

## Chapter 9

### Life form and species diversity on abandoned croplands in the Roggeveld, South Africa

#### Abstract

The Roggeveld mountain range forms part of the Fynbos Biome and consists of an island of Mountain Renosterveld vegetation surrounded by Succulent Karoo Biome vegetation. In order to improve our understanding of the vegetation recovery on abandoned croplands in the Mountain Renosterveld vegetation of the Roggeveld, a variety of species and life form diversity parameters were studied on abandoned croplands of different ages and compared with each other and to the natural vegetation.

Therophytes and chamaephytes were found to be the most abundant life forms on abandoned croplands, while hemicryptophytes, phanerophytes, lianas and parasites were the least abundant. Chamaephytes made an overwhelming contribution to the relative cover on abandoned croplands with phanerophytes, cryptophytes and therophytes contributing significantly less, while hemicryptophyte and liana contributions were negligible.

Species-area curves using the exponential function, differed significantly between the abandoned croplands of all ages and the natural vegetation. Species richness increased with the time since abandonment but no similar increase in species evenness, Shannon or Simpson indices were found. A regression using species richness values on age since abandonment predicted that an abandoned cropland of approximately 33-years should be as species rich as the natural vegetation, however a Principal Co-ordinate Analysis of floristic data indicated that all the abandoned croplands were floristically still extremely different from the natural vegetation. Across all nine survey plots only 15 species contributed to a high cover on the plots.

Vegetation recovery of abandoned croplands in the Mountain Renosterveld of the Roggeveld occurs naturally, yet the rate of recovery varies among the life forms and an important component of the flora, the geophytes (cryptophytes), still remains greatly underrepresented after 20 years of abandonment.

**Keywords:** Diversity indices, Fynbos Biome, old field, renosterveld, species richness, Succulent Karoo, Whittaker plots

## 9.1 Introduction

The Cape Floristic Region (CFR) of South Africa has one of the highest species densities and levels of endemism, at both local and regional scales, for any temperate or tropical continental region (Cowling et al. 1989, 1992) and is recognised as a global hotspot of biodiversity (Cowling & Hilton-Taylor 1994). The Fynbos Biome, as delineated by Rutherford and Westfall (1994), constitutes the major part of the CFR. This biome comprises three quite different, naturally fragmented vegetation types, namely fynbos, renosterveld and strandveld, that occur in winter- and summer-rainfall areas and are dominated by small-leaved, evergreen shrubs whose regeneration is intimately linked to fire (Rebelo et al. 2006). Renosterveld is one of the most threatened vegetation types in South Africa as a result of transformation by agriculture, alien invasive plants and urbanisation (Rebelo 2001, Rouget et al. 2006). The degree of transformation is strongly linked to topography and geographical location (Rebelo et al. 2006) with the lowlands usually showing a higher degree of transformation than the uplands mainly because the lowlands are more favourable for agriculture and urbanisation. Certain high-lying areas such as the Outeniqua and Tsitsikamma Mountains are, however vulnerable to transformation due to afforestation (Rebelo et al. 2006).

The vegetation of the Roggeveld mountain range was classified as renosterveld vegetation by Low and Rebelo (1996), Mucina et al. (2005) and Van der Merwe et al. (2008). This Mountain Renosterveld on the Roggeveld mountain range therefore constitutes an island of Fynbos Biome vegetation surrounded by the Succulent Karoo Biome. Although it is classified as part of the renosterveld vegetation (Fynbos Biome), it lies on the arid extreme of this vegetation type and differs from other renosterveld vegetation types further south in exhibiting many karroid properties.

Among the earliest references to the botanical wealth of the Mountain Renosterveld date from the early 1900s when Diels (1909) mentioned the presence of the Cape element in the flora and the high levels of endemism on the Hantam Mountain. Weimarck (1941) who proposed a classification of the Cape species into five phytogeographical groups treated the Hantam-Roggeveld as a subcentre of his North-Western Centre and stated that the subcentre constituted the last outlier of the Cape element in the inner parts of western South Africa. The Roggeveld was also one of the three centres of endemism that Hilton-Taylor (1994) identified within the Western Cape Domain, however, he considered the Western Cape Domain as part of the Succulent Karoo Biome.

The dominant shrub, *Dicerothamnus rhinocerotis*, renosterbos, after which the renosterveld is named, is an indigenous species with encroaching properties. Disturbed areas are quickly colonised and dominated by *D. rhinocerotis*, which is considered disadvantageous from an agricultural point of view since it is not grazed (Shearing 1997). Historical records of early

explorers indicate that renosterveld had abundant grasses and that as a result of high grazing pressure renosterbos was increasing in abundance and grasses becoming scarcer (transcriptions and translation of R.J. Gordon's travels, Cullinan 2003). The dominance of *D. rhinocerotis* was also mentioned by Marloth in 1908 who suggested that the frequent burning of vegetation by the early settlers to increase palatable vegetation available for their livestock actually increased the dominance of *D. rhinocerotis*. Marloth (1908) also mentions the monocultures of renosterbos on abandoned croplands and that within the first winter of land abandonment *D. rhinocerotis* seedlings colonise abandoned croplands and that the plants grow prolifically and become denser.

The first European farmers settled along the northern slopes of the Roggeveld mountains in the 1740s (Van der Merwe 1938). These settlements were restricted to the valleys and mountainous regions where permanent water could be found (Van der Merwe 1938, 1988). These first farmers cultivated crops on a small scale to be self-sustainable. During his travels to the region in 1778 Gordon (Cullinan 2003) noted that he saw planted trees, vegetables and garden fruit.

The higher rainfall of the Roggeveld in comparison to the surrounding Succulent Karoo areas has allowed farmers to plough large tracts of land to cultivate crops. Numerous utilised and abandoned croplands lie scattered throughout the Roggeveld landscape. Production costs have increased substantially over the years and farmers have been forced to cultivate fewer fields on their lands. This worldwide trend of the increased level of land abandonment is primarily as a result of environmental and socio-economic changes (Cramer et al. 2007).

In semi-arid to arid regions studies on secondary succession are rather scarce, possibly because succession proceeds very slowly under these harsh conditions (Otto et al. 2006). However, plant community succession is one of the most important aspects of vegetation ecology (Zhang 2005) since successional plant communities provide a model system for testing a variety of ecological hypotheses regarding the controls on biodiversity that could be applied to the management and restoration of plant communities (Huberty et al. 1998). Additionally, with the current predictions of climate change the study of plant succession and vegetation recovery take on an even stronger urgency (Bazzaz 2000). Climate change will add another layer of complexity to the restoration of old fields and could exacerbate the ecological thresholds to plant community assembly (Cramer et al. 2007).

The aim of the current study was to use a space-for-time approach to follow the recovery of the vegetation on abandoned croplands in the Roggeveld and to evaluate the rate of recovery in terms of the species composition and various parameters of species and life form diversity. Biodiversity parameters such as species richness, evenness and the Shannon and Simpson

indices were used to gain a better understanding of the process of recovery and how the abandoned croplands compare with the original natural vegetation.

## 9.2 Study area

The study was carried out on the farm Soekop (32° 02' 10.1" S and 20° 07' 06.9" E) in the Mountain Renosterveld vegetation of the Roggeveld (Figure 9.1). The Roggeveld mountain range forms the steep escarpment which separates the low-lying Tanqua Karoo basin from the interior plateau of South Africa. Rocks of the Ecca group cover most of the Roggeveld Mountains (Rubidge & Hancox 1999) with the study area belonging to the Waterford Formation which consists of sandstone, rhythmite, shale and mudstone with wave marks and slumping being common features (Council for Geoscience 2008). Shallow stony lithosol soils are characteristic of the Roggeveld (Francis et al. 2007).

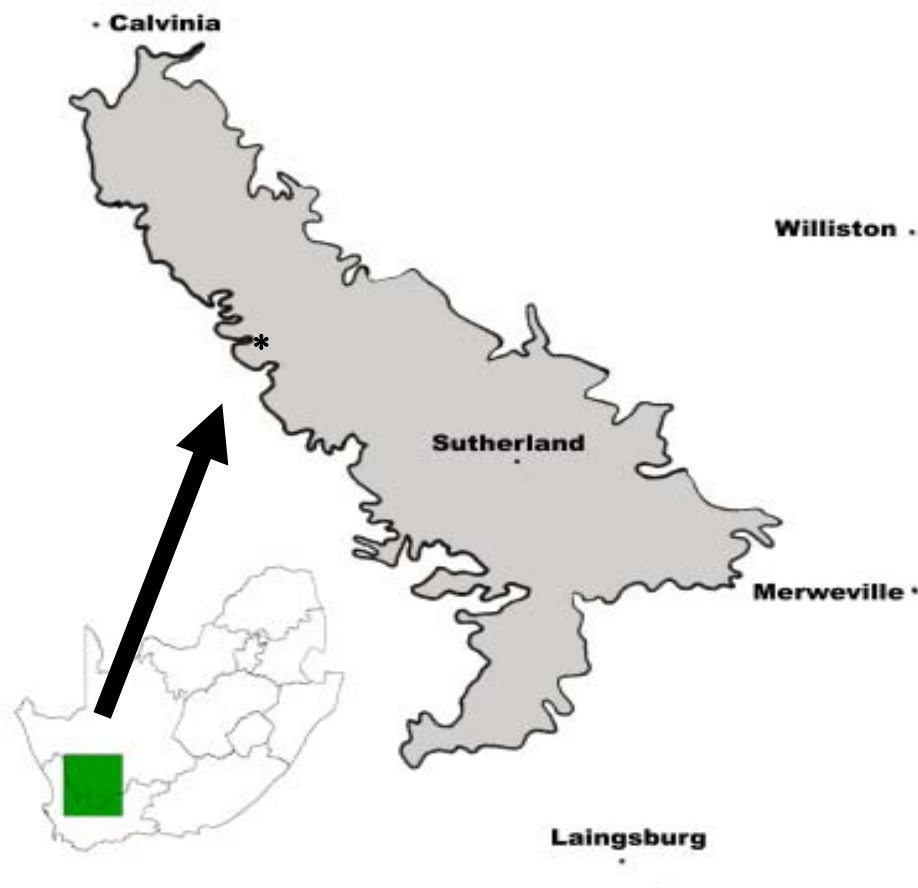


Figure 9.1 The location of the study site (\*) within the Roggeveld mountain range.

Rainfall in the study area ranges from 132 mm to 467 mm per year (Weather Bureau 1998) and although it falls mainly in winter it does include a few summer thunderstorms. In the winter, snowfalls occur with a mean of six snow days recorded per year over a 24-year period by the Weather Bureau (1998). At Sutherland, the mean daily minimum temperature for the

coldest month, July, is  $-2.4^{\circ}\text{C}$ , while the extreme minimum,  $-13.6^{\circ}\text{C}$ , was recorded in July 1970 and August 1978 (Weather Bureau 1998). The mean daily maximum for the warmest month, January, is  $27.1^{\circ}\text{C}$ , while the extreme maximum recorded was  $35.5^{\circ}\text{C}$  in January 1980 (Weather Bureau 1998).

The study area falls within the Roggeveld Shale Renosterveld vegetation type of Mucina et al. (2005, Rebelo et al. 2006). A recent finer scale classification and mapping of the vegetation associations of the area indicates that the study area falls within the *Dicerotheramnus rhinocerotis* Mountain Renosterveld vegetation association (Van der Merwe et al. 2008). This vegetation association is dominated by a high cover of *D. rhinocerotis* while *Merxmüllera stricta* and *Dimorphotheca cuneata* also characterise the vegetation unit. Strong annual and geophyte components in spring are usually present following good winter rains.

### 9.3 Materials and Methods

Nine sample plots using Whittaker's plant diversity plot technique (Shmida 1984) were surveyed. Eight of these were surveyed on abandoned croplands of various ages (3-, 4-, 8-, 10-, 15- and 20-years old). Additionally, a plot in the undisturbed natural vegetation close to the abandoned cropland of 20-years old was surveyed. All surveys were conducted on one farm in the same vegetation type and on the same geological substrate. Furthermore, the surveys were all conducted in one season. The only modification to the methodology as described by Shmida (1984) was the modification of the field form and notations used on the field form (see Chapter 6 for a full description of the methodology).

Species encountered in the surveys were separated into broad life form categories following Raunkiaer (1934) as modified in Mueller-Dombois and Ellenberg (1974 see Appendix 1). The relative contributions of each life form, in terms of species as well as plant cover, to the 1000 m<sup>2</sup> sample plots were calculated.

The total species number for seven plot sizes (1 m<sup>2</sup>, 5 m<sup>2</sup>, 10 m<sup>2</sup>, 20 m<sup>2</sup>, 50 m<sup>2</sup>, 100 m<sup>2</sup> and 1000 m<sup>2</sup>) were determined. These seven plot sizes were used to construct Type II species-area curves (Scheiner 2003, 2004) for each of the nine plots sampled using the exponential function since this function produced the best results in a study across the entire Hantam-Tanqua-Roggeveld subregion (Chapter 6). The exponential function is expressed as a semilog function:

$$S = z \times \log A + c \text{ (Veech 2000),}$$

Where: S = species richness

A = area of survey plot

z and c are constants.

Species richness (S), Shannon's index of diversity (H'), Simpson's index (D) and a measure of evenness (E) were calculated for each sampled plot at the 1000 m<sup>2</sup> (0.1 ha) size, using the PC-ORD computer program (PC-ORD Version 4 for Windows, MjM Software design) which calculates these four diversity measures as follows:

S = richness = number of species.

H' = Shannon diversity

$$H' = - \sum_i^s p_i \log p_i$$

Where  $p_i$  = importance probability in column  $i$ .

E = Evenness (equitability) = H' / ln (richness).

D = Simpson's index of diversity for an infinite population. This is the complement of Simpson's original index and represents the likelihood that two randomly chosen individuals will be different species.

$$D = 1 - \sum_i^s p_i^2$$

The Shannon index was also used to calculate a life form diversity index using frequencies of life forms instead of species.

The Chi-square test of the STATISTICA computer package (StaSoft, Inc. Version 8, 2300 East 14<sup>th</sup> Street, Tulsa, OK 74104) was used to compare the life-form distributions. Floristic data for all nine plots surveyed were ordinated using Principal Co-ordinate Analysis (PCoA) in the SYN-TAX computer program (Podani 2001) because the use of a wide array of distance measures in Principal Co-ordinate Analysis (PCoA) can give a marked improvement over Principal Component Analysis (PCA) (McCune & Grace 2002). The statistical significance of the differences between slope values and intercepts of the exponential function curves were analysed by an Analysis of Covariance (Quinn & Keough 2002) linear regression with GraphPad Prism 4.03 for Windows (GraphPad software, San Diego, California, USA, [www.graphpad.com](http://www.graphpad.com)).

## 9.4 Results and discussion

Whittaker's plant diversity plot technique has proved to be an efficient method of sampling used around the world, especially in semi-arid environments (Shmida 1984, Chapter 6, Chapter 7, Chapter 8). The data derived by this technique were used to determine various life form and species diversity parameters for abandoned croplands of various ages in the

Roggeveld. These data were compared to baseline data of the various plant diversity parameters compiled for the Roggeveld area derived with the same technique (Chapter 6, Chapter 7, Chapter 8)

The tradition of classifying plants and vegetation into major types on the basis of plant form has a long history (Vandvik & Birks 2002). The life form of a species refers to the vegetative form of the plant body and it is assumed to be a result of morphological adjustment to the climate and environment (Cain 1950, Barkman 1979, Van Rooyen et al. 1990, Semenova & van der Maarel 2000). Cain (1950) stated that the spectra for successional communities of various sorts might reflect edaphic conditions and give a good measure of the changing environment as succession proceeds. When considering the abundance of each life form at 1000 m<sup>2</sup> (Figure 9.2) and the contribution per life form expressed as a percentage of the total number of species (Figure 9.3), trends along the successional sequence are observed.

Generally, therophyte and chamaephyte species were the most abundant species throughout the various stages of secondary succession in the Roggeveld (Figure 9.2b, 9.2e, 9.3) while, liana species were scarce and only recorded on fields abandoned for 10 years or more (Figure 9.2f, 9.3). No parasite species were encountered in any of the plots surveyed. Therophyte species increased in number with age of the abandoned croplands up to croplands last ploughed 8-years ago and with a noticeable decrease in number found on the abandoned croplands of 10-years and older (Figure 9.2e, 9.3). The natural vegetation held less therophyte species than the 4- and 8-year old abandoned croplands (Figure 9.2e), with the relative contribution of therophyte species to the life form distribution demonstrating the same trend except for the 3-year old abandoned croplands where they constituted almost half of the species (Figure 9.3). Chamaephyte species generally increased in number as the age of the abandoned croplands increased, with the natural vegetation holding the highest number of chamaephyte species (Figure 9.2b). However, the relative contribution of chamaephyte species showed an initial decrease whereafter it increased to the 15-year old abandoned cropland and then decreased in the 20-year old abandoned cropland and in the natural vegetation (Figure 9.3).



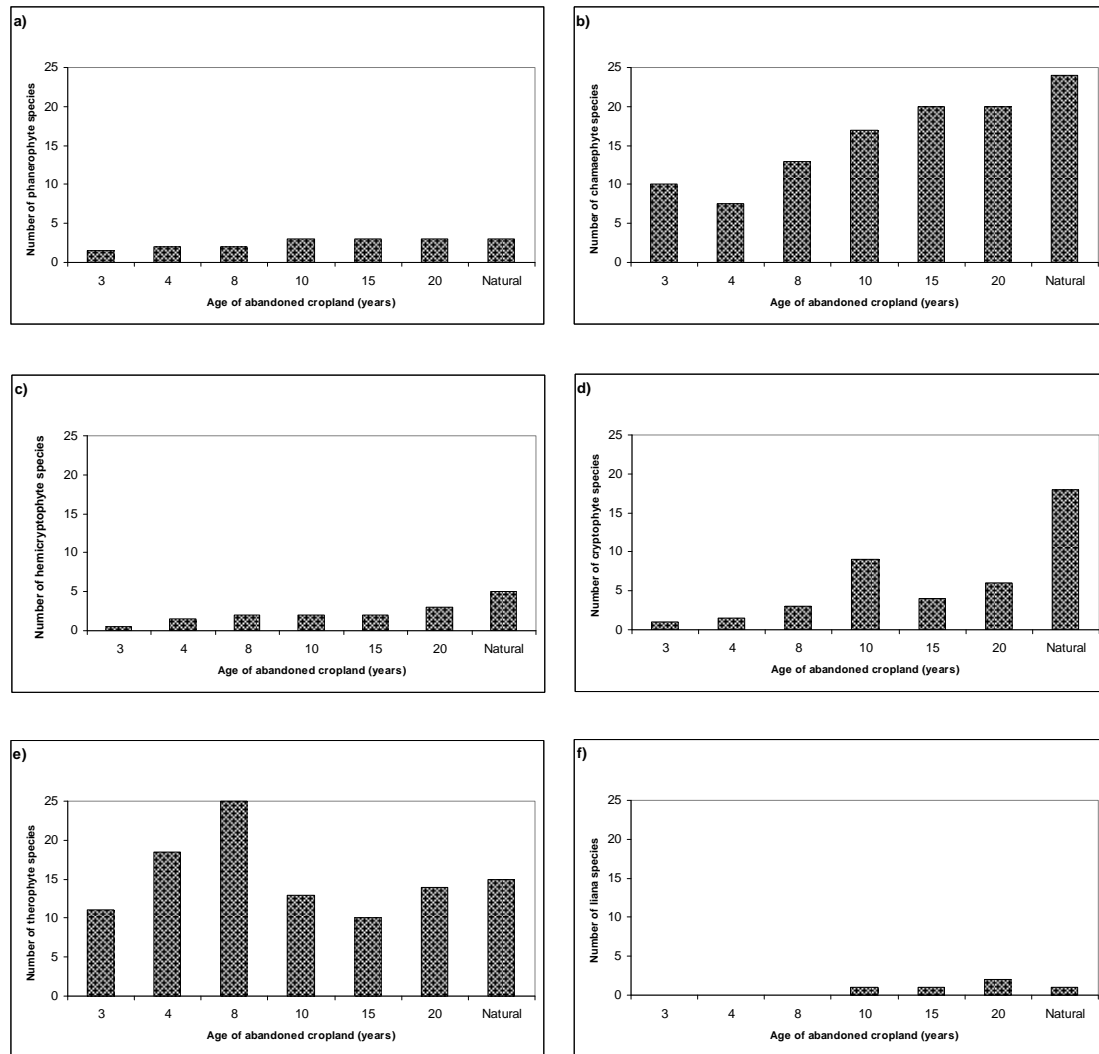


Figure 9.2 Total number of species per life form in 1000 m<sup>2</sup> plots on abandoned croplands of various ages and the natural vegetation in the Roggeveld for the following life forms: a) phanerophytes, b) chamaephytes, c) hemicytopytes, d) cryptophytes, e) therophytes and f) lianas.

Cryptophyte (geophyte) species generally increased gradually along the time scale since abandonment (Figure 9.2d) however, the relative contribution of cryptophyte species to the 20-year old abandoned cropland was still less than half the relative contribution to the natural vegetation (Figure 9.3). Different life forms have different sensitivities to soil disturbance (McIntyre et al. 1995) and cryptophyte species are severely depleted by continuous ploughing to produce crops. These effects of cultivation still prevail in the species composition on the abandoned croplands (Stromberg & Griffin 1996) and was particularly evident in the current study when considering the rich geophytic component of the Roggeveld (Van Wyk & Smith 2001).



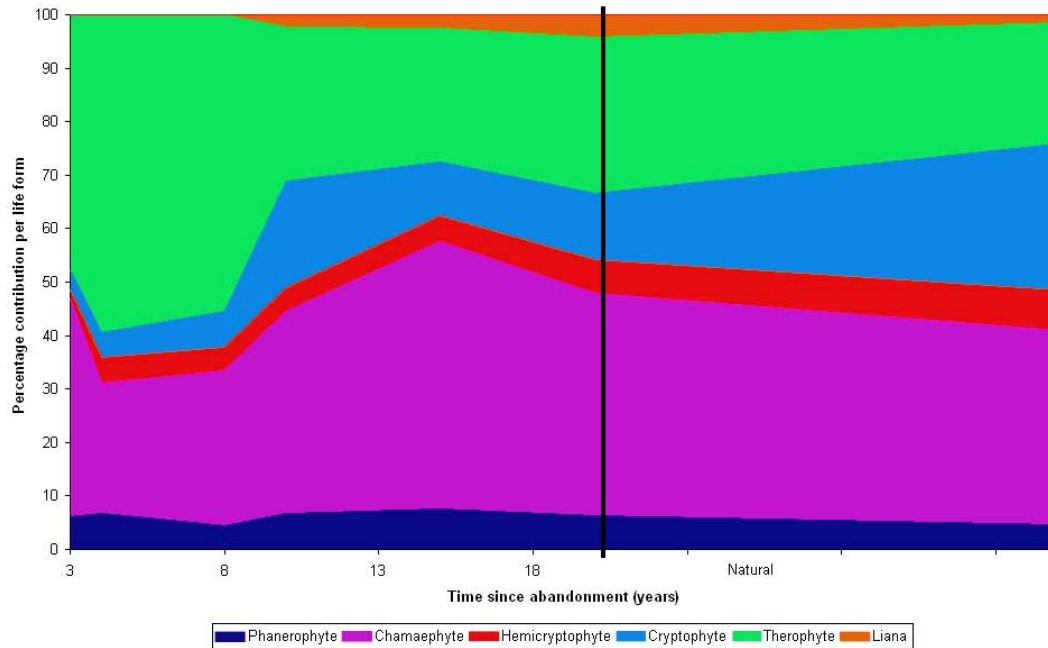


Figure 9.3 Number of species per life form per 1000 m<sup>2</sup> expressed as a percentage of the total number of species across the abandoned croplands of various ages and the natural vegetation in the Roggeveld.

The number and relative abundance of hemicryptophyte species increased with age since land abandonment (Figure 9.2c, 9.3) yet, the number of species remained small ( $\leq 5$  species per 1000 m<sup>2</sup>). Phanerophyte numbers remained relatively constant throughout all the plots of varying ages (Figure 9.2a, 9.3) and therefore the relative contribution of this life form showed a slight decrease. This could be ascribed to the ability of *Dicerotheramnus rhinocerotis* to quickly colonise disturbed areas throughout the Roggeveld region. Liana species were only present in abandoned croplands of 10-years and older (Figure 9.2f, 9.3).

Therophyte species were initially replaced predominantly by chamaephyte species and in later successional ages by a combination of chamaephyte and cryptophyte species. This replacement of therophyte species with mainly chamaephyte species differs from the 'classical' sequence of life forms on old fields where the annual species are replaced by biennials and herbaceous perennials (i.e. hemicryptophytes) before these are replaced by chamaephytes and eventually phanerophytes (Debussche et al. 1996, Huberty et al. 1998, Otto et al. 2006). However, which mechanisms of species replacement operate at a particular time and place in succession depends largely on the growth form of the dominant species of the site (e.g. annual vs. perennial life cycle, canopy-forming vs. understory species, clonal vs. non-clonal). Species replacement also depends on the life history characteristics, dispersal mode and growth form of the potential occupants of the site and the nature of natural disturbances (Armesto & Pickett 1986). Considering that the Roggeveld vegetation is generally rich in chamaephyte and cryptophyte species and poor in phanerophyte and

hemicryptophyte species, the successional transition from therophyte species to chamaephyte species and later a combination of chamaephyte and cryptophyte species can be understood.

The Shannon life form diversity index ranged from 0.628 (OL2) to 1.115 (OL6) along the successional sequence with no evidence of increasing complexity with increasing age since abandonment. Yet, when considering Figure 9.3, it seems as though there is a better spread of species amongst the life forms as succession proceeds.

By weighting every species by its relative cover and expressing this value as a percentage of the total relative cover, a very different life form distribution is obtained (Figure 9.4). Phanerophyte contribution decreased from the 3- to 8-year old abandoned croplands, then increased substantially on the 10-year old abandoned cropland and decreased again to the 20-year old abandoned cropland, thereafter remaining at a slightly increased lower level (Figure 9.4). The dominant life form, contributing to the highest cover, is the chamaephyte life form. Chamaephytes comprise a third of the vegetation cover on 3-year old abandoned croplands and continually increased in cover to a value of 80.3% on 20-year old abandoned croplands, with the natural vegetation holding 70.9% chamaephyte cover (Figure 9.4). Hemicryptophytes increased after three years of abandonment thereafter remaining relatively constant throughout all the abandoned croplands at approximately half the relative cover found in the natural vegetation (Figure 9.4). The relative contribution of cryptophytes (geophytes) to vegetation cover increased from the third year of abandonment and varied within a narrow band throughout the abandoned croplands, with the cryptophytes contributing to a higher cover (8.2%) in the natural vegetation (Figure 9.4). Therophytes' contribution to the total cover was highest during the first 8-years of cropland abandonment and decreased noticeably on the 10-year old abandoned cropland and remained at this lower level, which was similar to its contribution in the natural vegetation (Figure 9.4). The smallest contribution to total cover of any life form was that of the lianas which remained  $\leq 0.6\%$  of the total cover (Figure 9.4).

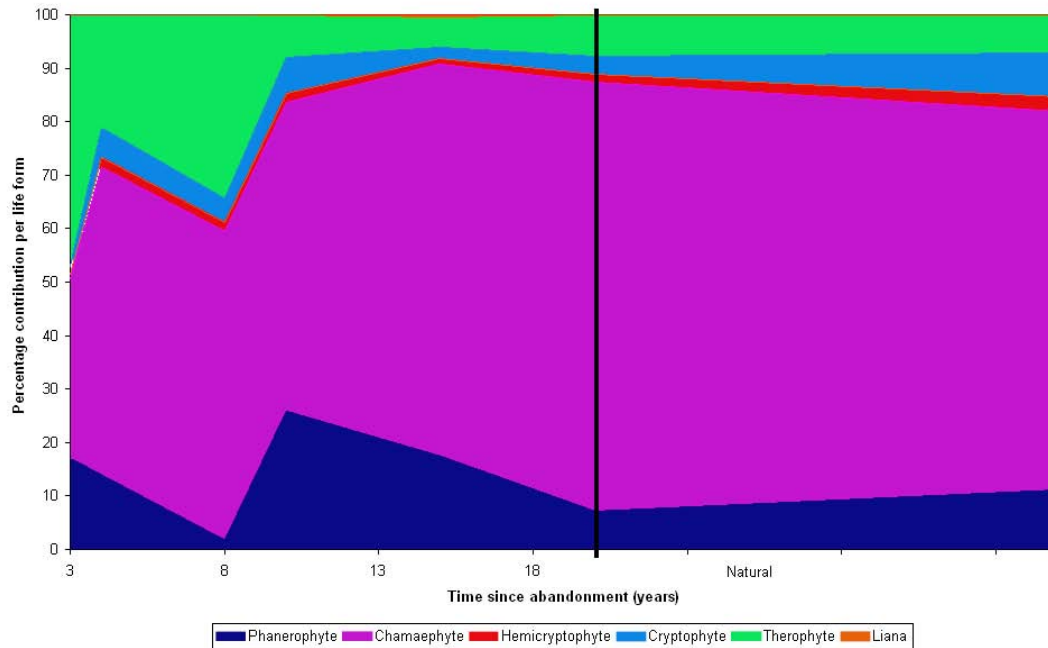


Figure 9.4. Relative cover per life form expressed as a percentage of the total cover across the abandoned croplands of various ages and the natural vegetation in the Roggeveld.

The Chi-squared test comparing the life form spectra on a species basis of the natural vegetation with the 3-, 4- and 8-year old abandoned croplands produced highly significant differences ( $p < 0.001$ ). No significant differences were found between the natural vegetation and abandoned croplands of 10- and 20-years old however, a significant difference ( $p < 0.05$ ) was found between the natural vegetation and the 15-year old abandoned cropland.

Species-area curves were constructed using the exponential function because this function generally performs well (Connor & McCoy 1979, Tjørve 2003) and was also found to produce the best fit in a study of the natural vegetation of the Hantam-Tanqua-Roggeveld (Chapter 6). Contrary to general theoretical expectations about species/area relationships, Bazzaz (2000) found that species number in successional habitats rarely rises smoothly and asymptotically with an increase in area because patchiness in the distribution of resources and species can generate abrupt changes in species/area relations. However, in this study no sudden increases in species number were evident and in all cases an asymptote seemed to be reached. A comparison of the slope and intercept values of the exponential curves between the abandoned croplands and the natural vegetation found that the curve for the natural vegetation was always significantly different from that of the abandoned croplands (Table 9.1). In most cases the slopes were different, but whenever the slope values were not different the intercept values were found to be significantly different.

Species richness, or the number of species, is currently the most widely used diversity measure (Stirling & Wilsey 2001) and is used extensively in secondary succession literature

(Squiers & Wistendahl 1976, Inouye et al. 1987, Lavorel 1994, Prieur-Richard et al. 2000, Tunnell et al. 2004, Gibson et al. 2005, Zhan et al. 2007) in comparisons between abandoned croplands of various ages and the natural vegetation to indicate the degree of recovery.

Table 9.1 Age of the abandoned cropland, survey plot number, exponential function, r-value and p-value (significance of fit) for the species-area curve for the plots surveyed on abandoned croplands of various ages and in the natural vegetation. The statistical significance of the comparisons of slope and intercept values between each abandoned cropland with the natural vegetation is also provided

Age of abandoned cropland	Survey plot number	Exponential (Semi-log) function			Significance of comparison of slope and intercept values between abandoned croplands and the natural vegetation	
		Linear equation	r-value	p-value	Slope value	Intercept value
3 years	OL1	$y=1.3686+8.2400x$	0.9621	0.0005***	0.0002***	
3 years	OL2	$y=0.4980+5.4866x$	0.9310	0.0023**	0.0001***	
4 years	OL3	$y=0.0107+8.5086x$	0.9596	0.0006***	0.0004***	
4 years	OL4	$y=5.1820+9.6119x$	0.9887	0.0000***	0.0004***	
8 years	OL5	$y=2.1718+13.9909x$	0.9888	0.0000***	0.0269*	
10 years	OL6	$y=-4.9583+13.2600x$	0.8841	0.0082**	0.1386	0.0002***
15 years	OL7	$y=1.1083+11.4901x$	0.9651	0.0004***	0.0064**	
20 years	OL8	$y=-4.4219+13.6977x$	0.8716	0.0106*	0.1980	0.0005***
Natural vegetation	OL9	$y=5.3234+18.9851x$	0.9810	0.0001***		

ns Not significant, \*  $p < 0.05$  Significant, \*\*  $p < 0.01$  Highly significant, \*\*\*  $p < 0.001$  Very highly significant

Generally, the species richness values acquired in this study for the abandoned croplands indicate the expected low species richness on abandoned croplands of three to four years in age (20 to 33 species per 1000 m<sup>2</sup>, Table 9.2). There is a marked increase in species richness at the ages between eight and 20 years (40 to 48 species per 1000 m<sup>2</sup>, Table 9.2). The undisturbed vegetation close to the 20-year old abandoned cropland had a species richness of 66 per 1 000 m<sup>2</sup> (Table 9.2). The latter value compares well with values obtained for other natural vegetation in the Roggeveld in which species richness varied from 62 to 99 species per 1000 m<sup>2</sup> with a mean value of 79 species per 1 000 m<sup>2</sup> (Chapter 7). A regression of the age of the abandoned cropland against the number of species found per 1000 m<sup>2</sup> suggests that theoretically an abandoned cropland of approximately 33 years after abandonment should be as species rich as the natural vegetation (Figure 9.5). However, such an extrapolation of the regression beyond the actual data points must be viewed with caution.

Table 9.2 Age of abandoned cropland, survey plot number, species richness, species evenness, Shannon's index of diversity and Simpson's index for abandoned croplands of different ages and the natural vegetation in the Roggeveld

Age of abandoned cropland	Survey plot number	Species richness	Species evenness (E)	Shannon index (H')	Simpson index (D)
3 years	OL1	28	0.613	2.044	0.744
3 years	OL2	20	0.404	1.211	0.435
4 years	OL3	29	0.734	2.471	0.856
4 years	OL4	33	0.613	2.144	0.743
8 years	OL5	45	0.797	3.014	0.884
10 years	OL6	45	0.594	2.260	0.770
15 years	OL7	40	0.579	2.138	0.760
20 years	OL8	48	0.573	2.218	0.781
Natural vegetation	OL9	66	0.592	2.480	0.762

A measure of species evenness (E) was calculated for each plot sampled. Evenness is constrained between zero and 1.0 with 1.0 representing a situation in which all species are equally abundant (Magurran 1988). Evenness values ranged from 0.573 (OL8, 20-year old) to 0.797 (OL5, 8-year old) with one 3-year old abandoned cropland (OL2, 3-year old) having an evenness value of 0.404 (Table 9.2). Species evenness values showed a marked increase up to the 8-year old abandoned cropland thereafter it dropped again and remained relatively steady at a lower level which is very close to the evenness value (0.592) of the natural vegetation in the vicinity of the 20-year old abandoned cropland (Table 9.2). Evenness values on the abandoned croplands were therefore comparable with previously determined values for the Roggeveld, which ranged from 0.501 to 0.820 (Chapter 7).

The Shannon indices calculated for the nine plots in this study ranged from 1.211 (OL2, 3-year old) to 3.014 (OL5, 8-year old) (Table 9.2), whereas values found in a study conducted in the natural vegetation ranged from 2.225 to 3.743 for the Mountain Renosterveld vegetation of the Roggeveld (Chapter 7). The Shannon and Simpson indices take both evenness and species richness into account (Magurran 1988). Shannon indices showed the same pattern as the evenness values with an increase up to eight years since abandonment and thereafter a sudden decline and remaining at that lower level. Simpson indices found for all nine plots surveyed showed little variation and ranged from 0.743 (OL4, 4-year old) to 0.884 (OL5, 8-year old) with the exception of OL2 (3-year old) with a Simpson index of 0.435 (Table 9.2). Simpson indices for the natural vegetation of the Roggeveld showed a greater variation and ranged from 0.604 to 0.944 (Chapter 7).

None of the diversity parameters, species evenness, Shannon or Simpson indices, reflected the trend in species richness, which showed a continuous increase in the number of species. This seems to indicate that although species richness increases, the dominance of a few species also increases disproportionately.

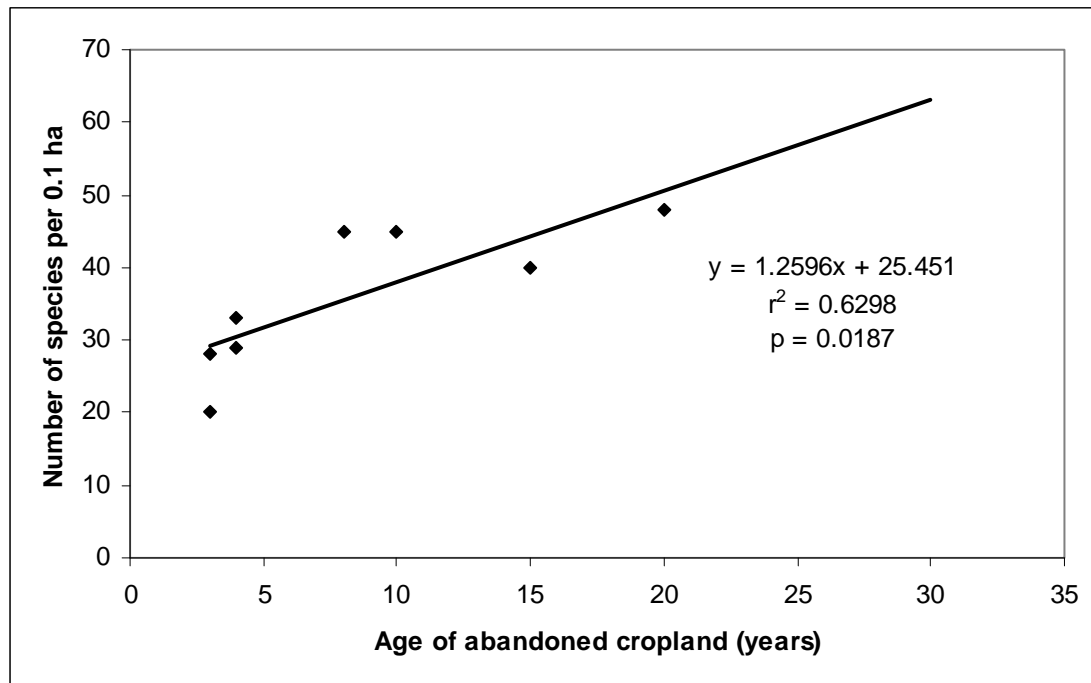


Figure 9.5 Regression of the number of species per 1000 m<sup>2</sup> (0.1 ha) on the age of abandoned cropland.

Across all the survey plots 15 species contributed most to the cover found within a plot (Table 9.3). Eight of these species (*Chrysocoma ciliata*, *Dicerotheramnus rhinocerotis*, *Dimorphotheca cuneata*, *Euryops laterifolius*, *Helichrysum hamulosum*, *Merxmuellera stricta*, *Oedera genistifolia* and *Poa bulbosa*) also contributed to the high vegetation cover of the natural vegetation. A maximum of five (*Chrysocoma ciliata*, *Dicerotheramnus rhinocerotis*, *Dimorphotheca cuneata*, *Medicago polymorpha* and *Selago cf. rigida*) of the 15 species contributed a high cover, at any one time, on the abandoned croplands. Four of the seven annual species with the highest abundances were abundant only on the abandoned croplands up to an age of 8-years, these species were *Cotula nudicaulis*, *Hordeum murinum*, *Karoochloa tenella* and *Medicago polymorpha*. Thus, no annuals at high abundances were found on abandoned croplands of 10-years and older. Furthermore, the two introduced weedy species (*Hordeum murinum* and *Medicago polymorpha*) were virtually absent on croplands of 10-years and older. The perennial component cover varied greatly across all the surveyed plots. All eight perennial species with the highest abundances were present in the natural vegetation, which confirms the statement by Van der Putten et al. (2000) that in succession the identity of the local species matter. The fact that three of the perennial

species were present from the very early stages of succession seems to support the tolerance and not facilitation model of Connell and Slatyer (1977, Gurevitch et al. 2002).

Table 9.3 The percentage cover of the 15 most abundant species in abandoned croplands of various ages and in the natural vegetation in the Roggeveld

Species	Annual/ Perennial	OL1	OL2	OL3	OL4	OL5	OL6	OL7	OL8	OL9
<i>Chrysocoma ciliata</i>	Perennial	10.0	35.0	0.5	1.0	10.0	5.0	40.0	25.0	5.0
<i>Cotula nudicaulis</i>	Annual			2.0	0.5	0.5			0.5	0.5
<i>Dicrothamnus rhinocerotis</i>	Perennial	25.0	2.0	5.0	0.5	0.5	15.0	15.0	5.0	2.0
<i>Dimorphotheca cuneata</i>	Perennial	3.0	0.5	0.5	1.0	5.0	25.0	10.0	2.0	10.0
<i>Erodium moschatum</i>	Annual	0.5	0.5	0.5	0.5	0.5	<0.1		0.5	0.5
<i>Euryops laterifolius</i>	Perennial	0.5		0.5			0.5	0.5	0.5	10.0
<i>Helichrysum hamulosum</i>	Perennial	0.5	<0.1			0.5	0.5	0.5	25.0	2.0
<i>Hordeum murinum</i>	Annual		0.5	3.0	10.0	0.5				
<i>Karoochloa tenella</i>	Annual		0.5	5.0	0.5	1.0	0.5	0.5		
<i>Medicago polymorpha</i>	Annual	1.0	3.0	10.0	20.0	0.5			<0.1	
<i>Merxmuellera stricta</i>	Perennial							<0.1	0.5	50.0
<i>Oedera genistifolia</i>	Perennial					0.5	0.5	5.0	0.5	2.0
<i>Pentaschistus aristifolia</i>	Annual	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
<i>Poa bulbosa</i>	Annual						0.5		5.0	2.0
<i>Selago cf. rigida</i>	Perennial	5.0	0.5	0.5	0.5		0.5	5.0	0.5	0.5

To analyse floristic patterns with respect to the data of the nine survey plots a Principal Coordinate Analysis (PCoA) was done. The resulting PCoA shows the relatively close proximity of the younger abandoned croplands (3-, 4- and 8-years old) to the older abandoned croplands (10-, 15- and 20-years old) and the large floristic gap between these abandoned croplands and the natural vegetation (OL9) (Figure 9.6). Thus, even although the regression of the age of abandoned cropland and number of species per 1000 m<sup>2</sup> indicates that after approximately 33-years an abandoned cropland will be as species rich as the natural vegetation (Figure 9.5) floristically, this abandoned cropland will still be appreciably different from the natural vegetation (Figure 9.6).



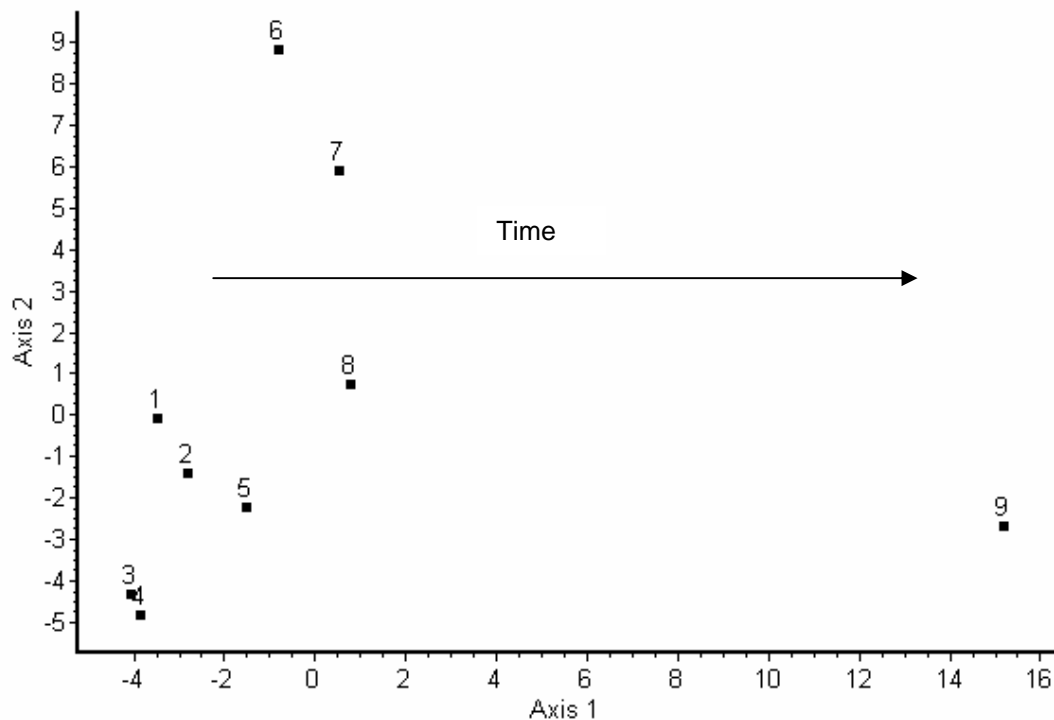


Figure 9.6 A Principal Co-ordinate Analysis (PCoA) of the floristic data of the abandoned croplands (1-8) and the natural vegetation (9).

When comparing the position of the natural vegetation with the abandoned croplands it is implied that succession proceeds on a single set pathway and that it leads to a predictable stable community. However, large variability in the recovery of the vegetation is likely to be found. Differences among fields may be due to pre-abandonment treatments, such as the type of crop or cultivation practice, climatic conditions after abandonment or grazing management. Cramer and Hobbs (2007) stated that within limitations imposed by climate and soil characteristics, it does appear that the combination of past land use type and land use intensity explains much of the difference in patterns within similar ecosystem types.

The 2005 year in which these data were collected was a poor rainfall year. This is expected to have underestimated the number of species, especially with respect to annuals and geophytes, which comprise a large part of the species diversity in the region. Thus the species richness values for both the abandoned croplands and the undisturbed vegetation are expected to be higher than the values reported here. Additional annuals would have affected both the abandoned croplands and the natural vegetation species richness values, whereas the geophytic component would have had a larger impact on the natural vegetation survey data.

The pattern of recovery of Roggeveld Mountain Renosterveld seems to differ from the West Coast Renosterveld of the Cape Floristic Region. Studies conducted on Elandsberg Private Nature Reserve on remnant renosterveld vegetation and abandoned croplands indicated the apparent slow return of indigenous renosterveld vegetation on abandoned croplands (Midokoponga et al. 2005). The main difference between the two areas is the dominance by introduced alien annual grasses on abandoned croplands in the West Coast Renosterveld. These weedy grasses arrest the whole recovery process. Current restoration efforts aim to reduce the cover of the introduced grasses while at the same time maintaining or even increasing species richness and diversity of indigenous target species (Krug & Krug 2007). In spite of the Roggeveld probably having harsher environmental conditions, recovery on abandoned croplands is occurring and seems to be continuing with a steady increase in species richness occurring and values of evenness, Shannon and Simpson indices of diversity being similar to those of the natural vegetation from approximately 10 years after abandonment.

All life forms are well represented within 20-years of cropland abandonment, however cryptophyte species are still underrepresented. This is to be expected since these species are eradicated by ploughing and reproduction, by vegetative means or seed set, occurs slowly. Geophyte species are an important component of the Roggeveld flora and from a diversity point of view, the return of these species on abandoned croplands is important.

No fires were experienced on any of the surveyed abandoned croplands, but it is expected that fire would simply slow down secondary succession with early successional species such as *Dicerothamnus rhinocerotis*, *Chrysocoma ciliata* and *Dimorphotheca cuneata* re-establishing within the next growing season. This is supported by data collected on post-fire monitoring plots in the Roggeveld that show *D. rhinocerotis* seedling established in plots within nine months following a fire (Chapter 10).

## 9.5 Conclusions

The Roggeveld, located within the Fynbos Biome, has a higher rainfall than the surrounding areas and has been used to cultivate wheat and other fodder crops for hundreds of years. Primarily due to an increase in production costs, many croplands are no longer utilised and now lie barren.

Chamaephyte and therophyte species were the most abundant life forms on abandoned croplands of all ages while hemicryptophyte, phanerophyte, liana and parasite species were the least abundant life forms. However, liana and parasite species were also seldom found in the natural vegetation. Therophyte species were the most abundant on young abandoned croplands and decreased in number from 10-years of age to values similar to those

encountered in the natural vegetation. Chamaephyte, cryptophyte and hemicryptophyte species increased in number with an increase in age of the abandoned croplands, the highest values being found for the natural vegetation. Phanerophyte species were few and did not differ much across the age range of the surveyed plots.

The relative cover of each life form expressed as a percentage of the total cover indicates the overwhelming contribution made by chamaephytes which increase along the successional sequence and remained at a high cover in the natural vegetation. Phanerophyte contributions fluctuated throughout the abandoned cropland succession, while therophyte cover was high on the 3- to 8-year old sites, thereafter decreasing substantially and remaining at a low value, similar to the natural vegetation. Hemicryptophytes contributed negligibly to cover on the abandoned croplands and in the natural vegetation. Cryptophyte cover fluctuated on abandoned croplands but at all times remained approximately a quarter lower than in the natural vegetation.

Comparison of slope and intercept values of the exponential function species-area curves across all the abandoned croplands and the natural vegetation found that the curves of the abandoned croplands differed significantly from those of the natural vegetation in all instances.

Species richness increased with the age of the abandoned cropland, with the species richness for the natural vegetation being the highest at 66 species per 1000 m<sup>2</sup>, however, a similar increase in the values of evenness, Shannon and Simpson indices were not found with increasing age of the abandoned cropland. A regression of species richness against age of abandoned croplands predicted that an abandoned cropland of approximately 33-years should be as species rich as the natural vegetation. Yet, a Principal Co-ordinate Analysis of the floristic data indicated that floristically all the abandoned croplands were still extremely different from the natural vegetation.

Across all the survey plots, 15 species contributed most to the high cover with eight of these also contributing to the high cover of the natural vegetation. Four annual species were present in high abundances on abandoned croplands of  $\leq 8$ -years of age, with no indigenous or alien invasive annual species at high abundances on older abandoned croplands. The perennial component cover varied greatly across all the surveyed plots.

The results of this study contribute to our understanding of restoration efforts on abandoned croplands in the Roggeveld. The Roggeveld Mountain Renosterveld abandoned croplands surveyed were not negatively influenced by alien annual grasses as in the West Coast Renosterveld and species richness increased continually. Recovery of abandoned croplands seems to occur naturally, however after 20-years, cryptophyte species were still largely

underrepresented in comparison to the natural vegetation. It is expected that the influence of fire would simply slow down secondary succession with early colonisers establishing again by the next growing season.

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## Chapter 10

### Vegetation trends following fire in the Roggeveld, South Africa

#### Abstract

The Mountain Renosterveld vegetation of the Roggeveld is an escarpment type renosterveld showing strong karroid affinities with fire playing an important role as a landscape scale disturbance that shapes these plant communities. Line transect data accumulated over ten years were analysed and this paper reports on the post-fire vegetation trends with respect to changes in vegetation cover, species numbers and life form categories over this timeframe.

Within the first nine months following fire, vegetation began to establish with the vegetation cover remaining at a higher level from year 3 to year 10. Species richness varied between 13 and 17 species at the first survey with the highest species richness generally encountered after three years at each transect. Shannon index values varied greatly between the five localities with four of the localities showing similar trends after the fire. The highest Shannon index values were generally found within the first three years and lowest Shannon index values found in year 9 and year 10. Species composition data for each plot over the ten year period were ordinated using Principal Co-ordinate Analysis. In all cases, these ordinations indicated a clear separation in species composition between the first two years (year 1 and year 2) following the fire and the remaining years (year 3 to year 10).

This study seems to lend support to the 'initial floristic composition' model of Egler (1954) with all or the majority of species encountered during succession already present at the beginning of the recovery phase and a rapid re-establishment of the initial plant community.

**Keywords:** Fynbos Biome, 'initial floristic composition' model, life forms, long-term monitoring, Mountain Renosterveld, post-fire vegetation recovery, vegetation cover

## 10.1 Introduction

The Mountain Renosterveld vegetation covering the Roggeveld mountain range is an island of Fynbos Biome vegetation surrounded by Succulent Karoo Biome vegetation (Van der Merwe et al. 2008). The Fynbos Biome coincides more or less with the area covered by the Cape Floral Kingdom which is recognised as one of the world's six floristic kingdoms (Good 1947), on par with much larger regions worldwide (Rebelo et al. 2006). The Fynbos Biome also constitutes the largest portion of the Cape Floristic Region (CFR) a region which is internationally renowned for its exceptional species diversity and which is recognised as one of 34 global hotspots of biodiversity ([www.biodiversityhotspot.org](http://www.biodiversityhotspot.org) – accessed 22 February 2009). This biome comprises three quite different, naturally fragmented vegetation types, namely fynbos, renosterveld and strandveld, that occur in winter- and summer-rainfall areas and are dominated by small-leaved, evergreen shrubs whose regeneration is intimately related to fire (Rebelo et al. 2006).

Renosterveld is an evergreen, fire-prone shrubland or grassland dominated by small, cupressoid-leaved, evergreen asteraceous shrubs (principally *Dicerothamnus rhinocerotis*, renosterbos, rhino bush) with an understory of grasses (Poaceae) and a high biomass and diversity of geophytes (Moll et al. 1984, McDowell & Moll 1992, Cowling et al. 1997, Rebelo et al. 2006). A major feature of renosterveld, at least the coastal units, is the extensive transformation that has taken place over the last 100 years (Rebelo et al. 2006). The escarpment renosterveld types, such as on the Roggeveld Mountains, show strong karroid affinities.

*Dicerothamnus rhinocerotis*, after which the renosterveld is named, is an indigenous perennial species with encroaching properties and is not grazed (Shearing 1997). Early explorers to the Roggeveld indicated the abundance of grasses in renosterveld and that as a result of high grazing pressure renosterbos was increasing in abundance and grasses were becoming scarcer (transcriptions and translation of R.J. Gordon's travels, Cullinan 2003). Marloth (1908) also mentioned *D. rhinocerotis* dominance and suggested that frequent burning of vegetation by the early settlers to increase palatable vegetation for their livestock was actually increasing the dominance of *D. rhinocerotis*.

Fire is a landscape scale disturbance that creates gaps in plant communities which provide space for plant establishment (Carson & Pickett 1990). Disturbance by fire can contribute to the maintenance of diversity in two manners: firstly, fire contributes to the maintenance of species richness by avoided competitive exclusion and secondly, fire can increase spatial heterogeneity (Lavorel et al. 1994).

The Mediterranean-type vegetation is one of the world's major fire-prone biomes (Capitania & Carcaillet 2008). In areas in which this type of vegetation occurs, as for example the Mountain Renosterveld of the Roggeveld, fire is a crucial process controlling vegetation dynamics and structure (Capitania & Carcaillet 2008), with the post-fire regeneration process highly dependent on the pre-fire vegetation (Hanes 1971, Trabaud & Lepart 1980, Pausas 1999, Lloret & Vilá 2003). Various studies have found that in such ecosystems species composition and structure rapidly recover after fire (Hanes 1971, Lloret & Vilá 2003). In fynbos, the effect of fire on species composition, vegetation structure and successional patterns depends on the frequency, intensity and season of the fire and it was found that there is also considerable variation in response between sites (Kruger & Bigalke 1984, Cowling et al. 1997).

One of the traits frequently used in attempts to classify species according to their response to disturbance, is growth form (McIntyre et al. 1995). A description of growth form, expressed in terms of dormant bud position, as developed by Raunkiaer (1934), encapsulates sets of correlated traits relating to persistence and architecture that are relevant to disturbance response (McIntyre et al. 1995, 1999). Guo (2001) found that using plant groups provided a useful framework for describing post-fire chaparral succession because they affect ecosystem processes in some predictable ways and may also reflect the underlying environmental changes after fire.

On 26 January 1999 more than 10 000 ha burnt in a lightning induced fire in the Roggeveld. This event created an opportunity to investigate the post-fire recovery of the vegetation in the Mountain Renosterveld. The aim of the current paper is to report on post-fire vegetation trends in the Mountain Renosterveld vegetation of the Roggeveld with reference to the changes in species numbers, vegetation cover and life form categories over a time-span of 10 years (1999-2008). Additionally, a Principal Co-ordinate Analysis was used to investigate species compositional changes over the ten-year period for each survey plot.

## 10.2 Study area

The study was conducted on three adjacent farms (Botuin, Klawervlei and Droëkloof) in the Mountain Renosterveld vegetation of the Roggeveld (Figure 10.1, Table 10.1). According to Mucina et al. (2005) and Rebelo et al. (2006), the study area falls within the Roggeveld Shale Renosterveld vegetation type, whereas the finer scale classification and mapping by Van der Merwe et al. (2008) indicated that the study area was part of the *Dicerotheramnus rhinocerotis* Mountain Renosterveld plant association (association 2). Plant association 2 is dominated by *D. rhinocerotis* with *Merxmuellera stricta* and *Chrysocoma ciliata* further characterising the vegetation unit. Following good winter rains the annual and geophyte component make up a large part of the vegetation.

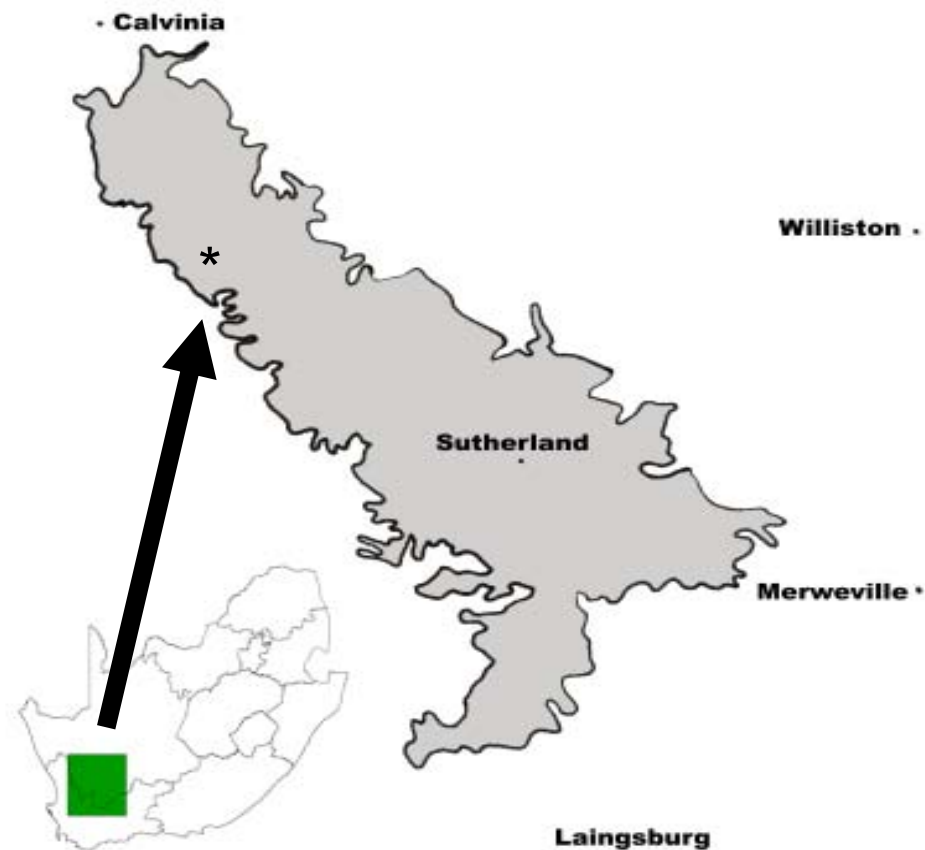


Figure 10.1 Location of the post-fire monitoring transects on three adjacent farms in the Roggeveld.

Although the rains within this region fall mainly in winter, a few summer thunderstorms contribute to the total annual precipitation of 132 mm to 467 mm per year (Weather Bureau 1998). Winter snowfalls occur with a mean of 6 snow days recorded per year over a 24-year period for Sutherland (Weather Bureau 1998). The mean daily maximum temperature for January (the warmest month) measured at the Sutherland is 27.1°C, while the mean daily minimum temperature for July (the coldest month) is -2.4°C.

Rocks of the Ecca Group cover most of the Roggeveld Mountains (Rubidge & Hancox 1999) with shallow stony lithosols characteristic (Francis et al. 2007). Three of the five post-fire monitoring sites were located on Land Type Da 69 with red B horizons, while the other two sites were located on Land Type Fa 650 with lime rare or absent in the entire landscape (Council for Geoscience 1989) (Table 10.1).

Table 10.1 Prominent features of the five post-fire monitoring sites in the Roggeveld, indicating GPS starting point co-ordinates, altitude, aspect, land type and dominant perennial plant species ten years after a fire

	Site 1	Site 2	Site 3	Site 4	Site 5
<b>GPS co-ordinates:</b>	31°58'35.6"S	31°59'15.2"S	31°58'39.6"S	31°55'49.7"S	31°55'19.8"S
<b>Starting point</b>	20°00'27.3"E	20°01'11.5"E	20°01'26.2"E	20°01'34.7"E	20°01'43.9"E
<b>Altitude</b>	1440 m	1371 m	1296 m	1334 m	1385 m
<b>Aspect</b>	East	North	West	South	South
<b>Land type</b>	Da 69	Da 69	Da 69	Fa 650	Fa 650
<b>Dominant perennial plant species after 10 years following a fire</b>	<i>Dicerothamnus rhinocerotis</i> , <i>Merxmuellera stricta</i> , <i>Muraltia vulnerans</i>	<i>Merxmuellera stricta</i> , <i>Chrysocoma ciliata</i> , <i>Dicerothamnus rhinocerotis</i>	<i>Merxmuellera stricta</i> , <i>Chrysocoma ciliata</i>	<i>Dicerothamnus rhinocerotis</i> , <i>Merxmuellera stricta</i>	<i>Leysera gnaphalodes</i> , <i>Lotononis hirsuta</i>

### 10.3 Materials and methods

To acquire objective quantitative data on the vegetation changes that occurred following a fire in 1999, a point or plotless method was used. Due to the steep slopes and rock-strewn areas, the descending point method (Roux 1963, Novellie & Strydom 1987) was deemed the most appropriate method to track post-fire vegetation trends at the five selected sites in the Roggeveld. A canopy strike was recorded when the descending point touched any plant material or fell within the canopy spread of the individual. When considering only basal strikes the perennial grasses are favoured above the karoo bush component, because perennial grasses have a small base to canopy spread ratio (Vorster 1982).

The transects were permanently marked with iron poles ('droppers') indicating the beginning and end points of a 50 m rope which was marked at 1 m intervals. Four lines, 1 m apart and parallel to one another were surveyed in order to limit the chance of surveying transitional areas between different vegetation types or habitats. The transects were monitored yearly in the last week of September or the first week of October. Ten years of data were collected between 1999 and 2008.

The number of strikes on a species were calculated as a percentage of the total number of point observations made and were not expressed as a percentage of all the strikes (Du Toit 1998a). Thus, in this study, the number of strikes per species were expressed as a percentage of the 200 points surveyed and these totals added to determine the percentage vegetation cover. The sum of the individual plant species percentages obtained rarely totals

one hundred because the number of strikes observed are fewer than the total number of point observations made (Du Toit 1998b).

Additionally, the species were classified into the dominant life forms as defined by Raunkiaer (1934) and modified by Mueller-Dombois and Ellenberg (1974, Appendix 1). Temporal changes in the post-fire vegetation were investigated in terms of (a) total vegetation cover (b) total species richness, (c) Shannon index of diversity, (d) vegetation cover per life form, (e) species richness per life form, and (f) changes in species composition across a 10 year period.

Shannon's index of diversity ( $H'$ ), often referred to as Shannon-Wiener index, was calculated for each sampled plot using the PC-ORD computer program (PC-ORD Version 4 for Windows, MjM Software design) which calculates this diversity measure as follows:

$H'$  = Shannon diversity

$$H' = - \sum_i^s p_i \log p_i$$

Where  $p_i$  = importance probability of species  $i$ .

The species compositional data for each of the five post-fire monitoring transects over the ten year period were ordinated using Principal Co-ordinate Analysis (PCoA) in the SYN-TAX computer program (Podani 2001). Principal Co-ordinate Analysis generally performs well with species data because it allows the use of a wide array of distance measures and therefore gives a marked improvement over Principal Component Analysis (McCune & Grace 2002).

#### 10.4 Results and discussion

The vegetation cover increased within the first nine months following the fire (Figure 10.2). Vegetation cover at sites 1 and 5 increased steadily from 1999 to 2001 (Figure 10.2a, 10.2e), while the vegetation cover at sites 2 and 3 decreased between 1999 and 2000 and then increased from 2000 to 2001 (Figure 10.2b, 10.2c). Post-fire transect 4 had no change in vegetation cover between 1999 and 2000 but vegetation cover increased in 2001 (Figure 10.2d). The high vegetation cover recorded in the 2001 season could be attributed to the region receiving good rains in that year. From 2001 until 2008 vegetation cover in all the post-fire monitoring transects remained higher than the vegetation cover found immediately following the fire in 1999 and 2000. In most instances there was a decrease in vegetation cover in 2003, 2004 and 2005. These three years were characterised by a low rainfall and drought conditions resulting in a low therophyte vegetation cover (Figure 10.2). The vegetation on Land Type Da had a far higher cover of perennial species (59.5% - 71%) than Land Type Fa (35.5% - 47%).



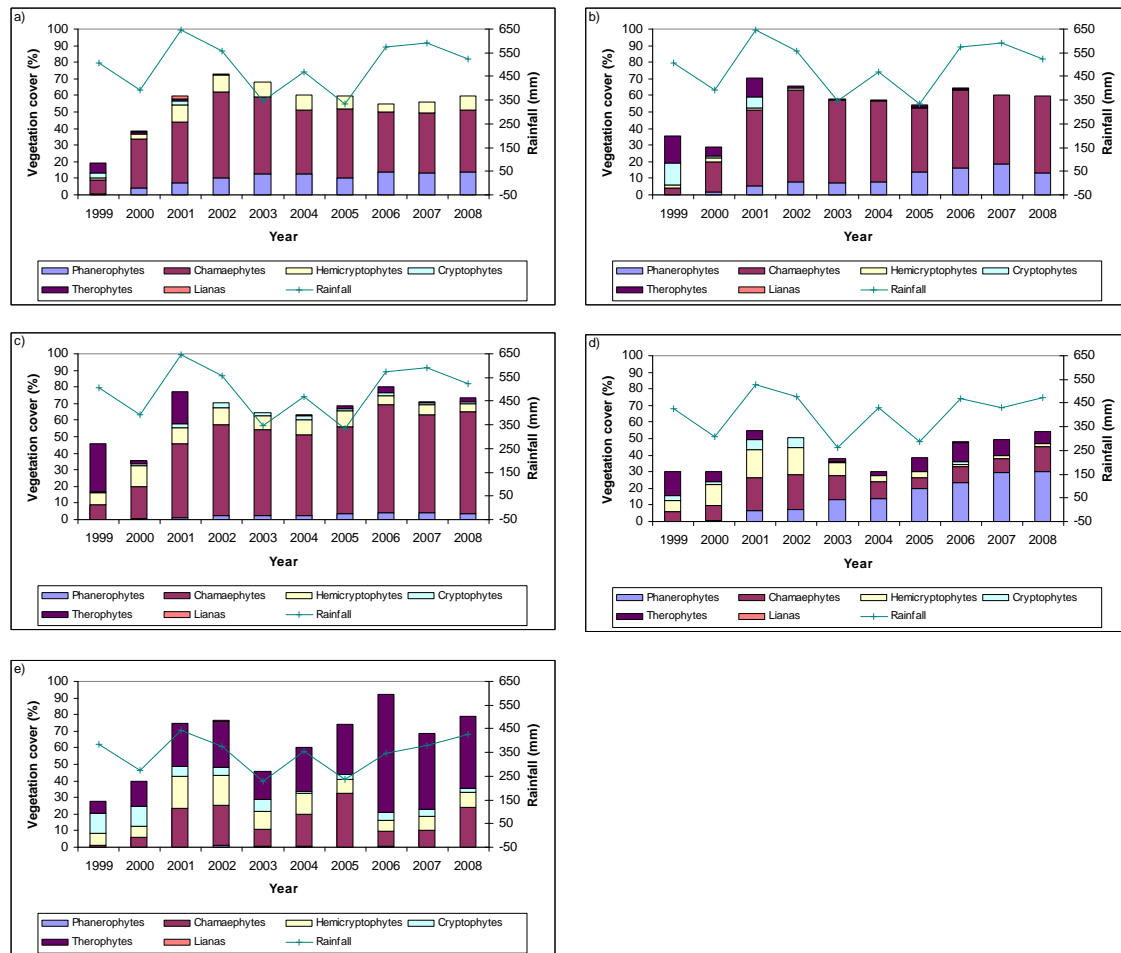


Figure 10.2 Vegetation cover changes per life form (columns) determined from a 200-point survey and annual rainfall (line) for five post-fire monitoring transects: a) site 1, b) site 2, c) site 3, d) site 4; and e) site 5.

Within nine months of the fire, the total number of species surveyed in the 200-point line transects ranged between 13 and 17 species per transect (Figure 10.3). At all sites on Land Type Da the highest species richness was reached within 3 years (2001) after the fire, whereafter species richness declined or remained more or less constant. A similar increase in the second and third post-fire year and subsequent decrease in species richness was reported in Californian chaparral (Guo 2001). In the case of the sites on Land Type Fa, species richness initially declined after the high value in 2001 but increased again to reach a maximum in 2006. Therophyte species contributed more to species numbers on Land Type Fa (Figure 10.3d & 10.3c) than on Land Type Da (Figure 10.3a-c). In all cases, chamaephyte species made a large contribution to the total species numbers.

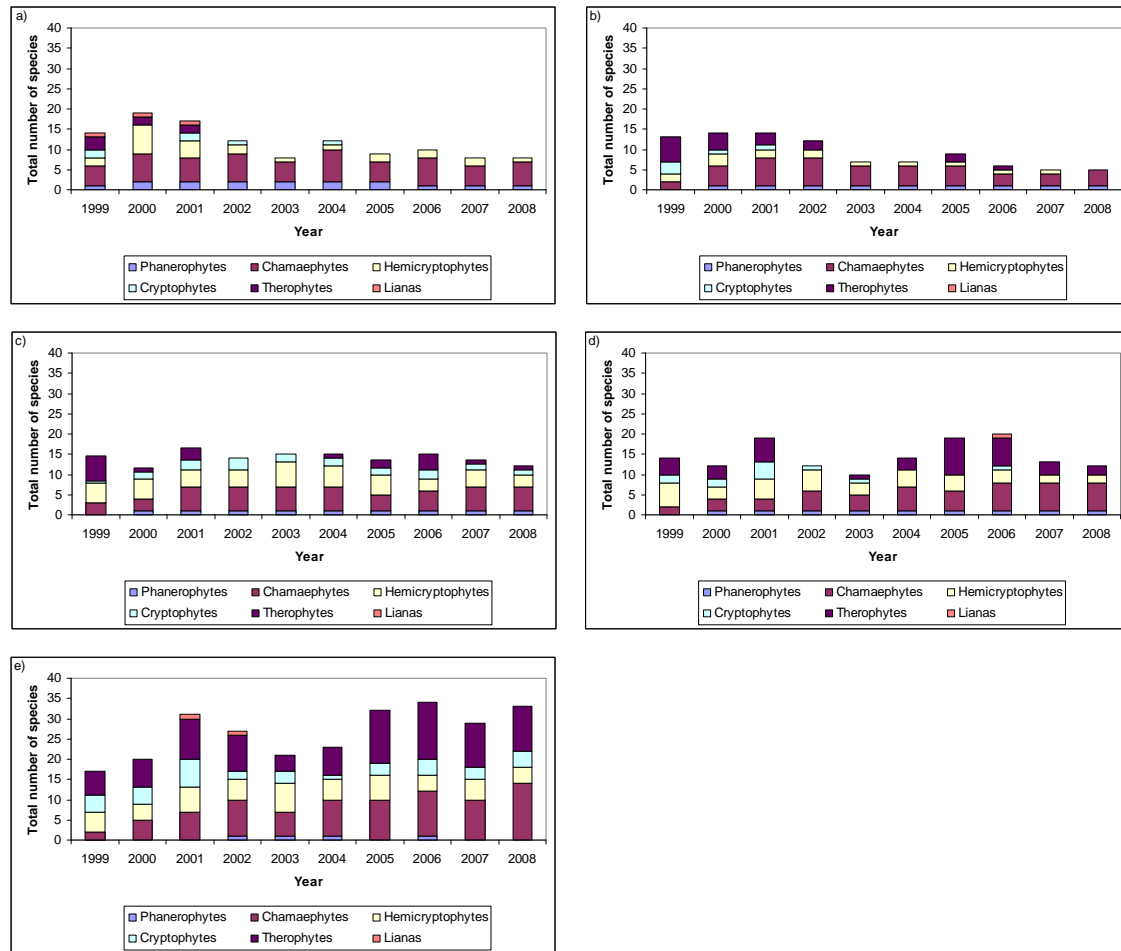


Figure 10.3 Total number of species per life form determined from a 200-point survey for the five post-fire monitoring transects: a) site 1, b) site 2, c) site 3, d) site 4; and e) site 5.

Various studies in Mediterranean-type ecosystems have indicated quick community recovery after fire and concluded that species richness was at its highest soon after fire (Capitania and Carcaillet 2008). Species diversity has been found to peak within the first year (Keeley et al. 1981, Schwilk et al. 1997) or second year (Potts et al. 2003) with Guo (2001) reporting the highest species richness in the second post-fire year on north-facing slopes and in the third year on south-facing slopes. In all instances species richness was reported to decline in the following years. Additionally, when studying the species composition soon after the fire it becomes evident that all, or the majority of, species present during the succession are in place from the beginning of the recovery phase. It appears that species richness in Fynbos vegetation is higher soon after fire and succession proceeds by successive elimination of species (Bond & Van Wilgen 1996). Since data collected in this study support the fact that nearly all of the species were already present in the early recovery phase and that the initial plant community established rapidly, the 'initial floristic composition' model of Egler (1954) seems to apply to this ecosystem, however, further research is needed to resolve which, if any, model of vegetation dynamics most accurately reflects post-fire dynamics in Mediterranean ecosystems (Capitania & Carcaillet 2008).

Shannon's index values ranged from 1.107 (site 2) to 3.030 (site 5) (Table 10.2) across the ten year period at the five monitoring sites. The highest two values for site 1 to site 4 were found within the first three years following fire, yet, the highest two values for site 5 were found in year 3 (2001) and year 10 (2008). Four of the sites (sites 1 to 4) showed similar trends, with the lowest Shannon values ranging between 1.107 (site 2) and 1.521 (site 1) and highest Shannon values varying from 2.093 (site 2) to 2.258 (site 1) (Table 10.2). In general, the lowest Shannon values in these sites were found in year 9 and year 10. The lowest Shannon value for site 5 was 2.564, which is higher than the highest values encountered in site 1 to site 4 (Table 10.2). This initial high Shannon value following fire results from the presence of a high number of geophytes (cryptophyte species) and annuals (therophyte species), which react quickly after fire.

Table 10.2 Shannon index values for five post-fire monitoring transects from 1999 to 2008

Year	Site 1	Site 2	Site 3	Site 4	Site 5
1999	2.258	2.093	2.151	2.043	2.564
2000	1.769	2.009	1.781	1.874	2.694
2001	2.078	1.973	2.058	2.195	2.979
2002	1.971	1.570	1.775	1.971	2.913
2003	1.445	1.147	1.454	1.751	2.613
2004	1.727	1.219	1.635	1.905	2.660
2005	1.604	1.340	1.466	1.983	2.927
2006	1.548	1.171	1.369	2.015	2.739
2007	1.568	1.107	1.296	1.410	2.939
2008	1.521	1.143	1.475	1.580	3.030

Upon classifying the species encountered in the field surveys into Raunkiaer (1934) classic life form categories (Appendix 1), two different patterns emerged across the 10 years of survey results. The three post-fire monitoring transects located on Land Type Da (site 1, site 2 and site 3) produced different life form spectra from the two post-fire monitoring sites located on Land Type Fa (Site 4 and Site 5) (Figure 10.4 and 10.5). In general, the contribution of phanerophyte and chamaephyte species was higher on Land Type Da (Figure 10.4a-c) than on Land Type Fa (Figure 10.4d, 10.4e), whereas the contribution of therophyte species was larger on Land Type Fa than Land Type Da (Figure 10.4a-e).

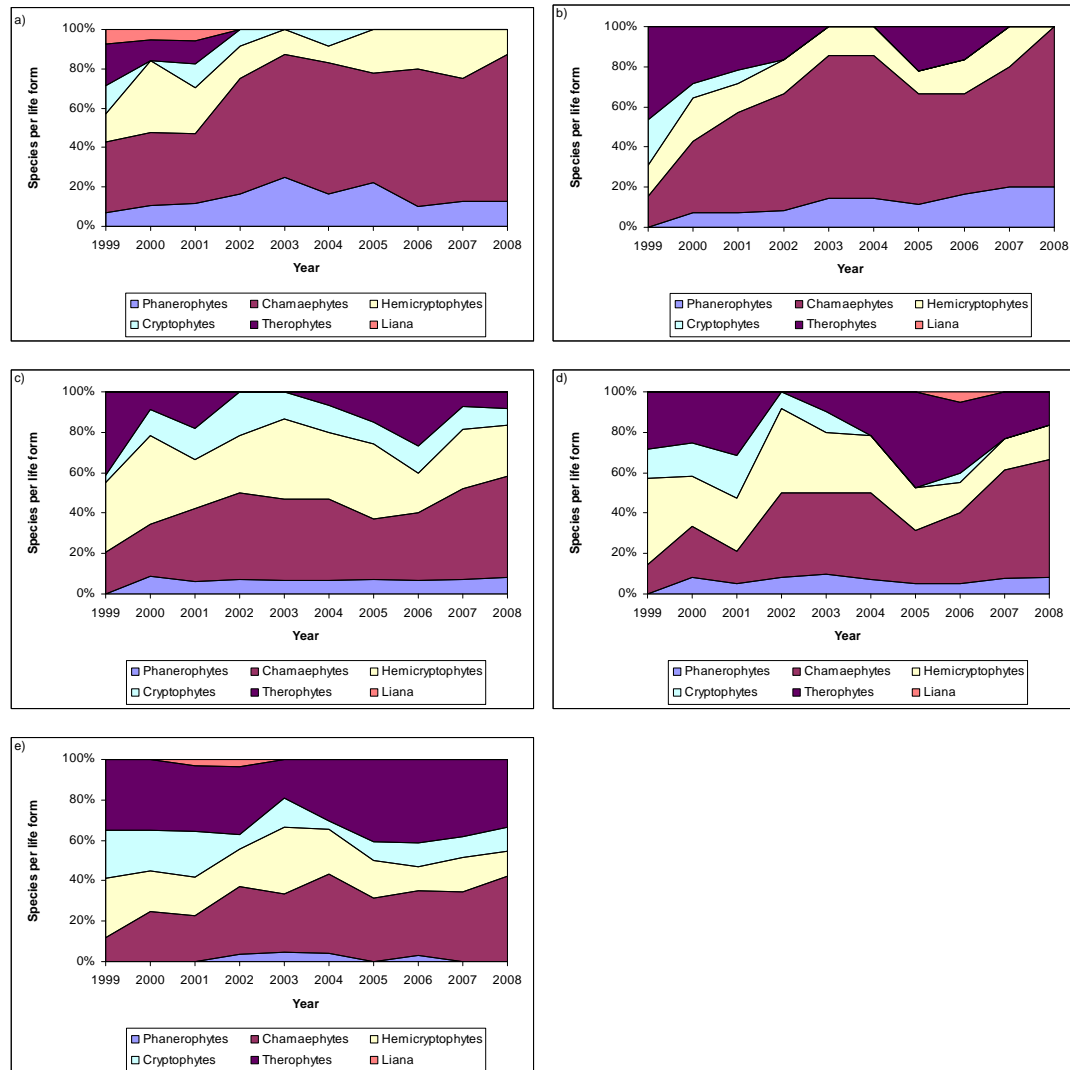


Figure 10.4 Number of species per life form expressed as a percentage of the total number of species for post-fire monitoring transects: a) site 1, b) site 2, c) site 3, d) site 4; and e) site 5.

The percentage contribution per life form to the vegetation cover produced different results (Figure 10.5) from the percentage contribution at a species level (Figure 10.4). Phanerophyte species contributed to a larger proportion of the vegetation cover than their species numbers suggested at site 1, 2 and 4 (Figure 10.5a, 10.5b and 10.5d). This was primarily as a result of the dominance by *D. rhinocerotis*. Site 3 was a *Merxmuellera stricta* grass dominated site with the grass limiting *D. rhinocerotis* establishment, hence, the lower phanerophyte species vegetation cover contribution (Figure 10.5c). Chamaephyte species cover dominated in the three Land Type Da post-fire monitoring transects (Figure 10.5a-c), whereas the contribution of therophyte species to the overall vegetation cover of these transects was limited to a small percentage in the first four years following the fire (Figure 10.5a-c). In contrast, therophyte species cover contribution on Land Type Fa (Figure 10.5d, 10.5e) remained relatively high throughout the first 10 years following the fire.

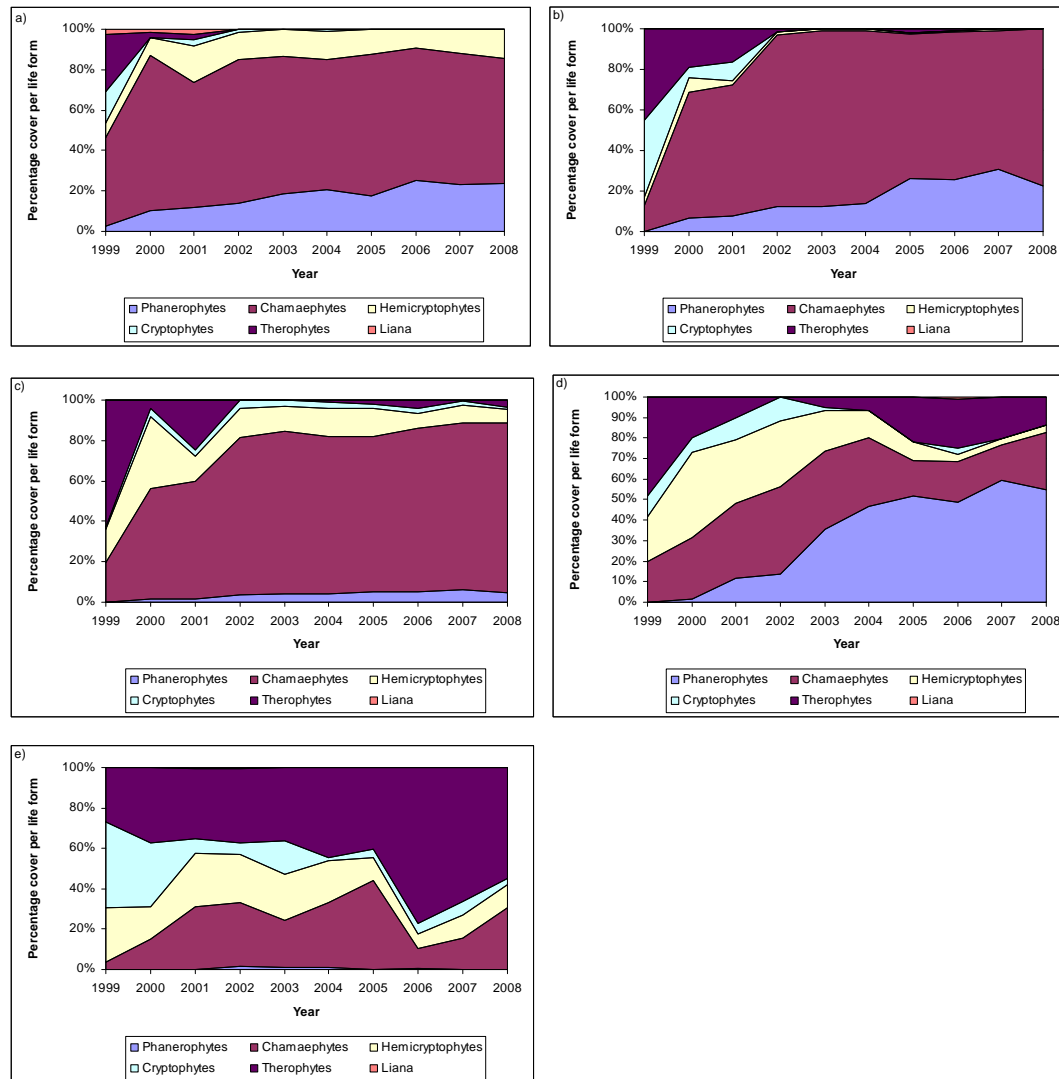


Figure 10.5 Percentage vegetation cover per life form expressed as a percentage of the total vegetation cover for post-fire monitoring transects: a) site 1, b) site 2, c) site 3, d) site 4; and e) site 5.

The prominent difference between site 4 and site 5 on Land Type Fa was the high cover contribution of phanerophyte species in site 4 and their near absence in site 5 (Figure 10.5d, 10.5e). This difference was due to the farmer removing all the *D. rhinocerotis* plants in site 5 in 2000 in order to limit their establishment and later dominance of the area. This intervention by the farmer has limited *D. rhinocerotis* to a few individuals and the percentage contribution of therophyte species to the vegetation cover is higher than in site 4 (Figure 10.5d, 10.5e). Also, species richness in site 5 was more than twice as high where the *D. rhinocerotis* individuals were removed (Figure 10.3). When considering only the perennial species, sites 1 to 4 had between five and ten perennial species in 2008, whereas 22 perennial species were encountered in site 5. Yet, at a vegetation cover level site 1 to site 4 had a perennial vegetation cover of between 47% and 71% while site 5 only had a perennial vegetation cover of 35.5%. In 2008, vegetation cover at site 5 was 79% of which 35.5% was contributed by

perennial species. In contrast, in 2008 at site 4 the total vegetation cover was 54.5%, but 47% was contributed by perennial species. Whether this annual dominated vegetation cover resulting from the removal of *D. rhinocerotis* is more desirable than the perennial *D. rhinocerotis* vegetation remains to be seen.

A Principal Co-ordinate Analysis of species compositional data for ten years following the fire at each post-fire monitoring transect produced varying results (Figure 10.6). There was, however, in all cases a clear spread along the two axes separating the ten years, with year 1 and year 2 found on the right hand side of the ordination diagram and subsequent years found towards the left of the ordination space. The three Da land type transects (site 1, site 2 and site 3) produced a similar ordination diagram in that year 1, year 2 and year 3 were spread progressively from the right hand side of the ordination diagram towards the left hand side of the ordination diagram (Figure 10.6a-c). Year 4 to year 10 occurred in various sequences however, in all cases towards the left hand side of the ordination space (Figure 10.6a-c).

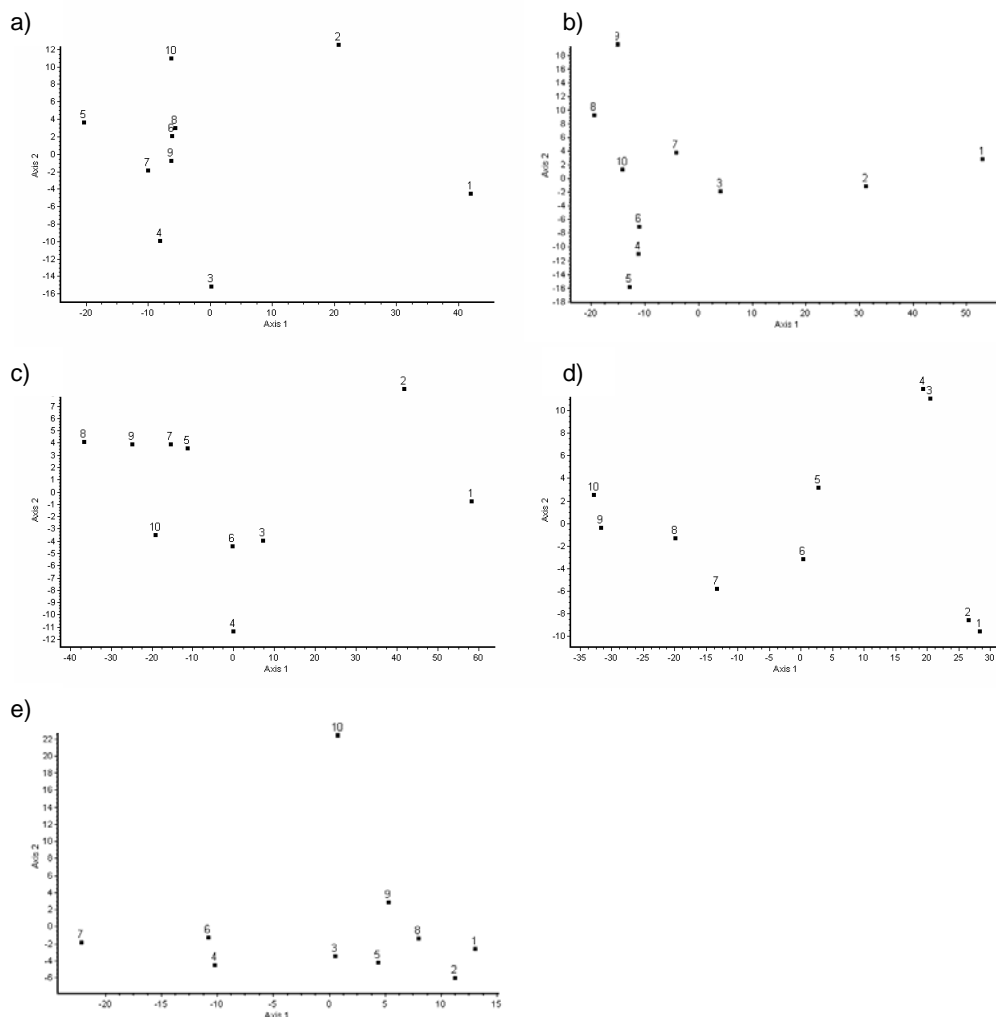


Figure 10.6 Principal Co-ordinate Analysis of species composition data for ten years (1-10) following a fire in the Roggeveld at post-fire monitoring transects: a) site 1, b) site 2, c) site 3, d) site 4 and e) site 5.

The two Land Type Fa transects (site 4 and site 5) were similar in that year 1 and year 2 occurred close together on the extreme right hand side of the ordination diagram (Figure 10.6d, 10.6e). The order of the subsequent years (year 3 to year 10) were chronologically spread out towards the left hand side of the ordination for site 4, but were rather haphazardly arranged for site 5 (Figure 10.6d, 10.6e). This haphazard arrangement in the ordination space of site 5 could be as a result of the removal of *D. rhinocerotis* seedlings in 2000.

These ordination results clearly indicated that in the first two years following fire, the species composition of all the survey transects were very different from the species composition in the subsequent years and that generally from year 3 to year 10, the species composition within a transect was more similar.

### 10.5 Conclusions

Vegetation began to establish within the first few months following fire in the Mountain Renosterveld vegetation of the Roggeveld. At all the post-fire monitoring sites, the vegetation cover remained higher from year 3 to year 10 than the vegetation cover found immediately following the fire (year 1 and year 2). Additionally, a single high rainfall year and three consecutive drought years had a large influence on the vegetation cover, increasing especially therophyte cover under good rainfall conditions and decreasing cover under poor rainfall conditions.

The total number of species per transect varied between 13 and 17 species within the first nine months following the fire. Species richness in most instances was highest (14 – 31 species) three years after the fire with chamaephyte species contributing the most throughout all the transects but, on the two Land Type Fa sites, therophyte species often contributed more to the total species richness of the transect.

Shannon index values generally ranged from 1.107 to 2.258 with one study transect an exception where the lowest Shannon value was 2.564 and the highest value 3.030. This transect also differed from the others in that the lowest Shannon value was found in the first year following fire and the highest value was found in the tenth year following the fire, all the other transects had the lowest Shannon values in year 9 and year 10 and the highest Shannon values in year 1 to year 3.

Temporal changes in life form composition were found at a species and vegetation cover level and depended on land type. Generally, at a species level, the phanerophyte and chamaephyte species contribution was higher on Land Type Da than on Land Type Fa, while therophyte species percentage contributions were higher on Land Type Fa than Land Type Da. Between the five post-fire monitoring transects, phanerophyte vegetation cover



contribution was highest on two transects on Land Type Da and one transect on Land Type Fa due to the dominance of *D. rhinocerotis*. Chamaephyte vegetation cover was highest on Land Type Da while therophyte or phanerophyte vegetation cover was highest on Land Type Fa.

A Principal Co-ordinate Analysis of species data for each survey plot, in all cases, placed year 1 and year 2 on the right hand side of the ordination diagram with the subsequent years spread along both axes towards the left hand side of the ordination space. This indicates the large difference in species composition between the first two years and subsequent years following fire.

These data seems to support Egler's (1954) 'initial floristic composition' model which states that all, or the majority of, species present during the succession are in place at the beginning of the recovery phase and re-establishment of the initial plant community is a rapid phenomenon (Capitanio & Carcaillet 2008).

## 10.6 Acknowledgements

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