea europaea</i>		2	1
Total area of survey (m ²)	650	236	800
Number of species	23	11	8
Diversity ()	4,5	1,4	1,1
Number of individuals	1261	341	799
Total sapling density/m ²	1,9	1,4	1,0
Sapling density (excluding <i>A. karroo</i> and <i>R. undulata</i>).	1,1	0,2	0,1

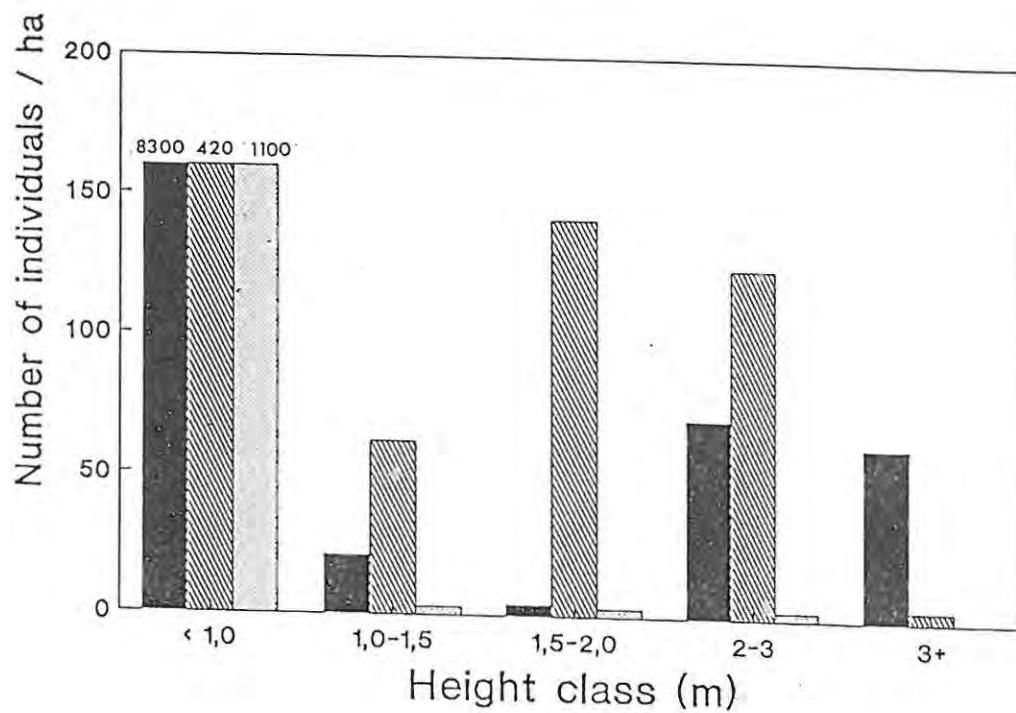


Figure 1. Height class distribution of established trees in the study area. *A. karroo* [solid black], *R. undulata* [hatched] and other trees [light gray]. The calculated number of saplings are indicated on top of the bars.

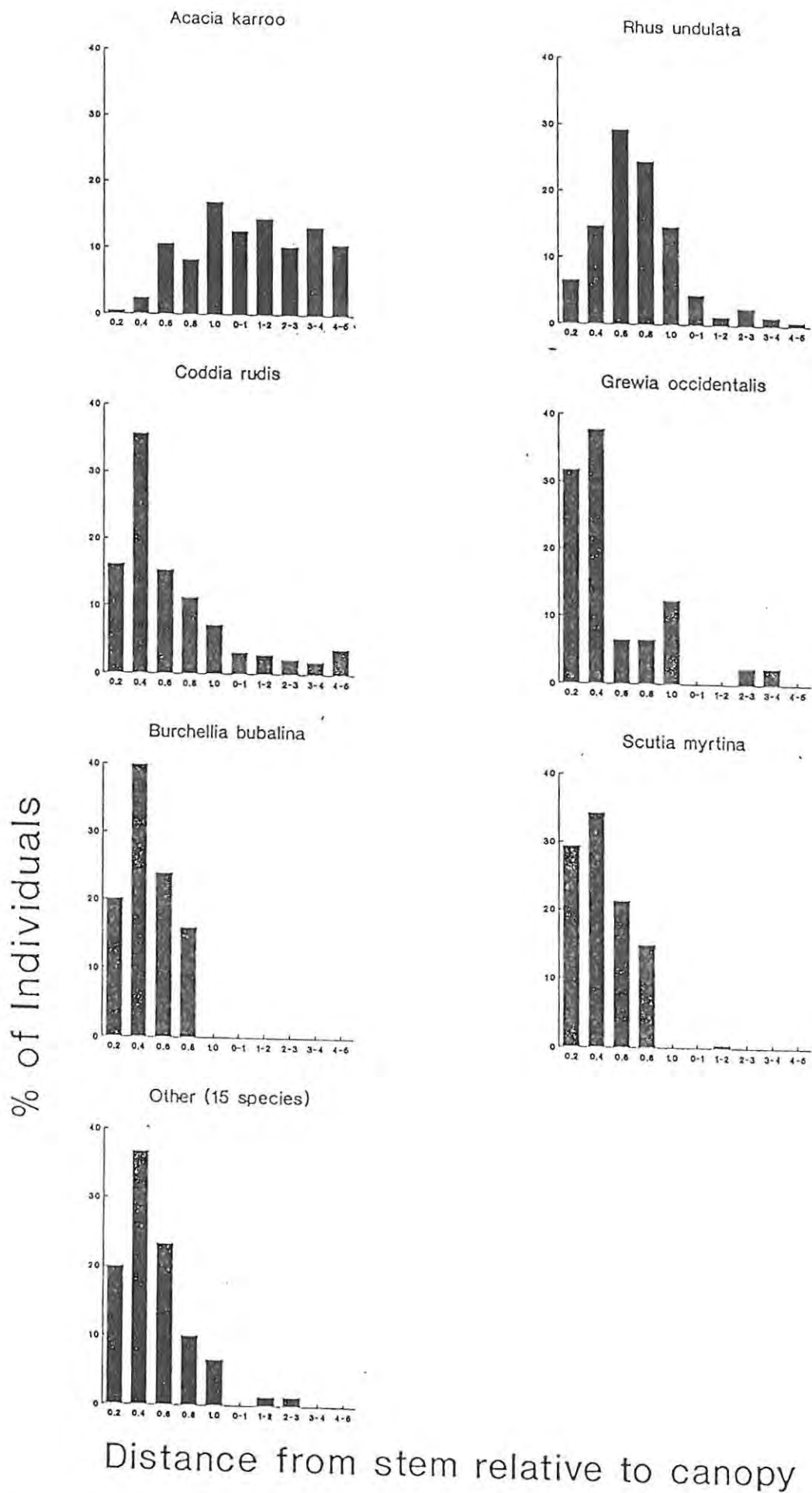


Figure 2. Established saplings relative to the canopy area of *A. karroo*.

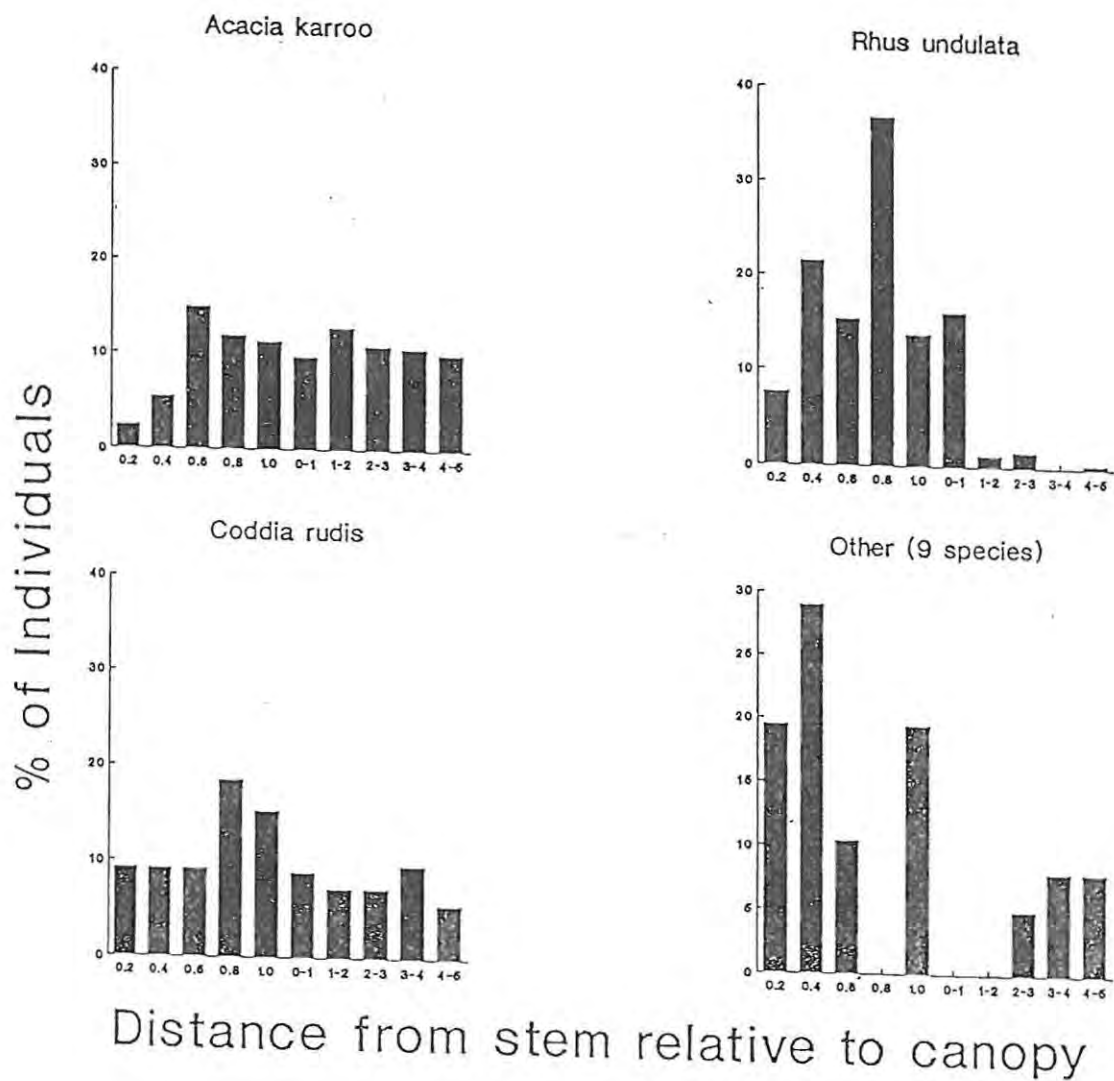


Figure 3. Established saplings relative to the canopy area of *R. undulata*.

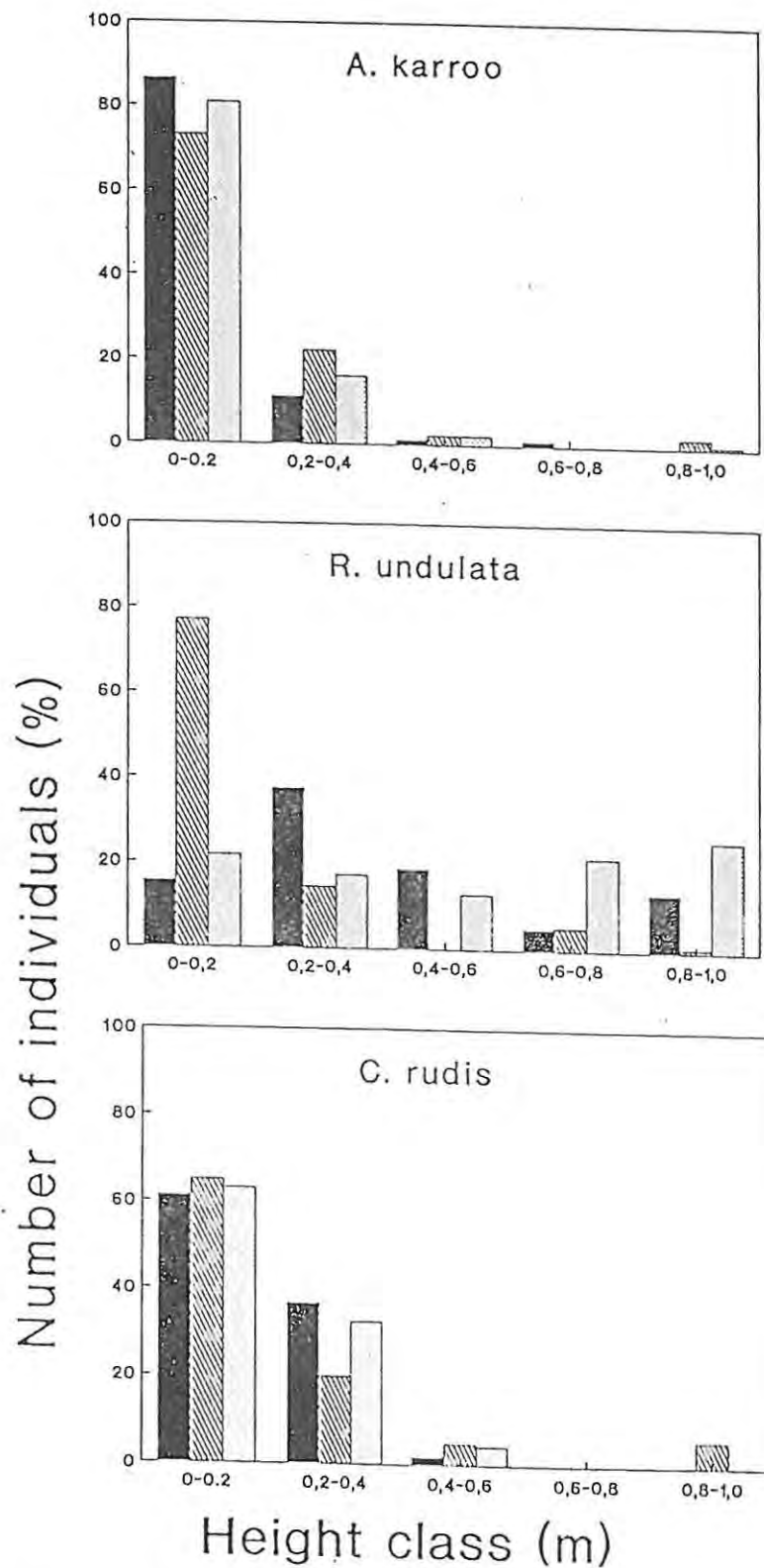


Figure 4. Height class distribution of saplings of *A. karroo*, *R. undulata* and *C. rudis* under the cover of *A. karroo*, *R. undulata*, and in the open.

RE-ASSESSMENT OF THE AREA AND CONSERVATION STATUS
OF SUBTROPICAL TRANSITIONAL THICKET (VALLEY BUSHVELD)
IN THE EASTERN CAPE, SOUTHERN AFRICA

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ABSTRACT

The Subtropical Transitional Thicket (STT) is the most extensive vegetation type in the eastern Cape, southern Africa, and the type most in need of conservation attention in the region. The STT is under increasing pressure from debushing and over-utilization by domestic herbivores.

Historically, the area of conserved STT was considered to be less than 2% from calculations based on the Valley Bushveld as mapped by Acocks in 1950. We re-mapped the STT using 1981 Landsat MSS imagery. Recent data on conservation areas within the STT were used to re-calculate the area conserved. The four suborders of STT were considered separately. We mapped two-thirds as much STT as Acocks. Xeric Succulent Thicket comprises half of the STT. Ten per cent of STT mapped in this exercise is conserved, and 6% of that mapped by Acocks is conserved. The Kaffrarian Thicket is poorly conserved (3%). Nine per cent of the natural vegetation of the eastern Cape is permanently transformed and of no conservation value.

INTRODUCTION

Valley Bushveld (Acocks, 1988), one of the most extensive vegetation types in the eastern Cape, southern Africa, is confined to the hot dry river valleys of the region (Lubke *et al*, 1988). Approximately 14 028 km² of the eastern Cape, here defined as the area of southern Africa south of 32°S and east of 24°E (Fig. 1), an area of 103 566 km², comprises Valley Bushveld (Palmer, 1989). The vegetation is less than 5 m in height, dominated by spiny woody shrubs, leaf, and stem succulents, and is possibly a recent (10 000 BP) colonizer of the region as evidenced by strong subtropical affinity, low endemism (Cowling, 1984) and archaeological and palaeoclimatic evidence (Palmer, 1990). Valley Bushveld, as well

as portions of Coastal Forest and Thornveld, Spekboomveld, Noorsveld and Alexandria Forest, of the order Subtropical Transitional Thicket (STT; Cowling, 1984), have been classified into syntaxonomic and structural units (Everard, 1987).

Large tracts of STT are being cleared for crops (Hoffman & Everard, 1987; Malan, 1988). The boom in the mohair industry has also led to an increase in the grazing pressure on the STT.

Little is known about the dynamics of disturbed and undisturbed STT, and its post-disturbance recovery. STT is considered to be stable, but with a low resilience (Cowling, 1984). Hoffman & Everard (1987) consider the recruitment levels of shrubs within the STT to be low, and although

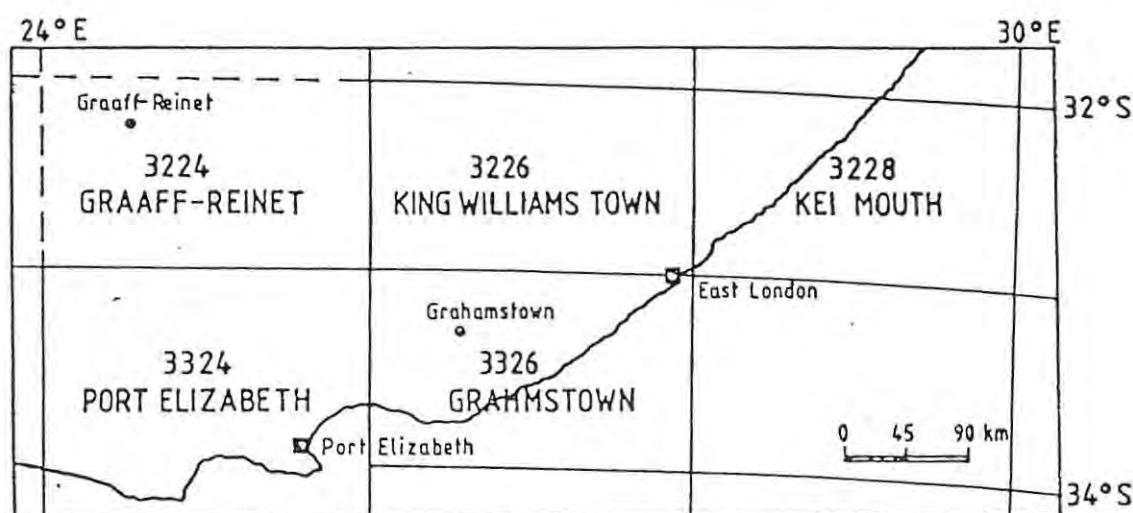


Fig. 1. South African 1:250 000 topographical sheets referred to in text.

adapted to a low disturbance regime, this vegetation will be slow to recover from high levels of disturbance, and unlikely to recover from severe disturbance. This poor recovery potential of the veld emphasizes the need for its conservation.

Lubke *et al* (1986) rate the subtropical thicket (= STT) as the vegetation type most in need of further investigation in the region, based on the number of threatened taxa, threat to and uniqueness of the vegetation, conservation status, and past study. The area of conserved Valley Bushveld in southern Africa has generally been considered to be less than 2% (e.g. Edwards, 1974; Scheepers, 1983; Lubke *et al*, 1986; Palmer, 1989). The majority of these calculations are based on the area of the Valley Bushveld as mapped in 1950 (Acocks, 1970). Subsequently, extensive debushing has taken place, and new conservation areas have been established.

Acocks (1970) produced his map following interpretation of monochromatic aerial photographs and extensive ground referencing. Since 1980, satellite-borne multi-spectral scanners (MSS) have provided another source of land-cover information in southern Africa. Recent mapping exercises in subtropical thicket of the eastern Cape (Palmer, 1982; Everard, 1985) investigated the possibility of mapping thicket from Landsat MSS data. The high aerial cover and greenness of thicket make it discernible in the infra-red spectral bands.

The aim of this study was to determine the total area and conserved area of STT in the eastern Cape; and the area which has been cultivated

or developed and is of no further conservation value.

METHODS

Manual interpretation techniques (Harrington & Dunn, 1980) were applied to Landsat imagery (1:1 000 000 edge-enhanced three band colour composites; Table 1) to map each suborder of the STT, and the area of transformed land.

Table 1

Listing of the five Landsat images which cover the valley bushveld in the eastern Cape. Scene ID uniquely identifies a particular Landsat Scene. The form of the ID is SDDDDHHMMS, where S = spacecraft number, DDDD = days since launch for that spacecraft, HHMMS = Greenwich Mean Time (GMT) of scene centre in hours minutes and tens of seconds. WRS is the world wide reference system, track and frame.

Scene ID	WRS	Date	Time	Centre
22314-07241	183-83	24/5/81	09H24	33° 14' S 25° 12' E
22169-07200	183-83/84	30/12/80	09H00	33° 54' S 26° 46' E
22169-07195	182-83	30/12/80	09H20	33° 19' S 26° 58' E
22456-07105	181-83	13/10/81	09H11	33° 07' S 27° 56' E
22456-07103	181-82	13/10/81	09H00	31° 40' S 28° 24' E

The 1:1 000 000 images were projected at a scale of 1:250 000 and registered with the relevant South Africa 1:250 000 Topo-cadastral sheets. Using Everard's (1985) map as ground reference

data, each image was manually classified into: the four suborders of STT (Table 2); transformed land; and undifferentiated natural vegetation (non-STT) for each of the South Africa 1:250 000 Topo-cadastral sheets on which Everard (1987) had mapped STT (3226 King Williams Town, 3228 Kei Mouth, 3324 Port Elizabeth, and 3326 East London).

Table 2

Conservation status of Subtropical Transitional Thicket in the eastern Cape

Vegetation type	Area (km ²)	% of STT	Area cons. (km ²)	% cons.
order: Kaffrarian succulent thicket				
suborder: mesic succulent thicket	1 488	16	283	19
suborder: xeric succulent thicket	4 657	51	531	11
Total: Kaffrarian succulent thicket	6 145	67	814	13
order: Kaffrarian thicket				
suborder: mesic Kaffrarian thicket	842	9	17	2
suborder: xeric Kaffrarian thicket	2 192	24	63	3
Total: Kaffrarian thicket	3 034	33	80	3
Subtropical transitional thicket	9 179	100	894	10

Everard's (1985) map of STT is at a scale of 1:2 500 000, and proved unsuitable for the calculation of areas of land. We enlarged this map to a scale of 1:250 000 and we accepted his boundaries between the suborders of STT for our maps. We considered the width of the coastal strip of Xeric Kaffrarian Thicket as depicted in Everard (1987) to be an over-representation of the actual width of this strip, which was seldom discernible on the imagery.

The polygons representing each suborder of STT and transformed land were cut out and their areas determined using a calibrated AAC-400 Automatic Areameter. Calculations were based on the area of each South Africa 1:250 000 Topo-cadastral sheet (Palmer, 1989), with details of

conserved areas extracted from Anon (1987), Van Wyk *et al* (1988) and personal communications from conservation authorities.

RESULTS

The total land area is 61 645 km² (Palmer, 1989), of which 5 436 km² (9%) has been permanently transformed by debushing and is no longer of any conservation value. Acocks (1970) mapped 13 730 km² of the area as STT, whereas this survey recorded 9 179 km² (67% of Acocks, 1970). Xeric Succulent Thicket comprised 51% (4 657 km²) of STT (Table 3), and had the largest conserved area (531 km²; 11%). Mesic Succulent Thicket had the highest percentage area under conservation (19%; 283 km²). The Mesic and Xeric Kaffrarian Thicket are both poorly conserved (2% and 3% respectively). Ten per cent of the STT mapped in this exercise is conserved, and 6% of Acocks (1970).

Table 3

Area of STT (km²) per 1:250 000 Topographical map: Acocks (1970) vs this survey

1:250 000 map	1950	1981	% remaining
3226 King Williams Town	4 251	1 309	31
3228 Kei Mouth	1 404	661	47
3324 Port Elizabeth	4 304	3 494	81
3326 East London	3 771	3 715	99
Total	13 730	9 179	67

Six conservation sites contain Mesic Kaffrarian Thicket (Table 3), ranging in size from 10–691 ha. Xeric Kaffrarian Thicket occurs in nine conservation sites, and ranges in extent from 67–4 259 ha., with eight sites under 550 ha. The six areas of conserved Mesic Succulent Thicket range in size from 15–17 675 ha. including two of over 5 000 ha. The nine conserved areas of Xeric Succulent Thicket range in size from 10–15 895 ha. Five of these are over 5 000 ha. and two over 2 500 ha.

DISCUSSION

A proportion of the difference between the area of STT in Acocks (1970) and this study (Table 3) could be attributable to Acocks (1988) recognising

Table 4

Area of STT in conservation areas in the eastern Cape

	Size (km ²)
Mesic Succulent Thicket	
Uitenhage Nature Reserve	3,50
Yellowwoods Nature Reserve	0,15
Loerie Nature Reserve	7,00
Groendal Wilderness Area	83,47
Alexandria State Forest	12,50
Formosa/Cockscomb/Kouga-Baviaanskloof Wilderness area	176,75
Total	283,37
Xeric Succulent Thicket	
Addo Elephant National Park	85,96
Andries Vosloo Kudu Reserve	56,76
Sam Knott Nature Reserve	158,95
Ecca Nature Reserve	1,28
Double Drift Game Reserve	100,00
Grahamstown Military Training Area	31,95
Adelaide Nature Conservation Station ...	0,10
Zuurberg National Park/Boplaas	95,31
Total	530,27
Mesic Kaffrarian Thicket	
Bridle Drift Nature Reserve	1,50
Fort Pato Nature Reserve	6,91
King Williams Town Nature Reserve	0,60
Umtiza Nature Reserve	5,55
Amalinda Nature Conservation Station...	0,10
Fort Gray Nature Reserve	1,97
Total	16,63
Xeric Kaffrarian Thicket	
Thomas Baines Nature Reserve	5,50
Waters Meeting Nature Reserve	42,59
Kowie Nature Reserve	2,60
Blaauwkrantz Nature Reserve	1,69
Cycad Nature Reserve	0,89
T. Fitzgerald Private Nature Reserve	2,00
Ghio Wetland Reserve	0,67
Kap River State Forest	2,86
Merville Private Nature Reserve	4,00
Total	62,80

Veld Types as units of 'farming potential' and not excluding areas where natural vegetation had been cleared (Moll & Bossi, 1984). Acocks (1970) included areas which had been previously cleared such as Port Elizabeth and East London as Valley Bushveld. These urban areas as well as irrigation schemes have increased significantly in size since early mapping efforts.

It is evident that much of what was previously STT has been permanently transformed, especially the narrow strips along the fertile river valleys and in areas suitable for crops. A recent development has been the debushing of marginal areas for wheat in the Patterson district (Malan, 1988). This attempted use of marginal ground has failed due to the rainfall patterns in the STT (Hoffman & Everard, 1987).

Areas over-utilized by livestock probably constitute a major source of transformed land in the STT. They could not be differentiated from healthy STT using the method applied because the dominant perennial shrubs are the last component to disappear and continue to provide good aerial cover and greenness. Aucamp & Tainton (1984) consider these over-utilized sites to be permanently transformed. Further research effort should be made to differentiate between healthy and over-utilized STT.

CONCLUSIONS

STT has changed from having one of the lowest percentage areas conserved to having one of the highest, however the conservation status of the order Kaffrarian Thicket remains inadequate. The remaining areas of STT are almost exclusively used for farming, and the future conservation effort lies in educating the farmers not to over-utilize the vegetation and not to debush marginal areas for crops. We suggest that future conservation status calculations be based on these data.

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APPENDIX 3. Assembled data of each seedling occurrence for successive surveys. Three data sets are presented, arranged with (i) seedlings, (ii) nurse plants, and (iii) side of tree, in the first column respectively. Each data set is presented in order from south poorly vegetated to north well vegetated.

Codes used for species mentioned in the tables.

<i>Azima tetracantha</i>	AT
<i>Brachylaena illicifolia</i>	BI
<i>Capparis sepiaria</i> var. <i>citrifolia</i>	CS
<i>Cussonia spicata</i>	CU
<i>Diospyros scabrida</i>	DS
<i>Ehretia rigida</i>	ER
<i>Euclea undulata</i> var. <i>undulata</i>	EU
<i>Grewia occidentalis</i>	GO
<i>Grewia robusta</i>	GR
<i>Jatropha capensis</i>	JC
<i>Jasminum multipartitum</i>	JM
<i>Maytenus capitata</i>	MC
<i>Olea europaea</i> subsp. <i>africana</i>	OE
<i>Ozoroa mucronata</i>	OM
<i>Pappea capensis</i>	PC
<i>Portulacaria afra</i>	PA
<i>Ptaeroxylon obliquum</i>	PO
<i>Phyllanthus verrucosus</i>	PV
<i>Rhigozum obovatum</i>	RO
<i>Rhus</i> sp	Rhus
<i>Schotia afra</i> var. <i>angustifolia</i>	SA

Explanation of columns used in tables, with reference to the first entry.

EU EU2S A9a S: EU = seedling species, according to above codes.
 EU2S = plot identification. Nurse plant according to above codes.
 A9a = grid reference to seedling location within quadrat.
 S = side of tree (also from plot identification).

POORLY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
EU EU2S A9a S	EU	EU	EU	EU	EU	EU	EU	EU	EU
EU EU2S C9d S			EU	EU	EU	EU	EU	EU	EU
EU EU2S F8a S			EU	EU	EU	EU	EU	EU	EU
EU EU2S H8c S			EU	EU	EU	EU	EU		
EU EU2W J8a W				EU	EU				
EU GR3S C9d S		EU							
EU GR3W H5b W			EU	EU	EU	EU	EU	EU	EU
EU GR3W I6a W			EU	EU	EU	EU	EU	EU	EU
EU GR3W I6c W			EU	EU	EU	EU	EU	EU	EU
EU OM5E H2b E		EU							
EU OM5S A3d S				EU	EU				
EU PA2S B5d S		EU	EU						
EU PA2S F0a S				EU	EU	EU	EU	EU	
EU PC5S E9b S		EU							
EU PC5S F8c S		EU	EU						
EU P03W A7 W			EU						
EU P03W D1 W				EU	EU	EU	EU		
EU SA4S A4b S	EU	EU	EU	EU	EU	EU	EU	EU	EU
GO BI2E A3 E	GO	GO	GO	GO					
GR OM2W B1d W	GR	GR							
GR OM2W C1c W	GR	GR							
GR OM3S B3b S					GR				
GR SA3N J6b N	GR								
MC GR3S B6d S									MC
MC OM4W H1d W		MC	MC	MC	MC	MC	MC		
PA AT2E H9b E	PA	PA							
PA BI5E C9 E					PA	PA	PA	PA	PA
PA BI5E F6 E	PA								
PA BI5S C9 S	PA								
PA EU1S I4a S	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA EU2N B2b N			PA	PA	PA	PA	PA	PA	PA
PA EU2N B2c N			PA	PA	PA	PA	PA	PA	PA
PA EU3S F3c S	PA								
PA EU5N E9b N			PA						
PA EU5N G1d N									
PA EU5N I1 N									PA
PA EU5N I4a N	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA EU5S G0a S									PA
PA EU5S I8c S							PA	PA	PA
PA EU5S I9d S							PA		
PA GR3S B6d S				PA	PA	PA	PA	PA	PA
PA GR3S C7c S									PA
PA GR3S E5d S		PA	PA	PA	PA	PA	PA	PA	PA
PA GR3W I9c W			PA	PA	PA	PA	PA	PA	PA
PA GR3W J4a W						PA	PA	PA	PA
PA GR3W J9a W			PA	PA	PA	PA	PA	PA	PA
PA GR3W J0c W			PA	PA	PA	PA	PA	PA	PA
PA JC1N C8 N			PA	PA	PA	PA			

PA JC5W A6 W	PA								
PA MC3W C4c W	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA MC3W D7d W								PA	PA
PA MC3W E7d W				PA	PA				
PA MC4S J6d S		PA							
PA MC5N D4a N		PA							
PA QM2E I7a E	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA PA3S E8d S	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA P01S C3 S		PA	PA	PA					
PA R02S A5 S			PA	PA	PA	PA	PA	PA	PA
PA R02W H0 W			PA	PA					
PC MC3W H6c W			PC	PC	PC	PC	PC	PC	PC
PC QM4W J5a W		PC	PC	PC	PC	PC	PC	PC	
PC PC1W J2a W				PC	PC	PC	PC	PC	
PC PC5E I2c E		PC	PC	PC	PC	PC	PC	PC	
PC PC5S H8c S		PC	PC	PC					
PC PC5W G3d W		PC	PC	PC	PC	PC	PC	PC	PC
PC PC5W H3d W		PC	PC	PC	PC	PC	PC	PC	PC
PC SA3W H4d W						PC	PC	PC	
PC SA3W I5a W							PC	PC	
PC SA5E B3d E		PC							
PC SA5E D4a E							PC		
PV EU5S C4a S		PV	PV						
PV EU5S D4d S				PV					
PV PV2N D6 N			PV	PV	PV				
PV PV4N C6 N			PV						
PV PV4N D6 N						PV			

POORLY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT PA2N B3c N			AT	AT					
EU MC1S B5b S				EU	EU	EU	EU	EU	EU
EU OM5W H8c W				EU					
EU PA3N D4b N		EU	EU	EU	EU	EU	EU	EU	EU
EU PA5E A2b E			EU	EU					
EU PA5S G5c S		EU							
EU SA2E E7d E		EU	EU						
JC AT4S A9a S	JC	JC	JC						
MC MC1W H5b W				MC	MC				
MC OM3E H2c E						MC	MC	MC	MC
OE PO3S F4 S	OE					MC	MC	MC	MC
OM MC3E E5a E		OM							
OM PA2E A5a E		OM							
OM PA3E H2b E		OM							
OM PC3N A2b N		OM							
OM PC3N A3c N		OM							
OM PC3N B7a N		OM							
OM PC3N I2b N		OM							
OM PC3S H2c S		OM							
OM PC3W B2b W		OM							
OM PC3W D2c W		OM							
OM PC3W D5c W		OM							
OM PC3W E4d W		OM							
OM PC3W I2a W		OM							
OM PC3W I2d W		OM							
OM PC3W J4c W		OM							
PA BI1E I0 E		PA	PA						
PA BI3S C2 S	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA BI3S G8 S	PA	PA							
PA MC1E I4b E		PA	PA						
PA MC3S A7b S					PA	PA	PA	PA	PA
PA MC4W H1b W									
PA MC4W J2a W						PA	PA	PA	PA
PA MC4W J2c W				PA	PA	PA	PA	PA	PA
PA OM2E D8c E		PA	PA	PA					
PA OM4E G3c E		PA	PA						
PA PC5S A1d S	PA								
PA PV4N H2 N		PA	PA	PA	PA	PA	PA	PA	PA
PA SA2S A2d S	PA								
PV PV4W H8 W		PV	PV	PV	PV	PV	PV	PV	PV

MODERATELY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT P01N F5a N									AT
AT P01N G5 N				AT	AT	AT		AT	AT
CU EU5S E2d S		CU	CU	CU	CU	CU		CU	CU
CS P01E B2 E		CS	CS	CS	CS	CS		CS	CS
DS MC5E E3c E			DS	DS	DS	DS		DS	DS
ER OM4S I5d S									ER
EU BI3W A2 W			EU						
EU EU5E F1d E		EU							
EU MC2N I6b N								EU	EU
EU PA2E H1c E		EU							
EU PA2W A7c W			EU	EU	EU	EU	EU	EU	EU
EU PC1N G6a N		EU							
EU PC1W I4b W		EU							
EU P01E B6 E						EU			
EU P01W E1 W			EU			EU	EU	EU	EU
EU P01W F1 W				EU	EU	EU	EU		
GR GR5W B1a W	GR								
GR PC1E C1c E				GR					
GR SA4S A3b S				GR	GR				
JC OM1S D3c S			JC	JC		GR	GR	GR	GR
JC OM4S J1b S			JC						
JC P05S I5 S		JC							
MC GR2S F8c S									
MC OM2S I5a S		MC						MC	MC
MC PA2E D6a E									
MC P01E C1 E					MC	MC	MC	MC	MC
MC P01S F3 S					MC	MC	MC		
MC R05W J8b W				MC	MC				
MC SA1N J8d N		MC							
MC SA2E D5a E			MC	MC	MC	MC	MC	MC	
PA AT4E D5b E	PA								
PA AT4E E3a E	PA	PA							
PA AT4E E9d E	PA								
PA AT4S D5b S		PA	PA						
PA BI3E B2 E	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA MC4W A3a W	PA								
PA PA5N D6c N		PA							
PA PA5W E5b W		PA	PA						
PC PA2W C7c W									
PC PA4W I7b W				PC				PC	
PC PC2E E5d E				PC		PC	PC	PC	PC
PC PC2E G6a E		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4E B3a E		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4E B3b E		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4E B3c E		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4E D6a E									
PC PC4N A1b N			PC	PC	PC	PC	PC	PC	PC
PC PC4N A4d N			PC	PC	PC	PC	PC	PC	PC

PC PC4N B6b N		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4N D5c N			PC	PC					
PC PC4W A6b W		PC	PC	PC	PC	PC	PC	PC	PC
PC PC4W F7b W						PC	PC	PC	PC
PC PC4W F9d W		PC	PC						
PC P01E I1 E		PC	PC	PC	PC	PC	PC	PC	PC
PC P01N F9 N		PC	PC	PC	PC	PC	PC	PC	PC
PV JC4E B5 E	PV	PV							
PV MC5W E2b W		PV							
PV OM4N E5a N		PV	PV	PV	PV	PV	PV	PV	PV
PV PA5W I1a W			PV	PV	PV	PV	PV	PV	PV
PV PC2S C3c S		PV							
PV PV2E J3 E		PV	PV						
PV PV5W C6 W						PV	PV	PV	PV
Rhus MC3S F3a S				Rhus	Rhus				
Rhus SA2E C5b E			Rhus	Rhus	Rhus	Rhus	Rhus	Rhus	

MODERATELY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
ER MC4S G8b S		ER	ER	ER	ER	ER	ER		
EU AT1W H9b W	EU	EU	EU	EU	EU	EU	EU	EU	EU
EU AT1W I8c W	EU	EU	EU	EU	EU	EU	EU	EU	EU
GR AT1W H0c W	GR	GR	GR	GR	GR	GR	GR	GR	GR
GR AT2S I3b S		GR	GR	GR	GR	GR	GR	GR	GR
GR AT3E F7d E	GR	GR	GR	GR	GR	GR	GR	GR	GR
GR PA2W E4c W		GR	GR	GR	GR	GR	GR	GR	GR
GR PC1N H5c N	GR	GR	GR						
GR PV1S G2 S				GR	GR				
MC EU3E D8c E	MC	MC	MC						
OM BI1N E3 N		OM	OM	OM	OM	OM	OM	OM	OM
OM BI1W E9 W		OM							
OM JC4N F0 N									OM
PA AT2W G6b W									PA
PA AT2W G8b W									PA
PA AT3W C3b W	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)
PA AT4S G0c S					PA	PA	PA	PA	PA
PA AT4S I0b S	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA AT4W D4 W			PA	PA	PA				
PA AT4W E4c W		PA	PA	PA	PA				
PA B12E C4 E	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA EU2W C7b W		PA	PA	PA	PA	PA	PA	PA	PA
PA GR2N B8a N	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA GR2N C8a N	PA	PA							
PA GR2N C8c N	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA GR2N H4c N								PA	PA
PA GR2N H7b N								PA	PA
PA JC4S G6 S						PA	PA	PA	PA
PA OM1N G8a N	PA								
PA PO3S E6 S		PA							
PA PV3W F6 W	PA	PA							
PO AT1S I2d S	PO	PO	PO	PO	PO	PO	PO	PO	PO
PO PV1S G1 S	PO	PO	PO	PO	PO	PO	PO	PO	PO
PV MC1N B7b N		PV	PV						
PV OM1S F8a S	PV	PV							
PV OM1S H6a S	PV	PV							

WELL VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT GR5S E5c S		AT	AT	AT					
AT PA4W D8a W		AT	AT	AT	AT	AT	AT	AT	AT
AT PA4W F1b W					AT	AT	AT		
AT PA4W G1c W					AT	AT	AT		
AT PC4E A4d E					AT	AT	AT		
AT PC4S A4b S			AT						
ER R05E D2 E	ER	ER	ER	ER	ER	ER	ER		
EU MC3S E2c S		EU	EU						
EU PC2S A1d S				EU	EU	EU			
EU P03E A1 E	EU	EU	EU	EU	EU	EU	EU	EU	EU
EU P03N G1 N	EU	EU	EU	EU	EU	EU	EU	EU	EU
EU SA2S A3c S								EU	EU
GR AT3S A9a S			GR	GR	GR	GR	GR	GR	GR
GR AT4E E4c E									GR
GR AT4E E6d E									GR
GR MC2W H8a W		GR	GR	GR	GR	GR	GR	GR	GR
GR MC5E H3b E	GR	GR	GR	GR	GR	GR	GR	GR	GR
GR OM2S G1a S			GR						
JM OM2S B5c S		JM	JM	JM	JM	JM	JM		
JM PA3S D1a S				JM	JM	JM	JM	JM	JM
MC EU4E J7a E			MC(2)	MC(2)	MC(2)	MC	MC	MC	MC
MC P03E E4 E						MC	MC	MC	MC
OM AT5E F6c E									OM
OM GR4E E7b E									OM
OM OM1E F4d E		OM	OM	OM	OM	OM	OM	OM	OM
OM PA4W E0b W		OM	OM	OM					
OM PC2S H1d S				OM	OM				
PA AT2S E6d S			PA	PA					
PA AT4S D8c S									
PA MC1N A1b N									PA
PA PV1S B5 S					PA	PA	PA	PA	PA
PA PV3W H3 W					PA	PA	PA	PA	PA
PA PV3W I4 W				PA	PA	PA	PA	PA	PA
PA R03W J1 W				PA					
PA R05W J1 W	PA	PA	PA	PA	PA	PA	PA	PA	PA
PA SA4S I3d S	PA								
PA SA4S J3a S	PA								
PC GR3S A7c S			PC	PC					
PC PC2E D9d E					PC	PC	PC		
PC PC3E F3a E	PC	PC	PC	PC	PC	PC	PC	PC	PC
PC PC3E H5a E						PC	PC	PC	
PC PC3N D5b N						PC	PC	PC	PC
PC PC3N J1c N									PC
PC PC4S H4b S				PC	PC	PC	PC	PC	PC
PC PC4W B0a W					PC	PC	PC	PC	PC
PC PC4W C5d W						PC	PC	PC	
PC PC4W D0a W			PC	PC	PC	PC	PC	PC	PC
PC PC4W H3c W		PC	PC	PC	PC				

PC PC4W H8c W			PC	PC	PC				
PC PC4W I0a W			PC	PC	PC				
PC PC4W J9a W			PC						
PC PC5E B9b E							PC		
PC PC5E B9b E							PC	PC	
PC PC5S D7c S	PC	PC	PC	PC	PC	PC	PC		
PC PC5S D8a S							PC		
P0 AT4N J4a N	P0	P0	P0	P0	P0	P0	P0	P0	P0
P0 GR1E C3c E			P0	P0					
P0 GR1E C8 E					P0	P0	P0	P0	
P0 GR1S I8c S		P0	P0	P0	P0	P0	P0	P0	P0
P0 MC4W I2a W									P0
P0 PC3E I0a E									P0
P0 SA3E G6d E			P0	P0	P0	P0	P0	P0	P0
P0 SA3E H1c E	P0	P0	P0	P0	P0	P0	P0	P0	P0
P0 SA3N E5d N						P0	P0	P0	P0

SURVEY STARTING DATE

[illegible]

POORLY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT2E PA E H9b	PA	PA							
BI2E GO E A3	GO	GO	GO	GO					
BI5E PA E C9					PA	PA	PA	PA	PA
BI5E PA E F6	PA								
BI5S PA S C9	PA								
EU1S PA S I4a	PA	PA	PA	PA	PA	PA	PA	PA	PA
EU2N PA N B2b			PA	PA	PA	PA	PA	PA	PA
EU2N PA N B2c			PA	PA	PA	PA	PA	PA	PA
EU2S EU S A9a	EU	EU	EU	EU	EU	EU	EU	EU	EU
EU2S EU S C9d			EU	EU	EU	EU	EU	EU	EU
EU2S EU S F8a			EU	EU	EU	EU	EU	EU	EU
EU2S EU S H8c			EU	EU	EU	EU	EU	EU	EU
EU2W EU W J8a				EU	EU				
EU3S PA S F3c	PA								
EU5N PA N E9b			PA						
EU5N PA N G1d									PA
EU5N PA N I1									PA
EU5N PA N I4a	PA	PA	PA	PA	PA	PA	PA	PA	PA
EU5S PA S G0a									PA
EU5S PA S I8c							PA	PA	PA
EU5S PA S I9d							PA		PA
EU5S PV S C4a		PV	PV						
EU5S PV S D4d				PV					
GR3S EU S C9d		EU							
GR3S MC S B6d									MC
GR3S PA S B6d				PA	PA	PA	PA	PA	PA
GR3S PA S C7c									PA
GR3S PA S E5d		PA	PA	PA	PA	PA	PA	PA	PA
GR3W EU W H5b			EU	EU	EU	EU	EU	EU	EU
GR3W EU W I6a			EU	EU	EU	EU	EU	EU	EU
GR3W EU W I6c			EU	EU	EU	EU	EU	EU	EU
GR3W PA W I9c			PA	PA	PA	PA	PA	PA	PA
GR3W PA W J4a									PA
GR3W PA W J9a			PA	PA	PA	PA	PA	PA	PA
GR3W PA W J0c			PA	PA	PA	PA	PA	PA	PA
JC1N PA N C8			PA	PA	PA	PA	PA	PA	PA
JC5W PA W A6	PA								
MC3W PA W C4c	PA	PA	PA	PA	PA	PA	PA	PA	PA
MC3W PA W D7d								PA	PA
MC3W PA W E7d				PA	PA				
MC3W PC W H6c			PC	PC	PC	PC	PC	PC	PC
MC4S PA S J6d		PA							
MC5N PA N D4a		PA							
OM2E PA E I7a	PA	PA	PA	PA	PA	PA	PA	PA	PA
OM2W GR W B1d	GR	GR							
OM2W GR W C1c	GR	GR							
OM3S GR S B3b					GR				
OM4W MC W H1d		MC	MC	MC	MC	MC	MC		

OM4W	PC	W	J5a
OM5E	EU	E	H2b
OM5S	EU	S	A3d
PA2S	EU	S	B5d
PA2S	EU	S	F0a
PA3S	PA	S	E8d
PC1W	PC	W	J2a
PC5E	PC	E	I2c
PC5S	EU	S	E9b
PC5S	EU	S	F8c
PC5S	PC	S	H8c
PC5W	PC	W	G3d
PC5W	PC	W	H3d
P01S	PA	S	C3
P03W	EU	W	A7
P03W	EU	W	D1
PV2N	PV	N	D6
PV4N	PV	N	C6
PV4N	PV	N	D6
R02S	PA	S	A5
R02W	PA	W	H0
SA3N	GR	N	J6b
SA3W	PC	W	H4d
SA3W	PC	W	I5a
SA4S	EU	S	A4b
SA5E	PC	E	B3d
SA5E	PC	E	D4a

POORLY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT4S JC S A9a	JC	JC	JC						
BI1E PA E I0		PA	PA						
BI3S PA S C2	PA	PA	PA	PA	PA	PA	PA	PA	PA
BI3S PA S G8	PA	PA							
MC1E PA E I4b		PA	PA						
MC1S EU S B5b				EU	EU	EU	EU	EU	EU
MC1W MC W H5b				MC	MC	MC	MC	MC	MC
MC3E OM E E5a		OM							
MC3S PA S A7b					PA	PA	PA	PA	PA
MC4W PA W H1b									PA
MC4W PA W J2a						PA	PA	PA	PA
MC4W PA W J2c				PA	PA	PA	PA	PA	PA
OM2E PA E D8c		PA	PA	PA					
OM3E MC E H2c						MC	MC	MC	MC
OM4E PA E G3c		PA	PA						
OM5W EU W H8c				EU					
PA2E OM E A5a		OM							
PA2N AT N B3c			AT	AT					
PA3E OM E H2b		OM							
PA3N EU N D4b		EU	EU	EU	EU	EU	EU	EU	EU
PA5E EU E A2b			EU	EU	EU	EU	EU		
PA5S EU S G5c		EU							
PC3N OM N A2b		OM							
PC3N OM N A3c		OM							
PC3N OM N B7a		OM							
PC3N OM N I2b		OM							
PC3S OM S H2c		OM							
PC3W OM W B2b		OM							
PC3W OM W D2c		OM							
PC3W OM W D5c		OM							
PC3W OM W E4d		OM							
PC3W OM W I2a		OM							
PC3W OM W I2d		OM							
PC3W OM W J4c		OM							
PC5S PA S A1d	PA								
P03S OE S F4	OE								
PV4N PA N H2		PA	PA	PA	PA	PA	PA	PA	PA
PV4W PV W H8		PV	PV	PV	PV	PV	PV	PV	PV
SA2E EU E E7d		EU	EU						
SA2S PA S A2d	PA								

MODERATELY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT4E PA E D5b	PA								
AT4E PA E E3a	PA	PA							
AT4E PA E E9d	PA								
AT4S PA S D5b		PA	PA						
BI3E PA E B2	PA	PA	PA	PA	PA	PA	PA	PA	PA
BI3W EU W A2			EU						
EU5E EU E F1d		EU							
EU5S CU S E2d		CU	CU	CU	CU	CU	CU	CU	CU
GR2S MC S F8c								CU	CU
GR5W GR W B1a	GR							MC	MC
JC4E PV E B5	PV	PV							
MC2N EU N I6b									
MC3S Rhus S F3a				Rhus	Rhus			EU	EU
MC4W PA W A3a	PA								
MC5E DS E E3c			DS	DS	DS	DS	DS	DS	DS
MC5W PV W E2b		PV							
OM1S JC S D3c			JC	JC					
OM2S MC S I5a		MC							
OM4N PV N E5a		PV	PV	PV	PV	PV	PV	PV	PV
OM4S ER S I5d									ER
OM4S JC S J1b			JC						
PA2E EU E H1c		EU							
PA2E MC E D6a					MC	MC	MC	MC	MC
PA2W EU W A7c			EU	EU	EU	EU	EU	EU	EU
PA2W PC W C7c								PC	
PA4W PC W I7b				PC					
PA5N PA N D6c		PA							
PA5W PA W E5b		PA	PA						
PA5W PV W I1a			PV	PV	PV	PV	PV	PV	PV
PC1E GR E C1c				GR					
PC1N EU N G6a		EU							
PC1W EU W I4b		EU							
PC2E PC E E5d				PC	PC	PC	PC	PC	PC
PC2E PC E G6a		PC	PC	PC	PC	PC	PC	PC	PC
PC2S PV S C3c		PV							
PC4E PC E B3a		PC	PC	PC	PC	PC	PC	PC	PC
PC4E PC E B3b		PC	PC	PC	PC	PC	PC	PC	PC
PC4E PC E B3c		PC	PC	PC	PC	PC	PC	PC	PC
PC4E PC E D6a									
PC4N PC N A1b			PC	PC	PC	PC	PC	PC	PC
PC4N PC N A4d			PC	PC	PC	PC	PC	PC	PC
PC4N PC N B6b		PC	PC	PC	PC	PC	PC	PC	PC
PC4N PC N D5c			PC	PC					
PC4W PC W A6b		PC	PC	PC	PC	PC	PC	PC	PC
PC4W PC W F7b									
PC4W PC W F9d		PC	PC			PC	PC	PC	PC
P01E CS E B2		CS	CS	CS	CS	CS	CS	CS	CS
P01E EU E B6						EU	EU	EU	EU

P01E MC E C1					MC	MC			
P01E PC E I1		PC	PC	PC	PC	PC	PC	PC	PC
P01N AT N F5a									AT
P01N AT N G5				AT	AT	AT	AT	AT	AT
P01N PC N F9		PC	PC	PC	PC	PC	PC	PC	PC
P01S MC S F3				MC	MC	MC	MC	MC	
P01W EU W E1			EU						
P01W EU W F1				EU	EU	EU	EU		
P05S JC S I5		JC							
PV2E PV E J3		PV	PV						
PV5W PV W C6						PV	PV	PV	PV
R05W MC W J8b				MC					
SA1N MC N J8d		MC							
SA2E MC E D5a			MC	MC	MC	MC	MC	MC	
SA2E Rhus E C5b			Rhus	Rhus	Rhus	Rhus	Rhus	Rhus	
SA4S GR S A3b				GR	GR	GR	GR	GR	GR

MODERATELY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT1S PO S I2d	PO	PO	PO	PO	PO	PO	PO	PO	PO
AT1W EU W H9b	EU	EU	EU	EU	EU	EU	EU	EU	EU
AT1W EU W I8c	EU	EU	EU	EU	EU	EU	EU	EU	EU
AT1W GR W H0c	GR	GR	GR	GR	GR	GR	GR	GR	GR
AT2S GR S I3b		GR	GR	GR	GR	GR	GR	GR	GR
AT2W PA W G6b									PA
AT2W PA W G8b									PA
AT3E GR E F7d	GR	GR	GR	GR	GR	GR	GR	GR	GR
AT3W PA W C3b	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)
AT4S PA S G0c					PA	PA	PA	PA	PA
AT4S PA S I0b	PA	PA	PA	PA	PA	PA	PA	PA	PA
AT4W PA W D4			PA	PA					
AT4W PA W E4c		PA	PA	PA	PA				
B12E PA E C4	PA	PA	PA	PA	PA	PA	PA	PA	PA
B11N OM N E3		OM	OM	OM	OM	OM	OM	OM	OM
B11W OM W E9		OM							
EU2W PA W C7b		PA	PA	PA	PA	PA	PA	PA	PA
EU3E MC E D8c	MC	MC	MC						
GR2N PA N B8a	PA	PA	PA	PA	PA	PA	PA	PA	PA
GR2N PA N C8a	PA	PA							
GR2N PA N C8c	PA	PA	PA	PA	PA	PA	PA	PA	PA
GR2N PA N H4c								PA	PA
GR2N PA N H7b								PA	PA
JC4N OM N F0								PA	PA
JC4S PA S G6							PA	PA	OM
MC1N PV N B7b		PV	PV						PA
MC4S ER S G8b		ER	ER	ER	ER	ER	ER		
OM1N PA N G8a	PA								
OM1S PV S F8a	PV	PV							
OM1S PV S H6a	PV	PV							
PA2W GR W E4c		GR	GR	GR	GR	GR	GR	GR	GR
PC1N GR N H5c	GR	GR	GR						
P03S PA S E6		PA							
PV1S GR S G2				GR	GR				
PV1S PO S G1	PO	PO	PO	PO	PO	PO	PO	PO	PO
PV3W PA W F6	PA	PA							

SURVEY STARTING DATE

[illegible]

PC5S PC S D8a							PC		
PO3E EU E A1	EU	EU	EU	EU	EU	EU	EU	EU	EU
PO3E MC E E4						MC	MC	MC	MC
PO3N EU N G1	EU	EU	EU	EU	EU	EU	EU	EU	EU
PV1S PA S B5					PA	PA	PA	PA	PA
PV3W PA W H3					PA	PA	PA	PA	PA
PV3W PA W I4					PA	PA	PA	PA	PA
RO3W PA W J1					PA	PA	PA	PA	PA
RO5E ER E D2	ER	ER	ER	ER	ER	ER	ER	ER	ER
RO5W PA W J1	PA	PA	PA	PA	PA	PA	PA	PA	PA
SA2S EU S A3c								PA	PA
SA3E PO E G6d			PO	PO	PO	PO	PO	EU	EU
SA3E PO E H1c	PO	PO	PO	PO	PO	PO	PO	PO	PO
SA3N PO N E5d						PO	PO	PO	PO
SA4S PA S I3d	PA								
SA4S PA S J3a	PA								

WELL VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
AT2S AT S F9c					AT	AT	AT		
BI4N GR N C3						GR	GR	GR	GR
EU2E AT E I8c			AT	AT	AT	AT	AT		
EU2N MC N C2d				MC	MC	MC	MC	MC	MC
EU2S OM S C1c			OM	OM	OM	OM	OM	OM	OM
EU4E AT E C6c					AT	AT	AT		
EU4E EU E C5b								EU	EU
GR4E EU E C4d			EU	EU	EU	EU	EU	EU	EU
GR4N PA N D0a							PA	PA	PA
JC4E GR E A2			GR	GR	GR	GR	GR	GR	GR
JC4E GR E D5				GR	GR	GR	GR		
JC4S PA S F2		PA							
JC4S PA S G1		PA							
MC3S EU S I5c								EU	
MC3S PO S J5c								PO	PO
MC5N PA N E6b	PA								
PA3E GR E G6a								GR	GR
PA3E GR E G7c	GR								
PC1W EU W G0a			EU	EU	EU	EU	EU		
PC1W PC W A1d		PC							
PC1W PC W F6a	PC								
PC2S BI S F6c	BI	BI	BI						
PC2S CS S F6d				CS	CS	CS			
PC3N AT N A5a	AT	AT	AT	AT	AT	AT	AT	AT	AT
PC3W AT W A2b						AT	AT		
PC4W PC W H6c						PC	PC	PC	PC
PC5N PC N I2d		PC	PC	PC	PC	PC	PC	PC	PC
RO1E AT E J6			AT	AT	AT	AT	AT	AT	AT
SA3S PC S E9b		PC							
SA4E EU E D3a	EU	EU	EU						

POORLY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
E EU OM5E H2b		EU							
E GO BI2E A3	GO	GO	GO	GO					
E PA AT2E H9b	PA	PA							
E PA BI5E C9					PA	PA	PA	PA	PA
E PA BI5E F6	PA								
E PA OM2E I7a	PA	PA	PA	PA	PA	PA	PA	PA	PA
E PC PC5E I2c		PC	PC	PC	PC	PC	PC	PC	
E PC SA5E B3d		PC							
E PC SA5E D4a							PC		
N GR SA3N J6b	GR								
N PA EU2N B2b			PA	PA	PA	PA	PA	PA	PA
N PA EU2N B2c			PA	PA	PA	PA	PA	PA	PA
N PA EU5N E9b			PA						
N PA EU5N G1d									PA
N PA EU5N I1									PA
N PA EU5N I4a	PA	PA	PA	PA	PA	PA	PA	PA	PA
N PA JC1N C8			PA	PA	PA	PA			
N PA MC5N D4a		PA							
N PV PV2N D6			PV	PV	PV				
N PV PV4N C6			PV						
N PV PV4N D6						PV			
S EU EU2S A9a	EU	EU	EU	EU	EU	EU	EU	EU	EU
S EU EU2S C9d			EU	EU	EU	EU	EU	EU	EU
S EU EU2S F8a			EU	EU	EU	EU	EU	EU	EU
S EU EU2S H8c			EU	EU	EU	EU	EU	EU	EU
S EU GR3S C9d		EU							
S EU OM5S A3d				EU	EU				
S EU PA2S B5d		EU	EU						
S EU PA2S F0a				EU	EU	EU	EU	EU	
S EU PC5S E9b		EU							
S EU PC5S F8c		EU	EU						
S EU SA4S A4b	EU	EU	EU	EU	EU	EU	EU	EU	EU
S GR OM3S B3b					GR				
S MC GR3S B6d									MC
S PA BI5S C9	PA								
S PA EU1S I4a	PA	PA	PA	PA	PA	PA	PA	PA	PA
S PA EU3S F3c	PA								
S PA EU5S G0a									PA
S PA EU5S I8c							PA	PA	PA
S PA EU5S I9d							PA	PA	PA
S PA GR3S B6d				PA	PA	PA	PA	PA	PA
S PA GR3S C7c									PA
S PA GR3S E5d		PA	PA	PA	PA	PA	PA	PA	PA
S PA MC4S J6d		PA							
S PA PA3S E8d	PA	PA	PA	PA	PA	PA	PA	PA	PA
S PA P01S C3		PA	PA	PA					
S PA R02S A5			PA	PA	PA	PA	PA	PA	PA
S PC PC5S H8c		PC	PC	PC					

S	PV	EU5S	C4a								
S	PV	EU5S	D4d								
W	EU	EU2W	J8a			PV					
W	EU	GR3W	H5b			EU	EU				
W	EU	GR3W	I6a			EU	EU	EU	EU	EU	EU
W	EU	GR3W	I6c			EU	EU	EU	EU	EU	EU
W	EU	P03W	A7			EU					
W	EU	P03W	D1				EU	EU	EU		
W	GR	OM2W	B1d	GR	GR						
W	GR	OM2W	C1c	GR	GR						
W	MC	OM4W	HI d		MC	MC	MC	MC	MC		
W	PA	GR3W	I9c		PA	PA	PA	PA	PA	PA	PA
W	PA	GR3W	J4a					PA	PA	PA	PA
W	PA	GR3W	J9a		PA	PA	PA	PA	PA	PA	PA
W	PA	GR3W	J0c		PA	PA	PA	PA	PA	PA	PA
W	PA	JC5W	A6	PA							
W	PA	MC3W	C4c	PA	PA	PA	PA	PA	PA	PA	PA
W	PA	MC3W	D7d							PA	PA
W	PA	MC3W	E7d			PA	PA				
W	PA	RO2W	H0		PA						
W	PC	MC3W	H6c		PC	PC	PC	PC	PC	PC	PC
W	PC	OM4W	J5a		PC	PC	PC	PC	PC	PC	
W	PC	PC1W	J2a			PC	PC	PC	PC	PC	
W	PC	PC5W	G3d		PC	PC	PC	PC	PC	PC	PC
W	PC	PC5W	H3d		PC	PC	PC	PC	PC	PC	PC
W	PC	SA3W	H4d					PC	PC	PC	
W	PC	SA3W	I5a					PC	PC	PC	

POORLY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
E EU PA5E A2b			EU	EU	EU	EU	EU		
E EU SA2E E7d			EU						
E MC OM3E H2c						MC	MC	MC	MC
E OM MC3E E5a			OM						
E OM PA2E A5a			OM						
E OM PA3E H2b			OM						
E PA BI1E I0			PA	PA					
E PA MC1E I4b			PA	PA					
E PA OM2E D8c			PA	PA	PA				
E PA OM4E G3c			PA	PA					
N AT PA2N B3c				AT					
N EU PA3N D4b			EU	EU	EU	EU	EU	EU	EU
N OM PC3N A2b			OM						
N OM PC3N A3c			OM						
N OM PC3N B7a			OM						
N OM PC3N I2b			OM						
N PA PV4N H2			PA	PA	PA	PA	PA	PA	PA
S EU MC1S B5b				EU	EU	EU	EU	EU	EU
S EU PA5S G5c			EU						
S JC AT4S A9a	JC	JC	JC						
S OE PO3S F4	OE								
S OM PC3S H2c		OM							
S PA BI3S C2	PA	PA	PA	PA	PA	PA	PA	PA	PA
S PA BI3S G8	PA	PA							
S PA MC3S A7b					PA	PA	PA	PA	PA
S PA PC5S A1d	PA								
S PA SA2S A2d	PA								
W EU OM5W H8c				EU					
W MC MC1W H5b				MC	MC	MC	MC	MC	MC
W OM PC3W B2b		OM							
W OM PC3W D2c		OM							
W OM PC3W D5c		OM							
W OM PC3W E4d		OM							
W OM PC3W I2a		OM							
W OM PC3W I2d		OM							
W OM PC3W J4c		OM							
W PA MC4W H1b									
W PA MC4W J2a						PA	PA	PA	PA
W PA MC4W J2c						PA	PA	PA	PA
W PV PV4W H8		PV	PV	PV	PV	PV	PV	PV	PV

MODERATELY VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/5/90	17/7/90	23/8/90	1/10/90
E CS P01E B2		CS	CS	CS	CS	CS	CS	CS	CS
E DS MC5E E3c		EU	DS	DS	DS	DS	DS	DS	DS
E EU EU5E F1d		EU							
E EU PA2E H1c									
E EU P01E B6						EU	EU	EU	EU
E GR PC1E C1c				GR					
E MC PA2E D6a					MC	MC	MC	MC	MC
E MC P01E C1					MC	MC	MC	MC	MC
E MC SA2E D5a			MC	MC	MC	MC	MC	MC	MC
E PA AT4E D5b	PA								
E PA AT4E E3a	PA	PA							
E PA AT4E E9d	PA								
E PA B13E B2	PA	PA	PA	PA	PA	PA	PA	PA	PA
E PC PC2E E5d		PC	PC	PC	PC	PC	PC	PC	PC
E PC PC2E G6a		PC	PC	PC	PC	PC	PC	PC	PC
E PC PC4E B3a		PC	PC	PC	PC	PC	PC	PC	PC
E PC PC4E B3b		PC	PC	PC	PC	PC	PC	PC	PC
E PC PC4E B3c		PC	PC	PC	PC	PC	PC	PC	PC
E PC PC4E D6a		PC	PC	PC	PC	PC	PC	PC	PC
E PC P01E I1		PC	PC	PC	PC	PC	PC	PC	PC
E PV JC4E B5	PV	PV							
E PV PV2E J3		PV	PV						
E Rhus SA2E C5b			Rhus	Rhus	Rhus	Rhus	Rhus	Rhus	
N AT P01N F5a									AT
N AT P01N G5				AT	AT	AT	AT	AT	AT
N EU MC2N I6b								EU	EU
N EU PC1N G6a		EU							
N MC SA1N J8d		MC							
N PA PA5N D6c		PA							
N PC PC4N A1b			PC	PC	PC	PC	PC	PC	PC
N PC PC4N A4d			PC	PC	PC	PC	PC	PC	PC
N PC PC4N B6b		PC	PC	PC	PC	PC	PC	PC	PC
N PC PC4N D5c			PC	PC	PC	PC	PC	PC	PC
N PC P01N F9		PC	PC	PC	PC	PC	PC	PC	PC
N PV OM4N E5a		PV	PV	PV	PV	PV	PV	PV	PV
S CU EU5S E2d		CU	CU	CU	CU	CU	CU	CU	CU
S ER OM4S I5d									ER
S GR SA4S A3b				GR	GR	GR	GR	GR	GR
S JC OM1S D3c			JC	JC					
S JC OM4S J1b			JC						
S JC P05S I5		JC							
S MC GR2S F8c									
S MC OM2S I5a		MC						MC	MC
S MC P01S F3				MC	MC	MC	MC	MC	
S PA AT4S D5b		PA	PA						
S PV PC2S C3c		PV							
S Rhus MC3S F3a				Rhus	Rhus				
W EU B13W A2			EU						

W EU PA2W A7c			EU	EU	EU	EU	EU	EU	EU
W EU PC1W I4b									
W EU P01W E1			EU						
W EU P01W F1				EU	EU	EU	EU		
W GR GR5W B1a	GR								
W MC R05W J8b				MC					
W PA MC4W A3a	PA								
W PA PA5W E5b		PA	PA						
W PC PA2W C7c								PC	
W PC PA4W I7b				PC					
W PC PC4W A6b		PC	PC	PC	PC	PC	PC	PC	PC
W PC PC4W F7b									
W PC PC4W F9d		PC	PC			PC	PC	PC	PC
W PV MC5W E2b		PV							
W PV PA5W I1a			PV	PV	PV	PV	PV	PV	PV
W PV PV5W C6						PV	PV	PV	PV

MODERATELY VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/09	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
E GR AT3E F7d	GR	GR	GR	GR	GR	GR	GR	GR	GR
E MC EU3E D8c	MC	MC	MC						
E PA B12E C4	PA	PA	PA	PA	PA	PA	PA	PA	PA
N GR PC1N H5c	GR	GR	GR						
N OM BI1N E3		OM	OM	OM	OM	OM	OM	OM	OM
N OM JC4N F0									OM
N PA GR2N B8a	PA	PA	PA	PA	PA	PA	PA	PA	PA
N PA GR2N C8a	PA	PA							
N PA GR2N C8c	PA	PA	PA	PA	PA	PA	PA	PA	PA
N PA GR2N H4c								PA	PA
N PA GR2N H7b								PA	PA
N PA OM1N G8a	PA								
N PV MC1N B7b		PV	PV						
S ER MC4S G8b		ER	ER	ER	ER	ER	ER		
S GR AT2S I3b		GR	GR	GR	GR	GR	GR	GR	GR
S GR PV1S G2				GR	GR				
S PA AT4S G0c					PA	PA	PA	PA	PA
S PA AT4S I0b	PA	PA	PA	PA	PA	PA	PA	PA	PA
S PA JC4S G6						PA	PA	PA	PA
S PA PO3S E6		PA							
S PO AT1S I2d	PO	PO	PO	PO	PO	PO	PO	PO	PO
S PO PV1S G1	PO	PO	PO	PO	PO	PO	PO	PO	PO
S PV OM1S F8a	PV	PV							
S PV OM1S H6a	PV	PV							
W EU AT1W H9b	EU	EU	EU	EU	EU	EU	EU	EU	EU
W EU AT1W I8c	EU	EU	EU	EU	EU	EU	EU	EU	EU
W GR AT1W H0c	GR	GR	GR	GR	GR	GR	GR	GR	GR
W GR PA2W E4c		GR	GR	GR	GR	GR	GR	GR	GR
W OM BI1W E9		OM							
W PA AT2W G6b									PA
W PA AT2W G8b									PA
W PA AT3W C3b	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)	PA(2)
W PA AT4W D4			PA	PA					
W PA AT4W E4c		PA	PA	PA	PA				
W PA EU2W C7b		PA	PA	PA	PA	PA	PA	PA	PA
W PA PV3W F6	PA	PA							

WELL VEGETATED, SOUTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
E AT PC4E A4d					AT	AT	AT		
E ER R05E D2	ER	ER	ER	ER	ER	ER	ER		
E EU P03E A1	EU	EU	EU	EU	EU	EU	EU	EU	EU
E GR AT4E E4c									GR
E GR AT4E E6d					GR	GR	GR	GR	GR
E GR MC5E H3b	GR	GR	GR	GR	GR	GR	GR	GR	GR
E MC EU4E J7a			MC(2)	MC(2)	MC(2)	MC	MC	MC	MC
E MC P03E E4						MC	MC	MC	MC
E OM AT5E F6c									OM
E OM GR4E E7b									OM
E OM OM1E F4d		OM	OM	OM	OM	OM	OM	OM	OM
E PC PC2E D9d					PC	PC	PC		
E PC PC3E F3a	PC	PC	PC	PC	PC	PC	PC	PC	
E PC PC3E H5a						PC	PC	PC	PC
E PC PC5E B9b							PC	PC	
E PC PC5E B9b							PC	PC	
E PO GR1E C3c			PO	PO				PC	
E PO GR1E C8					PO	PO	PO	PO	
E PO PC3E I0a									PO
E PO SA3E G6d			PO	PO	PO	PO	PO	PO	PO
E PO SA3E H1c	PO	PO	PO	PO	PO	PO	PO	PO	PO
N EU P03N G1	EU	EU	EU	EU	EU	EU	EU	EU	EU
N PA MC1N A1b						PA	PA	PA	
N PC PC3N D5b						PC			
N PC PC3N J1c									PC
N PO AT4N J4a	PO	PO	PO	PO	PO	PO	PO	PO	PO
N PO SA3N E5d						PO	PO	PO	PO
S AT GR5S E5c		AT	AT	AT					
S AT PC4S A4b			AT						
S EU MC3S E2c		EU	EU						
S EU PC2S A1d				EU	EU	EU			
S EU SA2S A3c								EU	EU
S GR AT3S A9a			GR	GR	GR	GR	GR	GR	GR
S GR OM2S G1a			GR						
S JM OM2S B5c		JM	JM	JM	JM	JM	JM		
S JM PA3S D1a				JM	JM	JM	JM	JM	JM
S OM PC2S H1d				OM	OM				
S PA AT2S E6d			PA	PA					
S PA AT4S D8c									PA
S PA PV1S B5					PA	PA	PA	PA	PA
S PA SA4S I3d	PA								
S PA SA4S J3a	PA								
S PC GR3S A7c			PC	PC					
S PC PC4S H4b				PC	PC	PC	PC	PC	
S PC PC5S D7c	PC	PC	PC	PC	PC	PC	PC	PC	
S PC PC5S D8a							PC	PC	
S PO GR1S I8c		PO	PO	PO	PO	PO	PO	PO	PO
W AT PA4W D8a		AT	AT	AT	AT	AT	AT	AT	AT

WELL VEGETATED, NORTH FACING

SURVEY STARTING DATE

	7/11/89	12/12/89	30/1/90	12/3/90	25/4/90	5/6/90	17/7/90	23/8/90	1/10/90
E AT EU2E I8c			AT	AT	AT	AT	AT		
E AT EU4E C6c					AT	AT	AT		
E AT R01E J6			AT	AT	AT	AT	AT		
E EU EU4E C5b								AT	AT
E EU GR4E C4d			EU	EU	EU	EU	EU	EU	EU
E EU SA4E D3a	EU	EU	EU						
E GR JC4E A2			GR	GR	GR	GR	GR	GR	GR
E GR JC4E D5				GR	GR	GR	GR	GR	
E GR PA3E G6a								GR	
E GR PA3E G7c	GR							GR	GR
N AT PC3N A5a	AT	AT	AT	AT	AT	AT	AT	AT	AT
N GR BI4N C3						GR	GR	GR	GR
N MC EU2N C2d				MC	MC	MC	MC	MC	MC
N PA GR4N D0a							PA		
N PA MC5N E6b	PA								
N PC PC5N I2d		PC	PC	PC	PC	PC	PC	PC	PC
S AT AT2S F9c					AT	AT	AT		
S BI PC2S F6c	BI	BI	BI						
S CS PC2S F6d				CS	CS	CS			
S EU MC3S I5c								EU	
S OM EU2S C1c			OM	OM	OM	OM	OM	OM	OM
S PA JC4S F2		PA							
S PA JC4S G1		PA							
S PC SA3S E9b		PC							
S PO MC3S J5c								PO	PO
W AT PC3W A2b									
W EU PC1W G0a			EU	EU	EU	AT	AT		
W PC PC1W A1d		PC				EU	EU		
W PC PC1W F6a	PC								
W PC PC4W H6c						PC	PC	PC	PC