4 Regeneration Strategies in Fynbos Plants and Their Influence on the Stability of Community Boundaries After Fire

B.W. van Wilgen and G.G. Forsyth

4.1 Introduction

An analysis of the range of regeneration strategies present in fynbos communities was a major aim of the work conducted at Swartboskloof. Information on the mechanisms whereby plants survive fire (e.g. Bell et al. 1984) and the attributes which allow them to persist in vegetation subjected to repeated fire (e.g. Noble and Slatyer 1980) is required to develop a sound understanding of the dynamics of vegetation subjected to fire. Such information is often only available for all of the plants if the communities are species-poor (e.g. Hobbs et al. 1984). In species-rich communities, it is usually the case that detailed information is only available for the dominant plants. A detailed knowledge of the responses of the constituent species in fynbos is restricted to the dominant shrubs of the family Proteaceae (e.g. Bond et al. 1984). A few studies have listed survival mechanisms in other species (van der Merwe 1966; van Wilgen 1981; van Wilgen and Kruger 1981), but data on other vital attributes (juvenile periods, longevity, modes of seed dispersal, and seed bank longevity) are not available for the vast majority of fynbos species. Fynbos has a rich diversity of species, and fynbos communities may differ in the spectrum of responses (and therefore in their vulnerability to fire). In this chapter we quantify the range of regeneration strategies manifested in a sample of fynbos plants subjected to fire, and examine the differences between major vegetation communities in terms of these strategies. We also compare the data to those collected in other fire prone ecosystems.

4.2 Survival Mechanisms and Vital Attributes of Species

4.2.1 Systems for the Classification of Species

Several systems for the classification of plant species responses to fire have been developed (e.g. van der Merwe 1966; Noble and Slatyer 1980; Gill

1981a; Bell et al. 1984). In this study we examined the responses of plants and communities to fire in terms of the systems described by Bell et al. (1984) and Noble and Slatyer (1980). The systems are outlined briefly below.

Bell et al. (1984) defined five categories of species response to fire. Fire ephemerals (FE) include monocarpic therophytes and annuals, or short-lived polycarpic perennials which exhibit a degree of fire-stimulated germination. They have fast growth rates, early reproductive maturities, high reproductive efforts proportional to biomass, and relatively short (<4 years) life spans. Obligate seeders (OS) are long-lived (>15 years) and are likely to have their growth cycle terminated prematurely by fire, as they do not possess the ability to sprout. Sprouting species are a diverse group, and three categories are recognized. Obligate vegetative reproducing sprouters (OVS) display great powers of multiplication by vegetative (non-sexual) means, but virtually no ability to reproduce by seed. Facultative sprouter-seeders (FSS) sprout weakly, or only after mild fires, but recruitment from seed is highly effective. Autoregenerating long-lived sprouters (ALS) are both successful sprouters, and generate moderately dense stands of seedlings after fire.

Noble and Slatyer (1980) regarded a set of attributes as important in determining the response of a species to disturbance. These included (1) mechanism of persistence during a disturbance, or arrival of propagules afterwards; (2) ability to become established either immediately after a disturbance or later in the post-fire development; (3) the timing of critical life-history events. In regard to the first of these, species are divided into:

D species: arrival of widely dispersed seeds;
S species: seeds with a long viability, stored in the soil;
C species: seeds with short viability surviving disturbance within protective fruits or cones;
V species: persistence by part of the individual surviving the disturbance, and recovery by vegetative growth, with immature tissue;
U species: as for V species, but sprouting mature tissue;
Δ species: a species with both D and U characteristics.

Similarly, three sets of species were recognized in respect of the second group of attributes:

T species: tolerant species, able to establish at any time, tolerating competition with adults of the same or other species;
I species: intolerant species, able to establish only immediately after disturbance, when competition is reduced;
R species: requiring species, unable to establish immediately after a disturbance, but able to establish once mature individuals of the same or other species are present.

Thirdly, with reference to the times taken to reach certain stages in life history, the following were regarded as critical:

1. The time when a disturbance occurs (o) and the time for propagules to become available on a disturbed site (p);
2. The time taken for individuals to reach reproductive maturity (m);
3. The life span of individual plants of the species (l);
4. The time taken for all propagules to be lost from the community (e.g. for the seed store to become depleted) and for the species to become locally extinct (e).

4.2.2 Selection and Characterization of Species

We studied pre-fire composition and post-fire succession on ten permanently marked quadrats (5 × 10 m). These were placed in proteoid and ericoid-restioid shrublands prior to the March 1987 fire in Swartboskloof (see Fig. 1.3). Quadrats were surveyed once before the fire, and at intervals of 9, 18 and 30 months after the fire. Post-fire surveys were done in the spring (except the first one), when most species are in flower. At each survey, all the plant species occurring on the quadrats were identified and listed. Two more quadrats were laid out in the specialized hygrophilous communities after the 1987 fire, and these were also surveyed at three intervals after the fire.

The quadrats were subdivided into 50 sub-plots of 1 m^2 each. At each survey, the maximum height of the vegetation, and an ocular estimate of the percentage canopy cover was made on each of the 50 sub-plots within each quadrat. In addition, the three dominant species (in terms of visual estimates of live biomass) were listed and ranked on each sub-plot. Species were allocated importance values in proportion to their rank, as follows: rank 1 = 1, rank 2 = ⅔ and rank 3 = ⅓. These importance values were used in comparisons of the relative contribution of fire survival strategies and vital attributes between the major vegetation communities (see below).

We recorded the mode of post-fire regeneration (whether from seed or sprouting) and the date of first flowering after fire for each of the species. Each species was assigned a fire response category, and a description of the mechanism of persistence, based on morphological observations. Non-sprouting species were classified as either C, D, or S based on seed morphology and seed shed characteristics. C species are those where the seeds are retained on the parent plant; D species those with structures (such as wings or pappi) that enable the dispersal of seeds, or fruits that are dispersed by birds. The remaining non-sprouting species were classified as S species. Age to maturity (first flowering), where this was 3 years or less, was obtained from the quadrat data. For species that took longer to mature, data on age to maturity was obtained by searching for mature specimens of

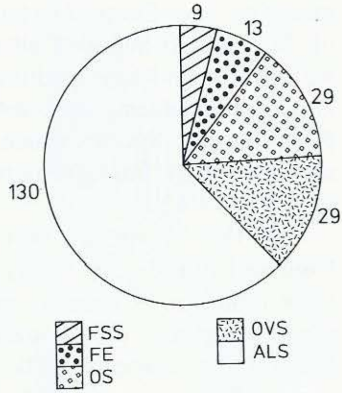

Fig. 4.1. Distribution of fire-response types among 210 plant species from Swartboskloof. The fire-response types are: *ALS* autoregenerating long-lived sprouters; *FE* fire ephemerals; *FSS* facultative sprouter-seeders; *OS* obligate seeders; OVS obligate vegetative reproducing sprouters. The number of species in each life-form is indicated on the diagrams

the species in adjacent areas of known post-fire ages. In addition, the comprehensive herbarium collection at Jonkershoek was searched for data on maturity. Data on longevity were obtained in a similar manner, but for species with longevities that exceeded 45 years (the longest that vegetation in the Jonkershoek valley had survived fire), longevity was simply given as >50 years. Fynbos that survives fire for longer than 50 years is almost unknown, and this assumption will have no effect on comparisons of fire frequencies of less than 50 years. For species which rely on soil-stored seed banks to regenerate, seed bank longevity was estimated as greater than the period between longevity and the occurrence of fire, where the given species was known to have regenerated after fire. For other species, seed bank longevity data were not considered essential to the analysis.

4.3 Results and Discussion

4.3.1 Spectra of Fire Response and Vital Attribute Types

Swartboskloof contains 651 indigenous species of flowering plants and ferns (McDonald and Morley 1988). We encountered 210 species on the 12 quadrats (Appendix 4.1). The most important fire response category (Fig. 4.1) was autoregenerating long-lived sprouters (62% of the species). This category included all of the species where all or most individuals sprouted after fire, and where seedlings of the species appeared after fire. The fate of the seedlings is not known, and many may die before they reach maturity (see Chap. 7). Obligate vegetative reproducing sprouters (14% of the species) included all species which sprouted strongly, but for which we did not find any seedlings. Of the 29 species classified as obligate vegetative reproducing sprouters, 16 were perennial herbs from the family Restionaceae. Species which reproduced by seed were made up by obligate seeders (14%), fire ephemerals (6%) and facultative seeder-sprouters (weak sprouters, 4%).

Of the 51 species that reproduce from seed, most (31) regenerate from soil-stored seed banks (SI and ST, Fig. 4.2). Widely dispersed seeds were found in 18 species, and canopy-stored seeds in only 2 species. Most sprouting species (70%) matured within the first year, and were classified as either U or Δ species. The remainder were classified as V species. Most species (91%) were classified as intolerant (I), while some (7%) were able to establish in mature vegetation and were classified as tolerant (T). Only five species (2%) were classified as requiring (R) a mature overstorey to establish from seed. Obligate vegetative reproducing sprouters were classified as I, but as no seedlings were found, they could be R species. Such a strategy would imply that the species only establish as seedlings if fire-free intervals are very long, as is the case with such species in Californian chaparral (Keeley 1986).

4.3.2 Age at Maturity

Of the 210 species, most (86%) flowered in the first year after fire; a further 7% flowered in the second, 5% in the third, 1% in the fourth, and 2% in the fifth year after fire. Almost all of the sprouting species (148 of 159 species) flowered in the first year after fire. Non-sprouting species were somewhat slower to mature, with 30, 10, 6, 2, and 3 out of 51 species flowering in the first, second, third, fourth and fifth years respectively.

4.3.3 Longevity of Individuals and Seed Banks

Most species in Swartboskloof are long-lived; 173 of the 210 species occur in vegetation with a post-fire age of >45 years as mature, long-established individuals. Twenty species were short-lived (<10 years), and only one annual species (*Sebaea exacoides*) occurred. There were 18 species of moderate longevity (15–40 years). Seed bank longevities were estimated only for those species that rely totally on a soil-stored seed bank in order to survive fires (see Appendix 4.1). Short-lived species, such as some *Aspalathus*, *Roella*, and *Thesium* species, must have fairly long-lived seed banks as they disappear early in the post-fire succession, and reappear after fire from the soil-stored seed bank. For longer-lived species, such as some *Blaeria*, *Cliffortia* and *Phylica* species, seed bank longevity could be much

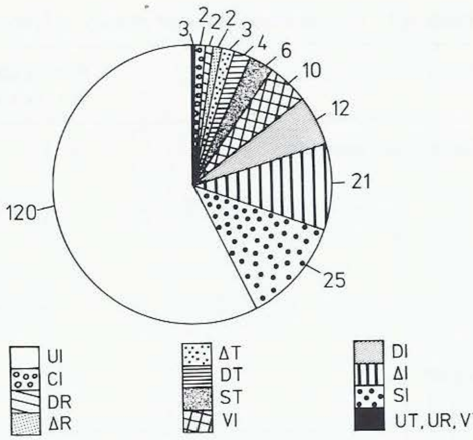

Fig. 4.2. Distribution of vital attribute types among 210 plant species from Swartboskloof. Each type indicates both the method of persistence and the requirement for establishment. The methods of persistence are: *C* canopy-stored seeds; *D* dispersed seeds; *S* soil-stored seeds; *U* sprouting mature tissue; *V* sprouting immature tissue; and Δ U and D features combined. The requirements for establishment are: *I* intolerant; *T* tolerant; and *R* requiring. The number of species in each type is indicated on the diagram

shorter. The population sizes of these species, and many *Erica* species, decline markedly with increasing age, but some individuals do remain in old vegetation.

4.3.4 The Timing of Critical Life History Events

The time at which plants reach critical stages in their life histories can be summarized with reference to the five recognized phases of post-fire succession in fynbos (Kruger and Bigalke 1984; Table 4.1). We recognized nine fire-response patterns (Table 4.2). A given pattern may apply to a range of different vital attributes or fire-response types, as illustrated in Table 4.2. Each of the patterns is discussed below.

The first pattern was the most common, and applied to 160 of the 210 species in the sample. These species persist on, or return to the site and mature within the youth period (1 year after fire). They have life spans in excess of 50 years, or are able to establish in the interfire period, and are found at all stages of the post-fire succession. The vast majority of these species have the ability to sprout, and are classified as ALS or OVS in terms of fire-response types, and as UI or ΔI in terms of vital attributes. Species classified as UI and ALS (the most common combination) may differ considerably in their ecology, although the survival mechanisms and outcomes of disturbances at different stages of their life cycles remain the same. Consider for example *Maytenus oleoides* (a tree) and *Cyrthanthus ven-*

Table 4.1. Post-fire successional phases in fynbos (After Kruger and Bigalke 1984)

Phase	Period after fire (years)	Characteristics
Immediate post-fire	0–1	Seed germination and vegetative regeneration takes place. Most annuals and some geophytes reproduce only in this phase.
Youth	1–5	Graminoid herbs and sprouting shrubs dominate. Canopy cover approaches pre-fire levels.
Transitional	5–10	All plants reach reproductive maturity. Non-sprouting shrubs emerge from the canopy.
Mature	10–30	Tall shrubs reach maximum height and flowering activity. Low shrubs begin to die.
Senescent	30–60?	Mortality of tall shrubs accelerates. Crowns open and litter builds up.

tricosus (a geophyte). Both sprout after fire, and both are long-lived. *Maytenus*, where it occurs, remains a dominant feature of the above-ground vegetation, and flowers and produces fruit annually. *Cyrthanthus*, on the other hand, flowers only immediately after fires, and appears to survive even long interfire periods as a dormant bulb. The first pattern also applies to a small number of long-lived, non-sprouting species, which are killed by fire.

The second pattern is almost identical to the first, but contains species which mature in the immediate post-fire phase (2–5 years after fire), rather than in the first year after fire. About half of these species possess the ability to sprout. The non-sprouters include plants such as the three *Cliffortia* species, which are long-lived but establish only immediately after fire, and

Table 4.2. Fire-response patterns (illustrated by the timing of critical life history events) in 210 species in Swartboskloof, and the range of vital attributes (Noble and Slatyer 1980) and fire-response types (Bell et al. 1984) in each response pattern

Phase of fynbos succession[a] Immediate post-fire	Youth	Transitional	Mature	Senescent	Vital attributes[b]		Fire-response types[b]		Total number of species
opm				le	UI	(122)	ALS	(122)	160
					ΔI	(21)	OVS	(26)	
					ST	(5)	OS	(10)	
					DT	(3)	FSS	(2)	
					SI	(4)			
					ΔT	(2)			
					UR	(1)			
					UT	(1)			
					ΔR	(1)			
op	m			le	SI	(10)	OS	(10)	24
					VI	(8)	ALS	(7)	
					DI	(2)	FSS	(4)	
					ΔT	(1)	OVS	(3)	
					ST	(1)			
					DT	(1)			
					VT	(1)			
opm	l			e	SI	(6)	FE	(11)	11
					DI	(5)			
opm			l	e	DI	(4)	OS	(5)	6
					SI	(2)	FSS	(1)	
o		p	m	le	DR	(2)	FSS	(2)	3
					ΔR	(1)	ALS	(1)	
op	m		l	e	DI	(1)	OS	(2)	2
					SI	(1)			
op	m		le		CI	(2)	OS	(2)	2
op	m	l		e	SI	(1)	FE	(1)	1
opm		l		e	SI	(1)	FE	(1)	1

[a] Symbols for critical life history events are: (o), time of disturbance; (p), time at which propagules are available on site; (m), time at which reproductive maturity is reached; (l), local loss of individuals from the community; (e), local extinction from the community.
[b] Abbreviations for vital attributes and fire-response types are explained in the text; number of species in parentheses.

Chrysanthemoides monilifera, which is short-lived but can establish between fires. Sprouting species exhibiting this pattern were classified as V in terms of the mechanism of persistence, as opposed to U, which applies to the first pattern.

The third pattern contains most of the plants classified as fire ephemerals. These species all establish from seed after fire. They complete their life cycles within the immediate post-fire phase, but none are annuals. They then either persist as soil-stored seeds, or disperse back to the site from adjacent areas after the next fire. Of the species that are able to disperse widely, two are exotics; the other three are herbaceous Asteraceae species.

The fourth and sixth patterns are similar, and represent non-sprouting plants that either flower within the first year of fire, or shortly thereafter, respectively. Some of these species, such as *Helichrysum cymosum*, *Pelargonium elongatum* and two *Senecio* species, possess the ability to disperse back into the site after fire. Some, such as *Blaeria dumosa*, and *Pentaschistis malouinensis* rely on a soil-stored seed bank. There are no data on the longevity of soil-stored seed banks for any of the species concerned, and this represents a critical gap in the ability to predict the effects of long interfire periods. *Sebaea exacoides*, the only annual species we encountered, fits this pattern as it is able to establish in the interfire period.

The fifth pattern applies to species which require an overstorey of mature vegetation to establish, and includes two trees (*Maytenus acuminata* and *Kiggelaria africana*) and one shrub (*Myrsine africana*). Seeds of these species are dispersed by birds and establish in the transitional phase of fynbos succession. The two tree species need to reach a large size before they can survive fires by sprouting, but it is possible that, given long (>50 years) interfire periods, the species could establish and create foci for further colonization by tree species with bird-dispersed propagules. Such foci would be fire-resistant (van Wilgen et al. 1990b) and could lead to the establishment of clumped forest patches.

The seventh pattern is essentially the same as the third. It represents plants which could best be described as long-lived fire ephemerals. These plants all regenerate from soil-stored seed banks, and complete their life cycles before the mature stage of fynbos succession is reached. Although no data on seed longevity are available, seed banks must persist for up to 40 years in some cases, as abundant regeneration occurs at some sites after long fire-free periods. The ninth pattern applies to only one species (*Aspalathus ciliaris*), which is a long-lived fire ephemeral that matures in the second year after fire.

The eighth pattern describes two shrub species (*Protea repens* and *P. neriifolia*) which are killed by fire, and rely on seed banks stored in the canopies of the shrubs for regeneration. The species have moderately long life spans (up to 35 years), but seed banks do not persist beyond the life span of the adults. The species will thus not survive fires which occur at intervals of longer than 35 years. Secondly, although the species mature within 3 to 4 years after fire, it takes at least 10 years for adequate seed banks to build up in the canopies of plants. Of the 210 species, these two species were considered the most vulnerable to both short and long interfire periods. Should the species be lost from the community, they represent a small proportion of the total diversity. However, they can contribute up to 89% of the above-ground and 53% of the below-ground biomass in some communities in Swartboskloof respectively (van Wilgen 1982; Higgins et al. 1987). The dominance of these species, combined with their relative vulnerability, has led to fire frequencies in fynbos being prescribed to accommodate these species.

4.3.5 Differences Between Communities

We examined the relative contribution of various categories of fire survival strategies and vital attributes to each of the major vegetation communities (see Chap. 1). The quadrat data from both pre- and post-fire surveys were divided into proteoid shrublands (five quadrats), ericoid-restioid shrublands (three quadrats), specialized hygrophilous communities (two quadrats), and a frequently burnt firebreak (one quadrat). For each sub-set thus defined, the contribution of each category of fire survival strategy and vital attributes to the community as a whole was examined in two ways. Firstly, the number of species in each category was listed for the combined pre- and post-fire data. Secondly, the relative contribution of the various categories in terms of surrogate measures of biomass was calculated for the pre-fire and last post-fire surveys. To do this, importance values for each species on each sub-plot (see above) were totalled per species for each quadrat. A surrogate measure of live biomass was calculated for each species, by multiplying the total importance value (described above) of each of the species per quadrat by the mean cover and height of the vegetation for that quadrat. Data for the quadrats were then pooled to obtain means, and summarized by vital attributes and fire survival strategies for each of the major communities.

The communities are remarkably similar in terms of the proportions of species in each of the categories (Figs. 4.3 and 4.4). Obligate seeders and fire ephemerals were less prominent in the firebreak and hygrophilous communities, but differences were not great. Similarly, the relative composition in terms of vital attributes was similar in all communities.

A total of 197 species were encountered on the ten quadrats that were surveyed pre-fire (the two quadrats in hygrophilous communities were not enumerated pre-fire). Of these, 134 occurred pre-fire, and 193 post-fire. Changes in the composition of the vegetation after the fire were not great, and similarity of pre- and post-fire vegetation ranged from 72 to 89% (Table 4.3) on the ten quadrats surveyed. Most of this difference is explained by the addition of new species post-fire. While 63 species were added to the list, only 4 species disappeared.

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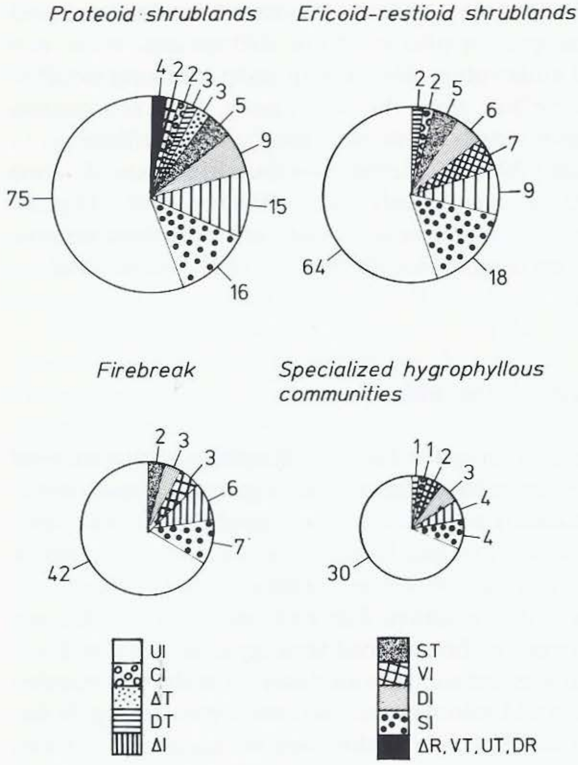

Fig. 4.3. The relative contribution of species, in terms of vital attributes, to four vegetation communities in Swartboskloof. The size of the circle reflects the total number of species encountered. The number of species in each category is indicated on the diagrams; abbreviations as in Fig. 4.2

Table 4.3. An analysis of the pre- and post-fire species composition on 10 × 10 m quadrats in three vegetation communities subjected to fire in Swartboskloof

Community	Number of species pre-fire	Number of species post-fire	Species lost after fire	Species gained after fire	Total species	Pre- to post-fire similarity (Sorenson's index)
Proteoid shrublands	88	131	3	46	134	77.6
Ericoid shrublands	67	109	4	46	113	71.6
Firebreak	53	60	3	10	63	88.5
Entire survey	134	193	4	63	197	81.7

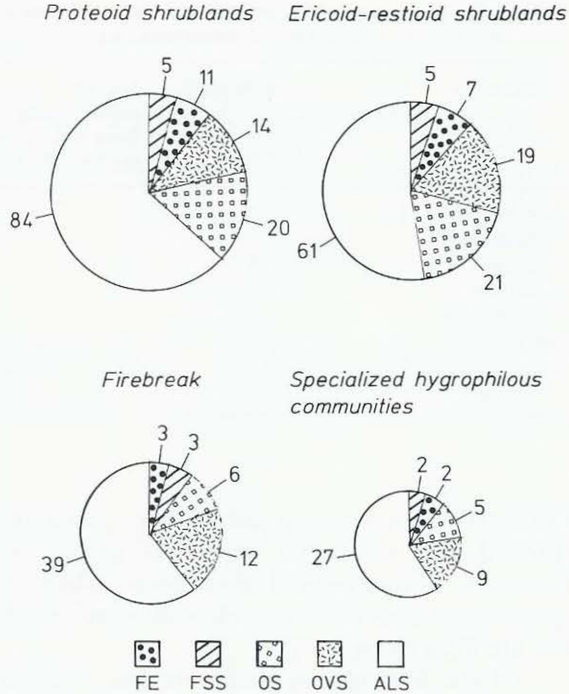

Fig. 4.4. The relative contribution of species, in terms of fire-response types, to four vegetation communities in Swartboskloof. The size of the circle reflects the total number of species encountered. The number of species in each category is indicated on the diagrams; abbreviations as in Fig. 4.1

All of the communities examined had more species after fire than before fire. The species that appeared after the fire were either fire ephemerals (regenerating from widely dispersed or soil-stored seed banks), geophytes (which were probably present as dormant bulbs but were undetected pre-fire), species that were present as soil-stored seed pools, or species with the ability to colonize the site by means of soil-stored seed banks (Table 4.4). Examples of the dispersed species include fire ephemerals such as *Ursinia pinnata*, *Solanum tomentosum* and *Senecio pubigerus*. Examples of species regenerating from seed pools includes all species of *Thesium*, *Roella ciliata* and *Aspalathus ciliaris*. Many geophytes, such as *Bulbine tuberosa*, *Cyrtanthus ventricosus*, *Ornithogalum hispidum* and *Urginea dregei*, flowered after the fire, but were either dormant, or remained undetected as they were inconspicuous before the fire. Some species that were added to the list were classified as long-lived sprouters, and should have been present before the fire. These may either have been overlooked in the dense vegetation before the fire, or may have regenerated from seed. Similar numbers of species were added to both the proteoid and ericoid-restioid shrubland communities

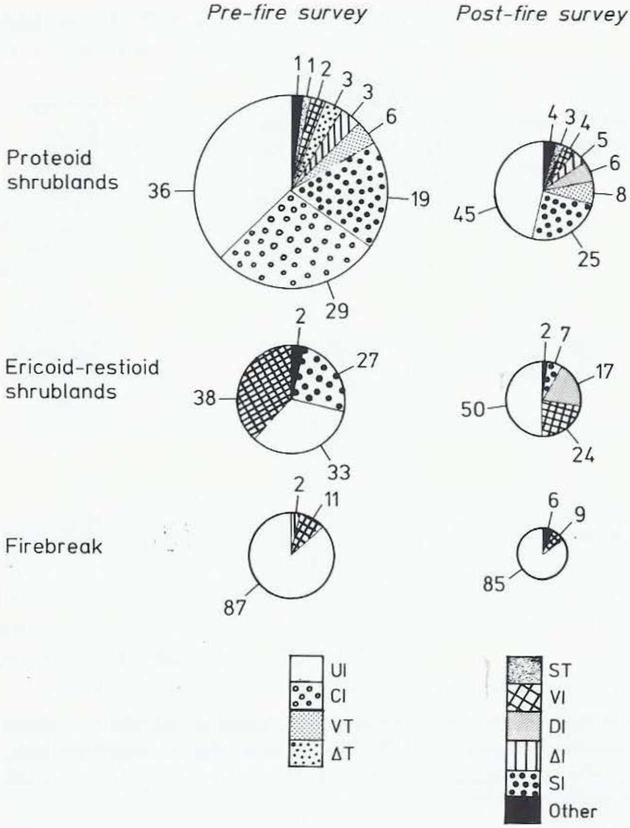

Fig. 4.6. The relative contribution of vital attributes, in terms of biomass, to three vegetation communities immediately before and 30 months after fire in Swartboskloof. The size of the circle reflects the relative biomass. The relative contribution (%) of each category is indicated on the diagrams; abbreviations as in Fig. 4.2

shrublands. The single species eliminated in specialized hygrophilous communities is *Protea neriifolia*, which occurred post-fire as isolated seedlings. None of the species occurring in the frequently burnt firebreak are eliminated by any fire frequency, as sensitive species no longer occur there. In all of the communities, some species are listed as potentially eliminated by long interfire periods. These are species with a longevity less than the fire frequency concerned, which rely on soil-stored seed pools for regeneration after fire. In the absence of data on seed pool longevity, these species can only be considered as potential losses from the community.

The hypothesis that a given fire frequency would favour one community over another is not supported by the above data. All communities are maintained by fire frequencies between 10 and 20 years, and no community is favoured over another by a given fire regime, so that other factors must

Table 4.5. The fate of species in four vegetation communities subjected to fire at different frequencies. Data show the number of species in each category. The species listed as potentially eliminated represent species for which data on seed bank longevity are not available

Fire frequency (yr)	5	10	15	20	25	30	35	40	45	50
Proteoid shrublands										
Species eliminated	3	1	1	1	0	0	0	2	2	2
Species potentially eliminated	0	0	7	8	8	8	8	9	12	12
Species surviving	131	133	126	125	126	126	126	123	120	120
Ericoid-restioid shrublands										
Species eliminated	2	0	0	0	0	0	0	3	3	3
Species potentially eliminated	0	0	5	5	5	6	6	8	12	12
Species surviving	111	113	108	108	108	107	107	105	101	101
Specialized hygrophilous communities										
Species eliminated	1	0	0	0	0	0	0	1	1	1
Species potentially eliminated	0	0	1	1	1	1	1	2	2	2
Species surviving	44	45	44	44	44	44	44	43	43	43
Firebreak										
Species eliminated	0	0	0	0	0	0	0	0	0	0
Species potentially eliminated	0	0	1	2	2	3	3	4	4	4
Species surviving	63	63	62	61	61	60	60	59	59	59
Entire survey										
Species eliminated	4	2	2	2	0	0	0	2	2	2
Species potentially eliminated	0	0	9	10	10	11	11	13	17	17
Species surviving	206	208	199	198	200	199	199	195	193	193

govern the extent of communities. While vegetation structure can be radically altered by changes in fire frequency through the elimination of non-sprouting *Protea* shrubs, it is only in the case of long intervals between fire that, for proteoid shrublands at least, a transition to forest is possible. This question is addressed in more detail in Chapter 5.

4.3.7 Comparison to Other Fire-Prone Shrublands

The flora of the Mediterranean Basin, and the Chilean mattorral, differs from the fynbos in the almost complete absence of non-sprouting plants (Keeley 1986; see also Chap. 7). Californian chaparral differs from fynbos in having an abundant annual flora, a paucity of sprouting herbaceous perennials, and very few non-sprouters that rely on canopy-stored seeds for survival (Keeley 1986). Unlike fynbos, chaparral non-sprouting shrubs are largely resilient to extended fire-free intervals of 100 years or more. Keeley

Table 4.6. The number of plant species in five fire-response categories in Swartboskloof, Australian kwongan (Bell et al. 1984) and Scottish heathland (Hobbs et al. 1984)

Fire-response category	Swartboskloof	Kwongan	Heathland
Fire ephemerals	13	20	0
Obligate seeders	29	31	2
Facultative sprouter-seeders	9	15	2
Autoregenerating long-lived sprouters	130	67	20
Obligate vegetative reproducing sprouters	29	18	3
Total species	210	151	27

(1986) also compared the range of post-fire regeneration characteristics for shrublands in mediterranean-climate regions of California, the Mediterranean Basin, Chile, South Africa and Australia. He rated the relative abundance of plants with soil-stored seeds as low, and those with seed storage on the plant as very abundant in fynbos shrublands. The data for Swartboskloof show that, in terms of the number of species present, soil-stored seed is the more important strategy. Fynbos does not necessarily have an abundance of species which store seeds on the plant, but the vegetation is often dominated by a few species which employ this strategy. Keeley also lists seeding herbaceous perennials as absent in fynbos, but the data for Swartboskloof show that some perennial re-seeding grasses (*Pentaschistis* and *Pentameris* species) do occur.

Data sets suitable for direct comparison with the data from Swartboskloof are rare, but two examples from Australian kwongan shrublands and Scottish heathlands are given in Table 4.6. The proportion of plants that sprout is higher in fynbos than in kwongan, and the proportion of non-sprouting plants and ephemerals is correspondingly lower in fynbos. The diversity of fynbos and kwongan, both in terms of the number of species and the range of fire-response types, is high in comparison to the depauperate Scottish heathlands. The heathlands also lack ephemerals, and have a very high proportion (85%) of sprouting plants.

4.3.8 Fire, Resilience and Dynamics in Fynbos

The resilience (i.e. the ability to return to the pre-fire equilibrium state) of vegetation is a function of species-specific mechanisms (Keeley 1986). Frequent perturbation often selects for species which specialize, and even become dependent on, the relevant disturbance regime. How resilient is fynbos, and how is this reflected in the spectrum of survival types? Most fynbos species are able to sprout. Sprouters can tolerate large deviations from normal fire frequencies, as they are long-lived and basically unaffected by fire. Fire ephemerals and other non-sprouters that rely on soil-stored seed banks may be vulnerable to long interfire periods that exceed the life span of the seeds. The two non-sprouting *Protea* species are vulnerable to both short and long interfire periods, and are therefore the least resilient component of the vegetation. The genera *Protea* and *Leucadendron* often employ the remarkably tenuous CI method of persistence and establishment after fire, and are frequently dominant in fynbos. This indicates evolution in an environment subjected to a narrow range of fire frequency between 10 and 30 years.

Data on the vital attributes of species can be used to predict the presence or absence of species given different frequencies of disturbance. However, the relative abundance of species within a community cannot be predicted from this knowledge. In addition, variation in the season and intensity of fires can have different effects on plant species under similar fire frequencies. The dynamics of fynbos ecosystems in relation to fire is currently best understood in the case of the Proteaceae, where it has been shown that fire frequency alone cannot explain the variation in recruitment observed after fires in different seasons (Bond et al. 1984), or of different intensities (Bond et al. 1990). In addition, the size of the seed bank varies considerably at different stages within the "mature" period (Kruger and Bigalke 1984), and this will affect the relative size of post-fire populations. Models of the factors controlling species coexistence are currently being developed for the Proteaceae, and these offer a substantial advancement in understanding the dynamics of populations of fynbos plants in relation to fire (Cowling and Gxaba 1990; Yeaton and Bond 1991). However, for many other groups of plants, little or nothing is known of the factors controlling their dynamics in relation to fire. For example, the genus *Erica* has many species which rely on soil-stored seed banks for regeneration, but there are no data on the seed production rates or seed bank dynamics of members of this genus. Data on the range of regeneration strategies, as presented here, represent a starting point from which the dynamics of the vegetation in relation to fire can be examined. However, the data are at best rudimentary for the provision of a sound understanding of vegetation dynamics. Future research should concentrate on selected species within the major fire response patterns (Table 4.2) in order to improve the understanding of fynbos dynamics in relation to fire.

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Appendix 4.1. Life-forms, fire survival types and vital attributes for 210 species in Swartboskloof. Seed longevity is only given for species which rely on soil-stored seed banks for survival

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
SCHIZAEACEAE						
Schizaea pectinata	H	ALS	ΔI	1	>50	–
DENNSTAEDTIACEAE						
Pteridium aquilinum	H	ALS	ΔT	1	>50	–
ADIANTACEAE						
Pellaea pteroides	H	ALS	ΔT	1	>50	–
CUPRESSACEAE						
Widdringtonia nodiflora	P	ALS	VI	5	>50	–
PINACEAE						
Pinus radiata (*)	P	OS	DT	5	>50	–
ALLIACEAE						
Agapanthus africanus	EG	ALS	UI	1	>50	–
AMARYLLIDACEAE						
Cyrtanthus ventricosus	DG	ALS	UI	1	>50	–
Haemanthus coccineus	DG	ALS	UI	1	>50	–
ASPARAGACEAE						
Protasparagus rubicundus	DG	ALS	UT	1	>50	–
ASPHODELACEAE						
Bulbine tuberosa	DG	ALS	UI	1	>50	–
Caesia contorta	H	ALS	UI	1	>50	–
Trachyandra hirsutiflora	DG	ALS	UI	1	>50	–
Trachyandra hirsuta	DG	ALS	UI	1	>50	–
Trachyandra tabularis	DG	ALS	UI	1	>50	–
CYPERACEAE						
Ficinia deusta	H	ALS	UI	1	>50	–
Ficinia filiformis	H	ALS	UI	1	>50	–

Ficinia nigrescens	H	ALS	UI	1	>50	–
Macrochaetum hexandrum	H	ALS	UI	1	>50	–
Neesenbeckia punctoria	H	OVS	UI	1	>50	–
Tetraria bromoides	H	ALS	VI	2	>50	–
Tetraria burmanii	H	ALS	UI	1	>50	–
Tetraria capillacea	H	ALS	UI	1	>50	–
Tetraria compar	H	ALS	UI	1	>50	–
Tetraria crassa	H	ALS	UI	1	>50	–
Tetraria cuspidata	H	ALS	UI	1	>50	–
Tetraria fasciata	H	ALS	UI	1	>50	–
Tetraria fimbriolata	H	ALS	UI	1	>50	–
Tetraria ustulata	H	ALS	UI	1	>50	–
HAEMODORACEAE						
Dilatris pillansii	EG	ALS	UI	1	>50	–
Wachendorfia paniculata	DG	ALS	UI	1	>50	–
HYACINTHACEAE						
Albuca canadensis	DG	ALS	UI	1	>50	–
Lachenalia orchioides	DG	ALS	UI	1	>50	–
Ornithogalum hispidum	DG	ALS	UI	1	>50	–
Urginea dregei	DG	ALS	UI	1	>50	–
HYPOXIDACEAE						
Spiloxene capensis	DG	ALS	UI	1	>50	–
IRIDACEAE						
Anapalina triticea	DG	ALS	UI	1	>50	–
Aristea africana	MiCh	OS	SI	1	15	>35
Aristea major	EG	ALS	UI	1	>50	–
Aristea spiralis	EG	ALS	UI	1	>50	–
Bobartia gladiata	EG	ALS	UI	1	>50	–
Bobartia indica	EG	ALS	UI	1	>50	–
Geissorhiza aspera	DG	ALS	UI	1	>50	–
Gladiolus blommesteinii	DG	ALS	ΔI	1	>50	–
Gladiolus carneus	DG	ALS	ΔI	1	>50	–
Micranthus alopecuroides	DG	ALS	UI	1	>50	–
Moraea bituminosa	DG	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Moraea tricuspidata	DG	ALS	UI	1	>50	–
Thereianthus spicatus	DG	ALS	UI	1	>50	–
Tritonia crispa	DG	ALS	UI	1	>50	–
Watsonia borbonica	DG	ALS	UI	1	>50	–
ORCHIDACEAE						
Acrolophia capensis	EG	OVS	UI	1	>50	–
Schizodium obliquum	DG	ALS	ΔI	1	>50	–
POACEAE						
Cymbopogon marginatus	H	ALS	UI	1	>50	–
Ehrharta bulbosa	EG	ALS	UI	1	>50	–
Ehrharta dura	H	ALS	UI	1	>50	–
Ehrharta ramosa	H	FSS	SI	1	>50	–
Festuca scabra	EG	ALS	UI	1	>50	–
Merxmuellera cincta	H	ALS	UI	1	>50	–
Merxmuellera rufa	EG	ALS	UI	1	>50	–
Merxmuellera stricta	H	ALS	UI	1	>50	–
Pentameris macrocalycina	H	ALS	UI	1	>50	–
Pentameris thuarii	H	FSS	SI	2	>50	–
Pentaschistis aristidoides	EG	ALS	UI	1	>50	–
Pentaschistis colorata	H	ALS	UI	1	>50	–
Pentaschistis curvifolia	H	FSS	SI	1	>50	–
Pentaschistis malouinensis	H	FSS	SI	1	25	>25
Pentaschistis pallescens	H	ALS	UI	1	>50	–
Themeda triandra	H	ALS	UI	1	>50	–
RESTIONACEAE						
Calopsis membranaceus	H	OVS	VI	2	>50	–
Cannomois virgata	H	OVS	UI	1	>50	–
Elegia asperiflora	H	OVS	UI	1	>50	–
Elegia juncea	H	OVS	UI	1	>50	–
Hypodiscus albo-aristatus	H	OVS	UI	1	>50	–

Hypodiscus aristatus	H	OVS	UI	1	>50	–
Hypodiscus willdenowia	H	OVS	UI	1	>50	–
Ischyrolepis capensis	H	OVS	UI	1	>50	–
Ischyrolepis gaudichaudiana	H	OVS	UI	1	>50	–
Ischyrolepis sieberi	H	OVS	VI	2	>50	–
Platycaulos depauperatus	H	ALS	UI	1	>50	–
Restio filiformis	H	OVS	UI	1	>50	–
Restio triticeus	H	OVS	UI	1	>50	–
Staberoha cernua	H	OVS	UI	1	>50	–
Thamnochortus fruticosus	H	OVS	UI	1	>50	–
Thamnochortus gracilis	H	OVS	UI	1	>50	–
Willdenowia sulcata	H	OVS	UI	1	>50	–
TECOPHILAEACEAE						
Cyanella hyacinthoides	DG	ALS	UI	1	>50	–
ANACARDIACEAE						
Heeria argentea	P	OVS	UR	1	>50	–
Rhus angustifolia	P	ALS	UI	1	>50	–
Rhus rosmarinifolia	P	ALS	UI	1	>50	–
Rhus tomentosa	P	ALS	UI	1	>50	–
APIACEAE						
Annesorhiza inebrians	H	ALS	UI	1	>50	–
Centella glabrata	MiCh	ALS	UI	1	>50	–
Lichtensteinia lacera	DG	ALS	UI	1	>50	–
Peucedanum sieberianum	EG	ALS	UI	1	>50	–
ASTERACEAE						
Anaxeton asperum	NaCh	OS	DI	2	20	–
Arctotis semipapposa	MeCh	ALS	UI	1	>50	–
Athrixia heterophylla	MeCh	OVS	UI	1	>50	–
Berkheya herbacea	H	ALS	ΔI	1	>50	–
Chrysanthemoides monilifera	P	OS	ST	2	10	–
Conyza bonariensis (*)	MeCh	FE	DI	1	3	–
Corymbium glabrum	H	ALS	ΔI	1	>50	–
Corymbium scabrum	H	ALS	ΔI	1	>50	–
Corymbium villosum	H	ALS	ΔI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Disparago ericoides	MeCh	OVS	UI	1	>50	–
Elytropappus glandulosus	MeCh	ALS	UI	1	>50	–
Gazania serrata	MiCh	ALS	ΔI	1	>50	–
Gerbera crocea	H	ALS	ΔI	1	>50	–
Haplocarpha lanata	H	ALS	UI	1	>50	–
Helichrysum cymosum	MeCh	OS	DI	1	30	–
Helichrysum nudifolium	MeCh	ALS	ΔI	1	>50	–
Helichrysum teretifolium	MeCh	ALS	ΔI	1	>50	–
Helichrysum zeyheri	MeCh	ALS	ΔI	1	>50	–
Hypochoeris radicata (*)	H	FE	DI	1	5	–
Mairea lasiocarpa	NaCh	OS	SI	1	35	>15
Metalasia muricata	P	OS	DI	2	>50	–
Osmitopsis afra	MeCh	OVS	UI	1	>50	–
Osmitopsis asteriscoides	P	ALS	UI	1	>50	–
Osteospermum junceum	P	ALS	UI	1	>50	–
Osteospermum tomentosum	NaCh	OVS	UI	1	>50	–
Senecio grandiflorus	P	OS	DI	1	25	–
Senecio paniculatus	P	OS	DI	1	25	–
Senecio pinifolius	MeCh	ALS	UI	1	>50	–
Senecio pubigerus	P	FE	DI	1	5	–
Stoebe plumosa	MeCh	FSS	DI	2	>50	–
Ursinia paleacea	P	FE	DI	1	5	–
Ursinia pinnata	P	FE	DI	1	5	–
BRUNIACEAE						
Berzelia lanuginosa	P	ALS	UI	1	>50	–
Brunia nodiflora	P	ALS	VI	3	>50	–
Nebelia paleacea	P	ALS	VI	3	>50	–
CAMPANULACEAE						
Cyphia bulbosa	DG	ALS	UI	1	>50	–
Cyphia volubilis	DG	ALS	UI	1	>50	–

Lobelia coronopifolia	MeCh	ALS	UI	1	>50	–
Prismatocarpus diffusus	MeCh	ALS	UI	1	>50	–
Roella ciliata	MeCh	FE	SI	1	5	>45
CELASTRACEAE						
Hartogiella schinoides	P	ALS	ΔR	1	>50	–
Maytenus acuminata	P	FSS	DR	5	>50	–
Maytenus oleoides	P	ALS	ΔT	1	>50	–
CRASSULACEAE						
Crassula capensis	EG	ALS	UI	1	>50	–
Crassula fascicularis	MeCh	OS	ST	1	20	–
DIPSACACEAE						
Scabiosa columbaria	MeCh	ALS	ΔI	1	>50	–
DROSERACEAE						
Drosera aliciae	EG	ALS	ΔI	1	>50	–
Drosera capensis	EG	ALS	ΔI	1	>50	–
EBENACEAE						
Diospyros glabra	P	ALS	ΔI	1	>50	–
ERICACEAE						
Blaeria dumosa	NaCh	OS	SI	4	35	>15
Eremia totta	NaCh	OS	SI	3	>50	–
Erica articularis	MeCh	ALS	UI	1	>50	–
Erica coccinea	P	ALS	VI	3	>50	–
Erica hispidula	P	OS	SI	3	>50	–
Erica longifolia	P	OS	SI	3	>50	–
Erica sphaeroidea	MeCh	OS	SI	2	>50	–
EUPHORBIACEAE						
Clutia alaternoides	P	ALS	UI	1	>50	–
Clutia rubricaulis	MeCh	OVS	UI	1	>50	–
Euphorbia genistoides	NaCh	OVS	UI	1	>50	–
FABACEAE						
Aspalathus ciliaris	P	FE	SI	2	6	>44
Cyclopia genistoides	P	ALS	UI	1	>50	–
Indigofera alopecuroides	NaCh	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Otholobium fruticans	P	ALS	UI	1	>50	–
Otholobium obliquum	P	OVS	UI	1	>50	–
Podalyria montana	P	ALS	UI	1	>50	–
Psoralea aculeata	P	ALS	UI	1	>50	–
Rafnia capensis	MeCh	ALS	UI	1	>50	–
Rhynchosia totta	L	ALS	UI	1	>50	–
FLACOURTIACEAE						
Kiggelaria africana	P	FSS	DR	5	>50	–
GENTIANACEAE						
Chironia baccifera	MeCh	OS	DT	1	10	–
Sebaea exacoides	T	OS	ST	1	1	–
GERANIACEAE						
Pelargonium cucullatum	P	ALS	ΔI	1	>50	–
Pelargonium elongatum	MeCh	OS	DI	1	35	–
Pelargonium longifolium	EG	ALS	ΔI	1	>50	–
Pelargonium myrrhifolium	MeCh	ALS	ΔI	1	>50	–
Pelargonium tabulare	MeCh	ALS	ΔI	1	>50	–
LAURACEAE						
Cassytha ciliolata	VP	OS	DT	1	>50	–
LINACEAE						
Linum africanum	MeCh	ALS	UI	1	>50	–
MESEMBRYANTHEMACEAE						
Erepsia anceps	NaCh	FE	SI	1	5	>45
MONTINIACEAE						
Montinia caryophyllacea	P	ALS	UI	1	>50	–
MYRSINACEAE						
Myrsine africana	P	ALS	ΔR	1	>50	–

OXALIDACEAE						
Oxalis bifida	DG	ALS	UI	1	>50	–
Oxalis lanata	DG	ALS	UI	1	>50	–
Oxalis purpurea	DG	ALS	UI	1	>50	–
Oxalis strigosa	DG	ALS	UI	1	>50	–
Oxalis tenuifolia	DG	ALS	UI	1	>50	–
PENAEACEAE						
Penaea mucronata	P	ALS	UI	1	>50	–
POLYGALACEAE						
Muraltia alopecuroides	MeCh	ALS	UI	1	>50	–
Muraltia heisteria	P	ALS	UI	1	>50	–
Polygala bracteolata	MeCh	FE	SI	1	8	>42
PROTEACEAE						
Aulax pallasia	P	OVS	VI	2	>50	–
Leucadendron salignum	P	ALS	UI	1	>50	–
Protea acaulos	H	OVS	UI	1	>50	–
Protea neriifolia	P	OS	CI	4	35	<1
Protea nitida	P	ALS	VT	2	>50	–
Protea repens	P	OS	CI	3	35	<1
RHAMNACEAE						
Phylica imberbis	MeCh	ALS	UI	1	>50	–
Phylica pubescens	P	OS	SI	3	40	>10
ROSACEAE						
Cliffortia cuneata	P	OS	SI	2	40	>10
Cliffortia polygonifolia	P	OS	SI	3	40	>10
Cliffortia ruscifolia	P	FSS	SI	2	40	>10
RUBIACEAE						
Anthospermum aethiopicum	P	OS	ST	1	8	–
Anthospermum galioides	MiCh	OS	ST	1	8	–
Carpacoce vaginellata	MeCh	ALS	UI	1	>50	–
RUTACEAE						
Coleonema juniperinum	MeCh	FSS	SI	2	>50	–
Diosma hirsuta	MeCh	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
SANTALACEAE						
Thesium capitatum	MeCh	FE	SI	1	5	>45
Thesium strictum	P	FE	SI	1	5	>45
Thesium virgatum	MeCh	FE	SI	1	5	>45
SCROPHULARIACEAE						
Agathelpis dubia	MeCh	OS	ST	1	8	–
Halleria elliptica	P	OVS	UI	1	>50	–
Oftia africana	P	ALS	UI	1	>50	–
Selago spuria	MeCh	FE	SI	1	5	>45
SOLANACEAE						
Solanum tomentosum	P	OS	DT	1	5	–
THYMELAEACEAE						
Gnidia oppositifolia	P	ALS	UI	1	>50	–
Struthiola ciliata	MeCh	OS	SI	1	35	>15

[a] Species marked (*) are exotics.
[b] Life-forms follow the system of Raunkiaer (1934) and modifications thereof (Pate et al. 1984). The abbreviations are: H = hemicryptophytes (renewal buds close to the ground); MiCh = microchamaephytes (renewal buds within 100 mm of the ground); NaCh = nanochamaephytes (renewal buds 100–200 mm from the ground); MeCh = megachamaephytes (renewal buds 200–800 mm from the ground); P = phanerophytes (renewal buds 800 mm or greater from the ground); EG = evergreen geophytes (shoots buried in the ground); DG = deciduous geophytes (shoots buried in the ground); L = lianas (phanerophytes fully supported on other plants); VP = vascular parasites (plants which grow on other living plants); and Th = therophytes (annuals which complete their whole life cycle in 1 year).
[c] Abbreviations are explained in the text.