Regeneration of grassy fynbos near Grahamstown (eastern Cape) after fire

Gaynor R. Richardson, R.A. Lubke and Amy Jacot Guillarmod
Rhodes University, Grahamstown

The regeneration of grassy fynbos was studied for a period of 13 months after the original vegetation had been totally destroyed by fire. Because the fire was preceded by a very dry spell and succeeded by months of high rainfall, regeneration proved to be rapid and the growth of some of the species was clearly related to rainfall. Species recolonization was very rapid and in a particular order. The classification of the species into regeneration type and phenological groups relates well to other studies on fire regeneration in the fynbos. After 13 months over 100 species had returned to the area, the plants showing a progressive increase in height, basal and aerial cover.
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Die hergroei van die grasagtige fynbos is vir 'n tydperk van dertien maande nadat die oorspronklike plantegroei heeltemal deur 'n brand vernietig is, bestudeer. Die hergroei het baie vinnig plaasgevind weens die feit dat die brand deur 'n baie droë tydperk voorafgegaan was en deur maande van baie hoë reën opgevolg is. Die groei van party spesies was duidelik aan die reënval gekoppel. Die herkolonisering van die verskillende spesies het baie vinnig en in 'n bepaalde volgorde plaasgevind. Die klassifikasie van die verskillende soorte in hergroeigroeperings en fenologiese groepe vergelyk goed met dié van ander studies van die hergroei van fynbos na brande. Na dertien maande het meer as 'n honderd spesies na die streek teruggekeer en hierdie plante het toenemende vermeerdering in hoogte, grond- en lugbedekking getoon.
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Gaynor R. Richardson and R.A. Lubke*
Department of Plant Sciences, Rhodes University, Grahamstown, 6140 Republic of South Africa
Amy Jacot Guillarmod
Institute for Freshwater Studies, Rhodes University, Grahamstown, 6140 Republic of South Africa
*To whom correspondence should be addressed

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1. Introduction

Although there has been some early research on the heathlands of the Cape, it was only in the last decade with the introduction of the Fynbos Biome Project that a precise definition of this vegetation type was forthcoming. Floristically fynbos varies markedly within the Cape Floral Region, the only consistent feature being the predominance of the family Restionaceae (Taylor 1978; Kruger 1972). In a recent study of the south eastern Cape fynbos, Cowling (1983) defines grassy fynbos as being similar to the more widespread mountain fynbos in which many of the restioids are replaced by grasses. Acocks' (1975) terminology of False Macchia for this vegetation is no longer acceptable (Cowling 1983) and within the area of this study the definition of Cowling (1983) is most suitable.

Fire appears to be a fairly natural phenomenon in fynbos vegetation. A number of studies have been made of fire and its effect on fynbos in the western Cape (Marloth 1924; Adamson 1935; Wicht 1945, 1948; Wicht & Banks 1963; van der Merwe 1966; Taylor 1973, 1978). Story (1952) and Martin (1966) gave early accounts of fire in grassy fynbos of the eastern Cape and more recent studies in this region have been centred around the eradication of fynbos species from sour grassveld communities (Trollope & Booysen 1971; Trollope 1973; Downing, Robinson, Trollope & Morris 1978; Tainton 1981). One of the earliest accounts of fire in the fynbos is that of Marloth (1908) who ascribed the prevalence of certain Cape geophytes to the frequent occurrence of fires. Most geophytes, such as *Cyrtanthus angustifolius*, flower profusely for the first season after a burn but they seem to flower less frequently as the vegetation ages. In 1945 Wicht made a detailed study of the effects of fire on fynbos and recognized four ways in which species can survive fire: (a) geophytes that regenerate from underground storage organs, (b) sprouters that regrow from rootstock, (c) plants with thick bark that protects dormant stem buds from fire and (d) woody shrubs that are killed by fire and regenerate from seed. Taylor (1973) ascribed the remarkable recovery of fynbos after a burn to the rapid growth of sprouting species.

Gill (1981) recognized the following plant traits which were adaptations to fire: vegetation survival; enhanced reproduction through fire-stimulated flowering; on plant, seed storage and fire-stimulated dispersal; in soil, seed storage with fire-stimulated germination. Martin (1966), in a study of fire in the Grahamstown Nature Reserve, demonstrated a close relationship between life form and type of regeneration. His phenological observations suggested that regenerating plants could be placed in five groups, four of which contained plants which regenerated vegetatively.

Following an accidental burn in the Grahamstown area in August 1980, an opportunity arose for the study of regeneration of grassy fynbos over a long time period. The vegetation in this area is comparable in structure, composition and other features with that of the Grahamstown Nature Reserve (Martin 1966) and thus a comparative study could be initiated. The main aims were:

(a) to monitor regeneration of grassy fynbos after being destroyed by fire with particular emphasis on:
(i) change in species composition,
(ii) increase in height, cover and abundance of the species.
(b) to examine the effects of fire on grassy fynbos species with respect to phenological changes and population dynamics of selected species.
(c) to categorize the species according to their survival mechanisms (Wicht 1945) and phenological groups (Martin 1966).

2. The study area and site of the fire

The farm Faraway, situated about 8 km from Grahamstown on the Highlands road (Figure 1), consists of 31 ha of land mostly sloping to the south. On the steepest slope about 5 ha of Afro-Temperate forest occur and apart from small numbers of exotic pines and Acacias and a small cultivated area around the house, the remaining 26 ha are composed of grassy fynbos.

On 23 August 1980, a very hot veld fire which was started by glowing embers from a passing steam locomotive on the previous evening, spread over most of the farm. A strong northwest wind fanned the flames and by 16h30 the whole valley had been ravaged by the fire. Twenty-four of the 31 ha of land were burnt with only the natural forest and a small portion of the grassy fynbos protected by the forest not being destroyed.

3. Methods

Species regenerating after the fire were recorded from September 1980 and early in November 1980 twelve relocatable one metre square quadrats were randomly sited in the burnt area. At monthly intervals from December 1980 until December 1981, the following data were recorded for each species:

(a) Number of plants present in each quadrat.
(b) Phenology — vegetative, flowering or fruiting.
(c) Height of tallest plants.
(d) Aerial and basal cover using the line-intercept method.

Height was recorded only for the dominant species in each quadrat. Aerial and basal cover were measured only for those plants which contributed significantly to the total cover. Using this information, percentage frequency, mean density and mean percentage cover were calculated. Voucher specimens were deposited in the Albany Museum (GRA) and the Rhodes University Herbaria (RUH).

4. Results

4.1 Climate

The climatogram (Figure 2) summarizes the temperature

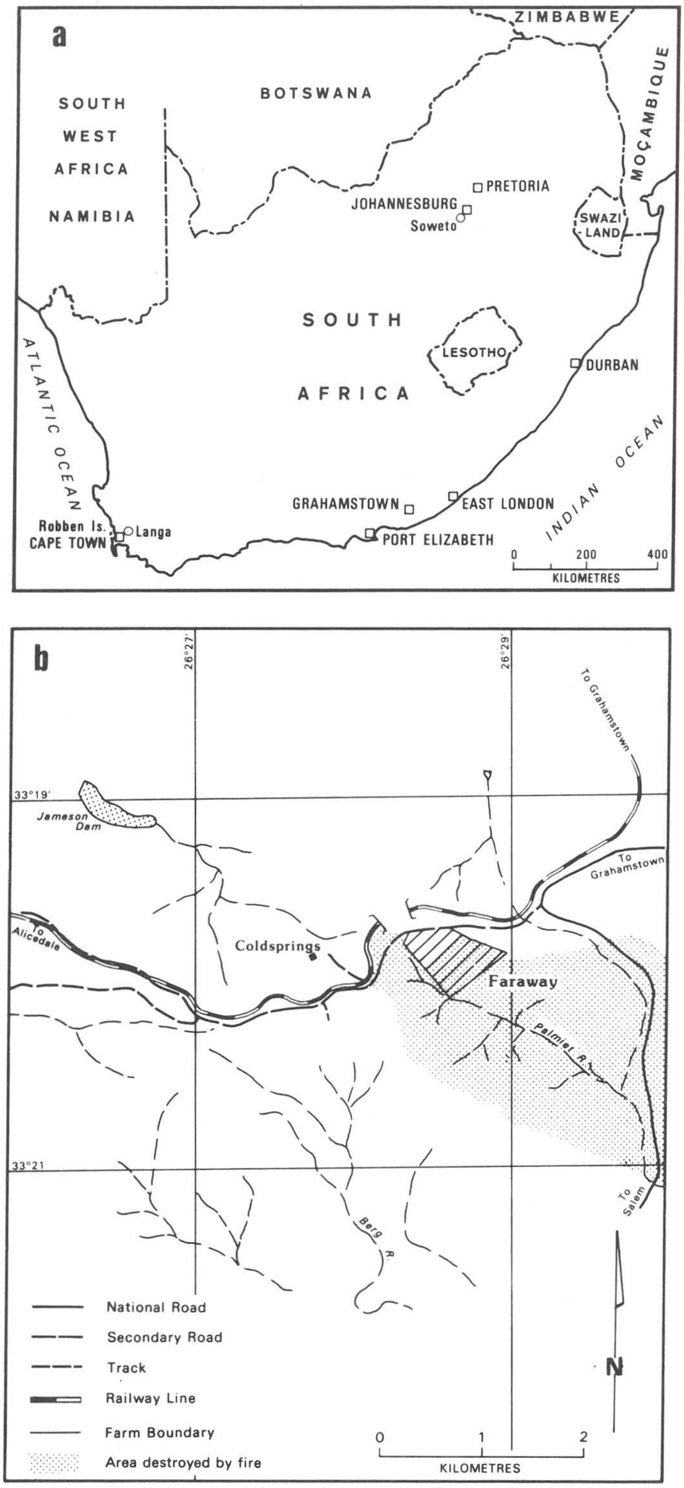

Figure 1 Map of the study area. (a) Location (b) Study site.

and precipitation in the months prior to and succeeding the fire. The fire was preceded by two months of low rainfall and thus the vegetation and ground were dry which aided the spread of the fire. Vines (1970) and Jackson (1968) have shown that fires tend to be more destructive in dry summers. Durand (1981) compared fynbos fire intensities with those of two different grassveld types and the results obtained showed clearly that the average fire in fynbos has a higher intensity than in the grasslands. He concluded that a fynbos fire is a very hot fire, particularly when initial temperatures are high as was the case here. The actual ambient air temperature (in the shade) on the day of the fire was 29,5°C and a strong

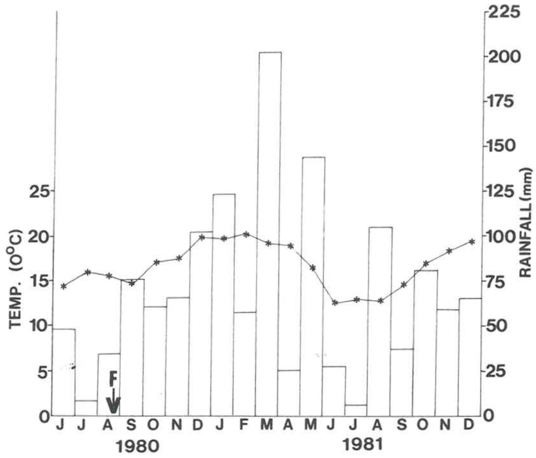

Figure 2 Climatogram showing average temperature and rainfall at Faraway. F = date of fire. (Source: A. Jacot Guillarmod, personal records.)

northwest wind fanned the flames.

The fire was followed by several months of unusually high rainfall for that time of the year. Martin (1966) noticed considerable differences in the response of some species depending on whether the fire was followed by a dry or wet spring. Some species would regenerate either vegetatively or by seed under conditions of good rainfall but failed to regenerate in drought.

4.2 Changes in species composition after the fire

On 28 August it was observed that burning was complete and no above ground vegetation had survived. Yet two days later, after only 0,19 mm of rain had fallen, the first plants, namely *Cyrtanthus angustifolius* — a typical 'fire lily' — were seen flowering and on 10 September 1980 over 300 plants of this species were counted in bloom. Furthermore, many more species had appeared, supporting the finding that plants that regenerate vegetatively after a fire begin to sprout within about fourteen days (Wicht 1948). At this time there were several unidentifiable species of grasses, *Restio* spp, *Hypoxis argentea, Bobartia macrocarpa, Senecio speciosus, Brunsvigia grandiflora, Berkheya decurrens, Athanasia dentata, Pteridium aquilinum* and many more, all of which had regenerated vegetatively.

A full list of species in order of appearance is listed in the appendix.

Although very little quantitative data on fynbos community structure is available, the unusually high species diversity of these communities is often mentioned (Wicht 1945; Acocks 1975; Boucher 1972). The increase in number of species appearing with time in the entire burnt area is shown in Figure 3. There is a fairly steep increase in species number during the months September to December and a slight increase during the months of April and May. This seems to correlate with variations in rainfall. The months September to January all received good rainfall but it decreased somewhat in February, becoming very heavy again in March when a total of 202,69 mm was recorded. This was probably responsible for the spurt in growth and regeneration during the succeeding months of April and May, although it is important to note that regeneration in the fynbos is a continuous process (Durand 1981).

4.3 Variations in cover and abundance of the species following the fire

The percentage cover increased fairly rapidly in the first six months after the fire and by February 1981 the ground was 44% covered (Figure 4). There followed a slower increase in canopy cover until March when increased growth occurred which, like species number, appears to be correlated with the rainfall. Wicht (1948) also found that sprouting accelerated after good rain causing geophytes to develop foliage although this could also be due to an increase in soil temperature. Gill (1981) showed that when the tops of plants were killed, often by fire, this resulted in the release of correlative inhibition and buds grew out to form new shoot systems. Twelve months after the initial measurements were recorded cover had increased to 70%. Kruger (1972) found, in a study of regeneration of fynbos after fire, that both canopy and basal cover had, within 25–30 months of burning, reached 70–90% of the levels measured before burning. This study shows similar trends of cover regeneration in grassy fynbos.

The increase in cover of individual species is indicated in Figure 4. In December 1980, *Alloteropsis semialata* had the greatest canopy cover followed by *Clutia heterophylla, Tristachya leucothrix* and *Bobartia macrocarpa*. By February

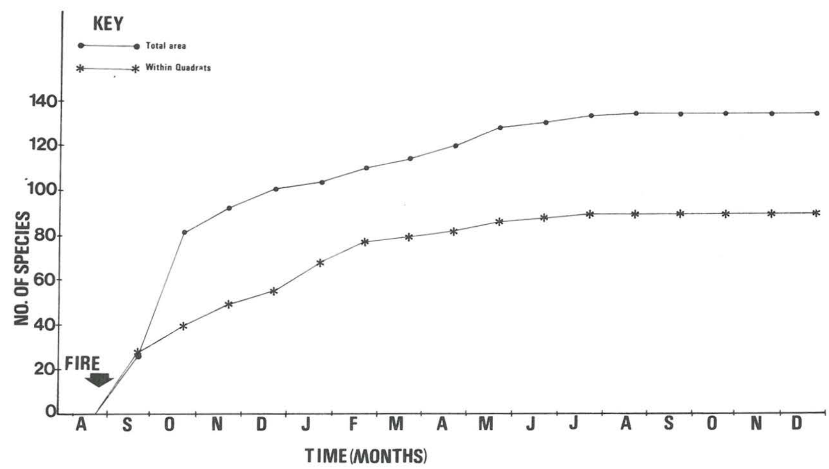

Figure 3 Increase in the number of species appearing with time.

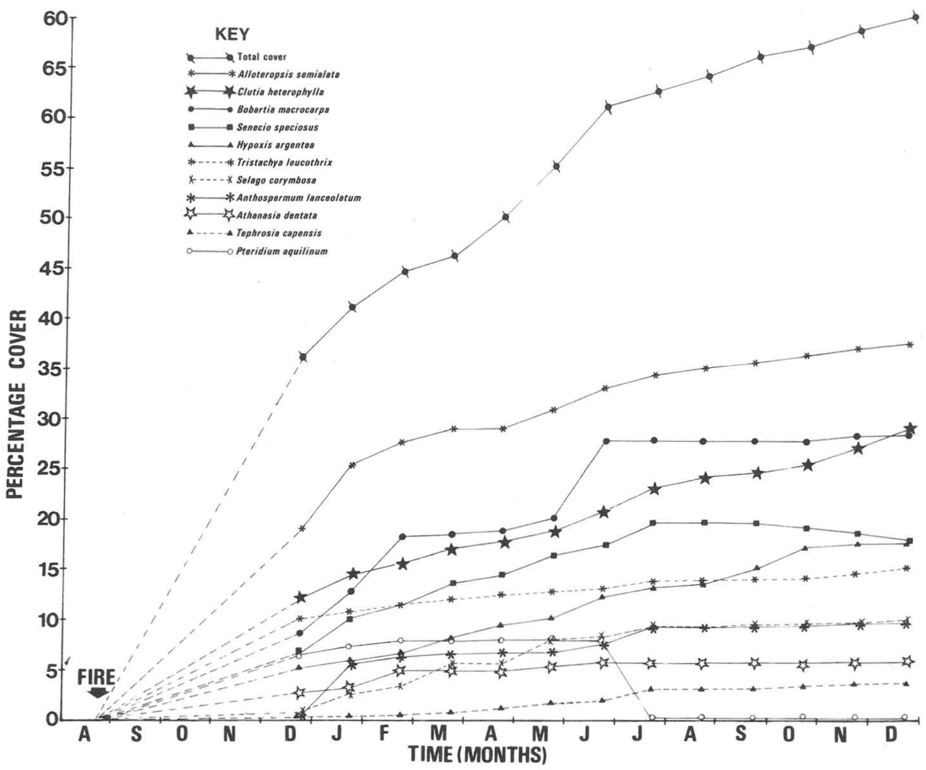

Figure 4 Increase in percentage canopy cover of eleven of the commonest species and total percentage cover over a 17-month period.

1981 the cover of *B. macrocarpa* had increased tremendously and it was pre-empted only by *Alloteropsis semialata*. It maintained its competitive advantage in the succeeding months. Graminoid and restioid species were the quickest to regenerate and become temporarily dominant but later there was an increase in cover of sprouting herbs and shrubs.

In Tables 1 and 2 the percentage frequency and mean density (plants m^{-2}) are listed. The arrangement of species is in order of highest frequency in December 1980. Plants which occurred in only one quadrat, i.e. very infrequently, are not included in this table. The most frequent species in December were *Alloteropsis semialata* (75%), *Bobartia macrocarpa* (66,67%), *Oxalis smithiana* (66,67%), *Hypoxis argentea* (59%), *Senecio speciosus* (41,67%) and *Senecio pterophorus* (25%). The most remarkable change in frequency was *Senecio pterophorus*. This species is absent from unburnt heath (Martin 1966) and was found to increase in frequency from 25% to 83,3%. This is probably because there is a large seed bank in the soil (Hitchings 1960; Roberts 1970). As with many weedy species the seeds possibly have a light requirement for germination (Brenchley & Warrington 1930). The fire may cause a disturbance of the soil fauna which in moving from the area bring seeds to the surface exposing them to light and thus enabling them to germinate. Up until August 1981 *Oxalis smithiana* increased in frequency from 66,7% to 91,7% and *Senecio speciosus* from 41,7% to 75%. *Oxalis* has deep-seated corms which are thus well protected against drying and fire, while *Senecio speciosus* also regenerates vegetatively but from an underground rootstock. Decrease of competition could also be responsible for the rapid spread of these species as they are effective colonizers of burnt areas. From October 1981 they decreased in frequency as other species replaced these primary colonizers. Gill (1981) reports that the nutritive qualities of ash may trigger a growth response in some species.

Helichrysum anomalum had the greatest density in December and showed an increase in density from 33,3 plants m^{-2} in December 1980 to 40,2 plants m^{-2} in July 1981. *Oxalis smithiana* increased from 6,38 to 25,18 plants m^{-2} while *Senecio speciosus* increased from 2,0 to 11,56 plants m^{-2}. Most of the dicotyledonous plants, especially the Asteraceae and Fabaceae showed numerical increases in density. On the other hand, the grasses and sedges did not show great increases in density although they increased in spread and in aerial cover.

4.4 Species dominance of the vegetation as reflected by height

The mean heights of the most prominent species were calculated and plotted (Figure 5). In the early stages after the fire *Pteridium aquilinum* was the tallest plant in most quadrats and was widespread over much of the burnt area. Although there were taller plants, e.g. *Cynoglossum enerve* and *Bobartia macrocarpa*, these were isolated in only one small area or in single quadrats. However, *Bobartia macrocarpa* soon outgrew *Pteridium aquilinum* and from March 1981 it was taller than this species. *Bobartia macrocarpa* retained its advantage until June 1981 when it was replaced by *Senecio pterophorus*. In the autumn of 1981 *Pteridium aquilinum* and *Cynoglossum enerve* died back to ground level as is usual in these species (Figure 5). In the spring these two species reappear and gradually increase in height.

4.5 Seedling establishment of *Bobartia macrocarpa*

By October, two months after the fire, *Bobartia macrocarpa* was in full bloom. This is one of the species which usually flowers after fire and very rarely at other times. Shedding of

Table 1 Percentage frequency of the dominant species occurring in more than one quadrat over a 13-month period

Species	Frequency												
	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1 *Alloteropsis semialata*	75%	75%	75%	75%	75%	75%	75%	75%	75%	75%	75%	75%	75%
2 *Bobartia macrocarpa*	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%	75%	75%	75%	83,33%	83,33%
3 *Oxalis smithiana*	66,67%	66,67%	83,33%	83,33%	83,33%	91,67%	91,67%	91,67%	91,67%	83,33%	75%	25%	25%
4 *Hypoxis argentea*	50%	58,33%	58,33%	58,33%	58,33%	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%	50%	50%
5 *Senecio speciosus*	41,67%	50%	50%	66,67%	66,67%	75%	75%	75%	75%	75%	75%	50%	41,67%
6 *Clutia heterophylla*	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	41,67%	41,67%
7 *Berkheya decurrens*	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	16,67%	16,67%
8 *Helichrysum anomalum*	33,33%	33,33%	33,33%	33,33%	33,33%	41,67%	41,67%	41,67%	41,67%	41,67%	41,67%	41,67%	41,67%
9 *Anthospermum aethiopicum*	25%	50%	50%	50%	50%	58,33%	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%	66,67%
10 *Helichrysum nudifolium*	25%	41,67%	41,67%	41,67%	41,67%	50%	50%	50%	50%	50%	50%	50%	50%
11 *Senecio pterophorus*	25%	33,33%	41,67%	50%	50%	75%	83,33%	83,33%	83,33%	83,33%	83,33%	83,33%	83,33%
12 *Pteridium aquilinum*	16,67%	25%	25%	25%	25%	25%	25%	8,3%	8,3%	8,3%	16,67%	16,67%	16,67%
13 *Tristachya leucothrix*	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%
14 *Alepidia capensis*	16,67%	25%	25%	25%	25%	25%	25%	25%	25%	25%	25%	16,67%	16,67%
15 *Erica cerinthoides*	16,67%	25%	25%	25%	25%	25%	25%	33,33%	33,33%	50%	50%	50%	50%
16 *Corymbium africanum*	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	8,33%	8,33%
17 *Gerbera piloseloides*	16,67%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	16,67%	16,67%	16,67%
18 *Argyrolobium tomentosum*	16,67%	25%	25%	25%	25%	25%	25%	25%	25%	25%	25%	16,67%	16,67%
19 *Geranium ornithopodum*	16,67%	25%	25%	25%	25%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%	33,33%
20 *Schizaea pectinata*	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	16,67%	25%	25%	25%	25%	25%	16,67%

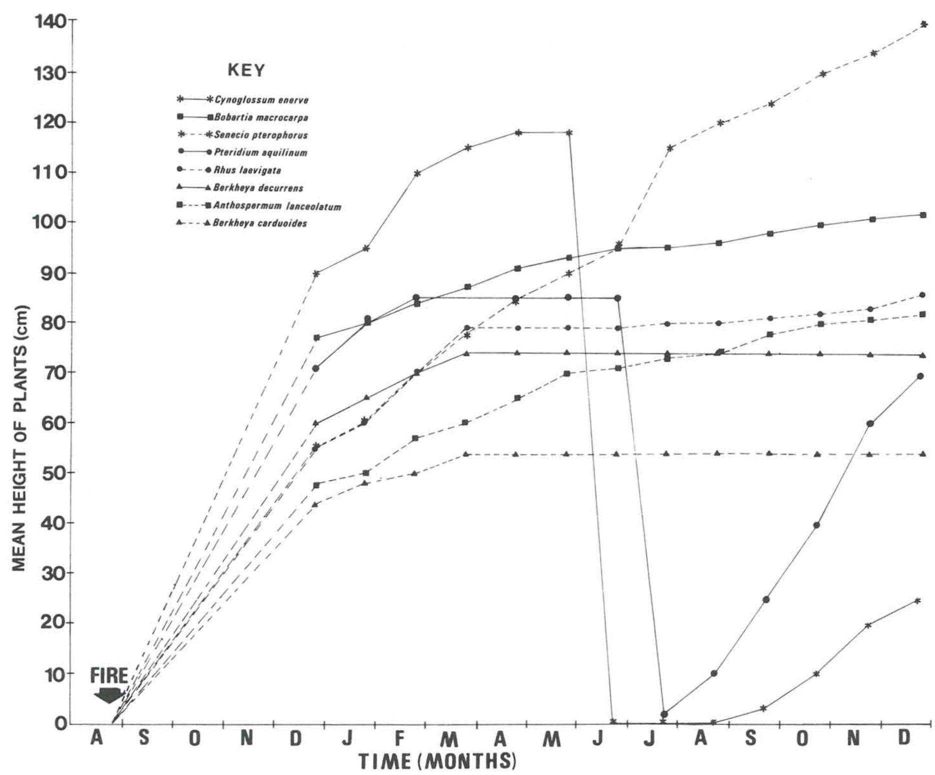

Figure 5 Increase in height of the most common species.

Table 2 Density in plants m^{-2} (mean ± standard error) of the dominant species occurring in more than one quadrat over a 13-month period

	Species	Density												
		December	January	February	March	April	May	June	July	August	September	October	November	December
1	*Alloteropsis semialata*	2,00 ± 0,47	2,22 ± 0,52	2,33 ± 0,50	2,44 ± 0,53	2,44 ± 0,53	2,44 ± 0,53	2,44 ± 0,53	2,44 ± 0,53	2,44 ± 0,53	2,44 ± 0,53	2,80 ± 0,65	2,80 ± 0,65	2,80 ± 0,65
2	*Bobartia macrocarpa*	5,50 ± 1,56	5,50 ± 1,56	5,50 ± 1,56	5,63 ± 1,55	5,63 ± 1,55	5,63 ± 1,55	5,75 ± 1,61	5,75 ± 1,61	5,75 ± 1,61	5,75 ± 1,61	5,75 ± 1,61	5,88 ± 1,61	5,88 ± 1,61
3	*Oxalis smithiana*	6,38 ± 1,73	8,63 ± 2,21	11,40 ± 2,63	18,60 ± 4,81	21,70 ± 5,52	21,18 ± 5,64	23,27 ± 5,60	25,18 ± 5,94	23,30 ± 5,14	19,10 ± 4,45	12,89 ± 2,72	12,50 ± 3,54	11,38 ± 1,45
4	*Hypoxis argentea*	1,17 ± 0,17	1,57 ± 0,30	1,57 ± 0,30	1,57 ± 0,30	1,57 ± 0,30	1,38 ± 0,26	1,38 ± 0,26	5,13 ± 3,98	5,50 ± 3,52	5,50 ± 3,52	4,44 ± 2,95	4,22 ± 2,73	3,33 ± 2,09
5	*Senecio speciosus*	2,00 ± 0,45	2,33 ± 0,67	5,67 ± 3,53	10,88 ± 6,58	16,88 ± 9,07	25,22 ± 11,86	25,89 ± 11,13	11,56 ± 3,88	11,56 ± 3,88	10,38 ± 4,14	9,56 ± 4,01	9,83 ± 3,96	12,00 ± 4,24
6	*Clutia heterophylla*	2,50 ± 0,65	2,75 ± 0,63	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	3,00 ± 0,71	2,80 ± 0,73	2,60 ± 0,68	2,20 ± 0,73
7	*Berkheya decurrens*	1,25 ± 0,25	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,50 ± 0,29	1,67 ± 0,33	1,67 ± 0,33	2,00 ± 1,00	2,00 ± 1,00
8	*Helichrysum anomalum*	19,25 ± 6,10	23,50 ± 6,76	26,75 ± 7,97	32,75 ± 9,25	36,25 ± 9,38	33,20 ± 13,26	36,40 ± 12,90	40,20 ± 12,41	40,20 ± 12,41	39,80 ± 12,25	39,40 ± 12,50	38,80 ± 12,35	37,80 ± 13,14
9	*Anthospermum aethiopicum*	1,33 ± 0,33	2,67 ± 1,28	2,67 ± 1,28	5,00 ± 2,21	7,33 ± 3,40	10,00 ± 5,37	5,00 ± 2,15	2,50 ± 0,85	2,50 ± 0,85	2,67 ± 1,12	2,67 ± 1,12	2,67 ± 1,12	2,67 ± 1,12
10	*Helichrysum nudifolium*	1,00 ± 0	1,20 ± 0,20	1,60 ± 0,40	1,80 ± 0,37	1,80 ± 0,37	1,67 ± 0,33	2,00 ± 0,37	2,83 ± 0,40	2,83 ± 0,40	2,83 ± 0,40	2,60 ± 0,68	2,60 ± 0,68	1,83 ± 0,40
11	*Senecio pterophorus*	2,00 ± 1,00	1,00 ± 0	1,20 ± 0,20	1,67 ± 0,67	1,67 ± 0,67	2,67 ± 1,03	5,10 ± 1,95	5,10 ± 1,95	5,10 ± 1,95	5,10 ± 1,95	5,10 ± 1,95	5,10 ± 1,95	5,10 ± 1,95
12	*Pteridium aquilinum*	8,50 ± 5,50	6,00 ± 4,04	7,33 ± 5,36	7,33 ± 5,36	7,33 ± 5,36	7,33 ± 5,36	7,33 ± 5,36	1,00 ± 0	1,00 ± 0	3,00 ± 2,00	4,00 ± 3,00	4,50 ± 3,50	6,00 ± 4,00
13	*Tristachya leucothrix*	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50
14	*Alepidia capensis*	2,00 ± 1,00	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,00 ± 0,58	2,50 ± 0,50	2,50 ± 0,50	1,50 ± 0,50	1,50 ± 0,50
15	*Erica cerinthoides*	2,00 ± 1,00	3,33 ± 1,20	3,33 ± 1,20	4,00 ± 1,53	4,00 ± 1,53	4,00 ± 1,5	4,00 ± 1,5	3,75 ± 1,38	3,75 ± 1,38	3,75 ± 1,38	3,75 ± 1,38	4,00 ± 1,22	4,00 ± 1,22
16	*Corymbium africanum*	1,50 ± 0,50	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	2,00 ± 1,00	1,00 ± 0	1,00 ± 0
17	*Gerbera piloseloides*	1,50 ± 0,50	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,75 ± 0,48	1,33 ± 0,33	– –	– –
18	*Argyrolobium tomentosum*	1,50 ± 0,50	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,33 ± 0,33	1,50 ± 0,50	1,50 ± 0,50
19	*Geranium ornithopodum*	8,50 ± 7,50	6,33 ± 4,84	7,67 ± 6,17	9,67 ± 8,17	11,00 ± 9,50	8,75 ± 7,09	10,00 ± 8,34	11,25 ± 9,59	11,25 ± 9,59	11,75 ± 9,76	12,25 ± 10,26	12,50 ± 10,51	12,75 ± 10,76
20	*Schizaea pectinata*	6,50 ± 3,50	6,50 ± 3,50	7,00 ± 3,00	7,00 ± 3,00	7,00 ± 3,00	7,00 ± 3,00	7,00 ± 3,00	6,67 ± 4,26	6,67 ± 4,26	6,67 ± 4,26	6,67 ± 4,26	6,67 ± 4,26	6,67 ± 4,26

seed started in December and by February of the following year the first seedlings were observed. By May they formed a dense covering on the bare patches of ground. Decreased competition as a result of the fire enabled many seedlings to become established. They grew in such close proximity that counting was difficult. A peak was reached in May (Figure 6) and the number of seedlings remained constant until July when there was a decrease in numbers which can probably be ascribed to increased intraspecific competition.

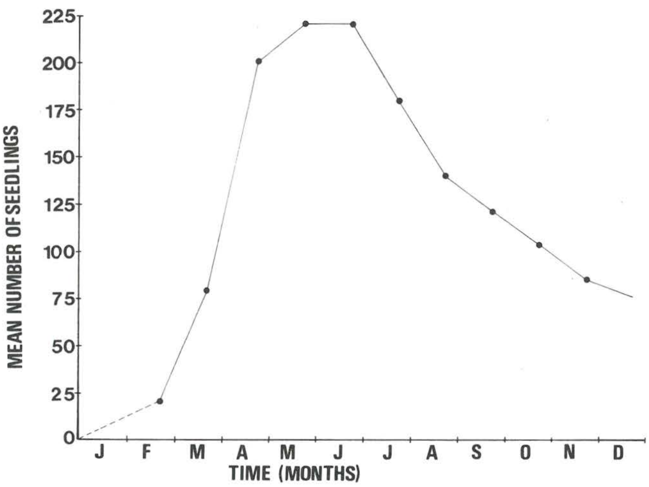

Figure 6 Change in the number of *Bobartia macrocarpa* seedlings in the quadrats during the period of study.

5. Discussion

The effect of fires on heath vegetation has been described for many parts of the world. In most cases a marked increase in herbaceous canopy cover, sometimes including grasses, was observed. Jarrett & Petrie (1929) reported a prolific production of seedlings of both woody and herbaceous species in south east Australia. In a study of chaparral by Sweeny (1956) it was found that numerous species of annuals regenerated from dormant seeds surviving fire in the soil. In South Africa annuals are of minor importance; for example, Adamson (1935) noticed only a poor representation of annuals after fire in the south western Cape fynbos but reported a prolific increase in some perennial shrubs, e.g. *Anthospermum aethiopicum* in the first few years after fire. In the present study we found great increases in some perennial shrubs, e.g. *Anthospermum herbaceum*, whereas the percentage of plants which regenerated only from seed was small (8,43%). According to van der Merwe (1966), 67% of the species at Swartboskloof regenerated vegetatively and 33% regenerated only from seed. These data confirm that, at least in early succession, the majority of the plants regenerate vegetatively. Kruger (1972) found that species regenerating vegetatively comprise the bulk of basal cover and help to reduce erosion during the period immediately after a burn because their basal tufts are seldom destroyed by fire and remain in position to anchor the surface soil.

Many of the fynbos species only flower or flower more profusely after fire. We found that many species were stimulated to flower by fire, e.g. *Cyrtanthus angustifolius, Gerbera viridifolia* and *G. piloseloides* while others showed an increase in flowering after burning, e.g. *Senecio speciosus*. These results correlate well with those of Martin (1966) in the Grahamstown Nature Reserve.

The good rains which occurred shortly after the fire obviously stimulated the regeneration of the geophytes and the germination of seeds in the soil. Martin (1966) found that *Themeda triandra* and *Restio triticeus* had delayed regrowth if fire was followed by dry weather (as for the 1948 fire) but grew rapidly with good rains (as for the 1951 fire). After the present fire both these species appeared by October owing to the good rains, thus substantiating Martin's findings. Species germinating from seed, such as *Senecio pterophorus* and *Bobartia macrocarpa* (which also regenerated from stock) showed rapid increases in number possibly owing to the increase in rainfall.

Fire survival can be examined with reference to two approaches to classification of regeneration, that of Wicht (1945) and that of Martin (1966). Wicht's observations were based mainly on the means by which plants regenerate or survive fires, whereas Martin was concerned with phenology. Of the four groups of fire survival plants which Wicht (1945) recognized, we observed the following:

(i) Geophytes, e.g. *Cyrtanthus angustifolius*, which was the first to appear after the fire, *Hypoxis argentea* and *Oxalis smithiana* among others.
(ii) Sprouters that regrow from rootstocks, e.g. *Themeda triandra, Eragrostis capensis, Euphorbia striata* and *Senecio speciosus*, appeared next, as Wicht also observed.
(iii) Plants with thick bark that protect dormant stem buds from fire. This group is also represented here by *Protea foliosa, Protea cynaroides, Rhus laevigata, Maytenus heterophylla* and *Leucadendron salignum*.
(iv) Woody shrubs that are killed by fire and regenerate from seed in this study, e.g. *Anthospermum aethiopicum* and *Selago corymbosa*.

Martin (1966) suggested that regenerating plants could be placed in five groups and our observations substantiate these findings:

(i) Geophytes such as *Cyrtanthus angustifolius* producing flower heads almost immediately after burning without the intervention of a leafy period.
(ii) Herbs and a few suffruticose subshrubs which regenerate vegetatively very quickly and flower about a month later than those in group (i). We found many plants regenerated from rootstocks e.g. *Senecio speciosus, Pteridium aquilinum, Clutia heterophylla, Hypoxis argentea, Anemone caffra, Alloteropsis semialata, Gerbera piloselloides, G. ambiqua, Euphorbia striata*.
(iii) Plants which begin to flower about one month later than those in group (ii). These included *Aster bakeranus, Elionurus muticus, Panicum ecklonii, Euphorbia silenifolia, Bobartia macrocarpa* in our study.
(iv) Mainly woody plants and some herbs which regenerate very slowly in the first year but flower the following year in spring, e.g. *Maytenus heterophylla* and *Leucadendron salignum*.
(v) Plants which are destroyed by fire and regenerate slowly from seed. *Anthospermum aethiopicum* was observed on 4 October, *Cliffortia graminea* on 2 November and *Selago corymbosa* appeared at the end of January 1981. The seed regenerating Ericas (*Erica demissa* and *Erica chamissonis*) had not reappeared by

December 1981. Martin found that these *Erica* spp. only regenerated two years after the fire. As they regenerate solely from seed brought in by wind, a time-lag may occur, especially if a poor seed season occurs after fire. *Anthospermum aethiopicum* regenerated rapidly after the fire and was so widespread that we assume that dormant seed was present in the soil. Levyns (1935) found that 59% of the seed was viable after five years. Other plants found to regenerate solely from seed were *Senecio pterophorus, Drosera cuneifolia, Solanum retroflexum, Geranium ornithopodum* and the exotic trees *Pinus pinaster* and *Acacia longifolia*.

Data are not available on the species composition of the study area before the fire but one would expect a greater diversity of species following the burn. The number of species reappearing in the area (Figure 3) could be related to rainfall and the total of 134 species appeared to be stable at the time of our last recording in December 1981. The mean percentage canopy cover for the study area (Figure 4) is apparently still on the increase, although most of the individual species have reached an equilibrium or in some cases show a decline in the normal cyclic population change over the seasons or with varying climatic factors.

The increased density and frequency of some species such as *Oxalis smithiana* and *Senecio speciosus* and the rapid rate at which the plants appear can be related to the non-competitive situation that occurs following the fire. The primary colonizers of burnt fynbos rapidly invade the area. For example, *Senecio pterophorus*, which is absent from unburnt natural heath, rapidly increases in frequency and was one of the tallest species in the regenerating area (Figure 5). With the exception of this colonizing species most of the species had attained their normal height in this type of vegetation. However, many of the woody species such as *Erica* spp., had not yet appeared so that the overall height of the vegetation is still increasing.

Apart from providing favourable conditions for flowering the fire also stimulated the production of an abundance of seed to replace the seed in the seed bank of the soil which had germinated. *Bobartia macrocarpa* produced a copious supply of seed which germinated immediately resulting in a dense mat of seedlings in some areas. Owing to competitive thinning, the numbers of seedlings of *B. macrocarpa* were gradually reduced to a stable level (Figure 6).

Although there is complete devastation of the grassy fynbos after fire, there is a rapid regeneration of vegetation, very often with an increase in production vegetatively or by means of seeds. In the initial stages the grasses and restioid plants become more abundant but there is an increase in the herbs as well. Although some of the woody species returned to the area, many of the climax species, such as *Erica demissa* and *E. chamissonis* take longer to reappear, as they are carried in as wind-borne seed. Continued studies of the changes in species composition will give an indication of the time taken for this vegetation to mature.

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Appendix

A list of all the species arranged according to the date of first appearance following the fire (F = Forb, G = Graminoid, Fy = Fynbos, S = Shrub).

August 30 1980

Cyrtanthus angustifolius Ait. F

September 10 1980

Alepidia capensis (Berg.) R.A. Dyer F
Athanasia dentata L. S
Berkheya decurrens (Thunb.) Willd. F
Bobartia macrocarpa Strid F
Brunsvigia grandiflora Lindl. F
Bulbine frutescens (L.) Willd. F
Clutia heterophylla Thunb. F
Geranium ornithopodum Eckl. & Zeyh. F
Helichrysum herbaceum (Andr.) Sweet F
Hypoxis argentea Harv. ex Bak. F
H. rooperi S. Moore F
Leonotis leonurus (L.) R.Br. F
Pteridium aquilinum (L.) Kuhn. F
Satyrium membranaceum Swartz F
Senecio speciosus DC. F

September 13 1980

Cyperus usitatus Burch. G
Restio triticeus Rottb. G
Themeda triandra Forssk. G

September 26 1980

Berkheya carduoides (Less.) Hutch. ex Fourc. F
Gazania krebsiana Less. F
Gerbera ambigua (Cass.) Sch.Bip. F
G. piloseloides (L.) Cass. F
Helichrysum anomalum Less. F
Scabiosa columbaria L. F
Scilla sp. F
Senecio albanensis DC. F
Watsonia meriana (L.) Mill. F

October 1 1980

Struthiola argentea Lehm. F
Tarchonanthus camphoratus L. S

October 4 1980

Acalypha ecklonii Baill. F
Anthospermum herbaceum L.f. S
A. aethiopicum L. S
Asparagus asparagoides (L.) Wight F
Clematis brachiata Thunb. F
Crassula vaginata Eckl. & Zeyh. F
Dierama pendulum Bak. F
Elegia parviflora Kunth. G
Halleria lucida L. S
Mohria caffrorum (L.) Desv. F
Pellaea viridis (Forssk.) Prantl. F
Poa annua L. G
P. binata Nees. G
Rubus pinnatus Willd. S
Senecio oxyriifolius DC. F
Sonchus asper (L.) Hill F
S. oleraceus L. F

October 10 1980

Anemone caffra Eckl. & Zeyh. F
Arctotheca calendula (L.) Levyns F
Centella coriacea Nannfd. F
Clutia pulchella L. F
Erica cerinthoides L. Fy
Kniphofia rooperi (Moore) Lem. F
Kohautia amatymbica Eckl. & Zeyh. F
Protea cynaroides L. Fy
P. foliosa Rourke Fy
Solanum retroflexum Dun. F

October 11 1980

Agapanthus africanus (L.) Hoffmg. F
Alloteropsis semialata (R.Br.) Hitch. G
Cotula sericea Thunb. F
Leucadendron salignum Berg. Fy
Rhus laevigata L. S
Trachyandra sp. F
Tristachya leucothrix Nees. G

October 19 1980

Aster bakerianus Burtt Davy ex O.A. Sm. F

October 26 1980

Albuca baueri Baker F
Cyperus rotundus L. G
Ehrharta capensis Thunb. G
Festuca caprina Nees. G
F. costata Nees. G
Harpochloa falx (L.f.) O.Ktze. G
Helichrysum nudifolium (L.) Less. F
Pelargonium caffrum (Eckl. & Zeyh.) Harv. F
Vernonia capensis (Houtt) Druce. F
V. dregeana Sch. Bip. F

October 28 1980

Acacia longifolia (Andr.) Willd. S
Argyrolobium tomentosum (Andr.) Druce. F
Athrixia crinita (L.) Druce. F
Elionurus muticus (Spreng.) Kunth. G
Eragrostis capensis (Thunb.) Trin. G
Eucomis comosa (Houtt.) Wehrh. F
Euphorbia silenifolia (Haw.) Sweet F
E. striata Thunb. F
Hibiscus aethiopicus L. F
H. trionum L. F
Lobelia erinus L. F
Maytenus heterophylla (Eckl. & Zeyh.) N.K.B. Robson S
Pinus pinaster Ait. S
Tephrosia capensis (Jacq.) Pers. F
Thesium fruticosum A.W. Hill S
T. junceum Bernh. S

November 2 1980

Cliffortia graminea L.f. Fy
Cynoglossum enerve Turcz. F
C. lanceolatum subsp. *eu-lanceolatum* Brand. F
Haplocarpha scaposa Harv. F
Indigofera stenophylla Eckl. & Zeyh. F
I. stricta L.f. F
Polygala hispida Burch. F
Psoralea pinnata L. Fy
Rhoicissus tomentosa (Lam.) Wild & Drumm. S
R. tridentata (L.f.) Wild & Drumm. S

November 8 1980

Panicum ecklonii Nees. G
Schizaea pectinata (L.) Sw. F

November 15 1980

Wahlenbergia capillacea (Thunb.) A.DC.	F
W. zeyheri Eckl. & Zeyh.	F
November 30 1980	
Eriospermum sp.	F
December 1 1980	
Dipcadi ciliare (Zeyh. ex Harv.) Bak.	F
December 8 1980	
Metalasia muricata (L.) D.Don.	S
December 28 1980	
Acrolophia capensis (Berg.) Fourc.	F
Corymbium africanum L.	F
December 29 1980	
Acacia saligna (Labill.) Wendl.	S
Alectra sessiliflora (Vahl.) Kuntze	F
Gnidia stypheloides Meissn.	F
Nidorella undulata (Thunb.) Sond ex Harv.	F
N. auriculata DC.	F
January 31 1981	
Anapalina caffra (Ker-Gawl. ex Bak.) G.J. Lewis	F
Rhynchosia caribaea (Jacq.) DC.	F
Selago corymbosa L.	S
February 2 1981	
Gladiolus permeabilis Delaroche.	F
Monopsis scabra (Thunb.) Urb.	F
February 28 1981	
Drosera cuneifolia L.f.	F
Hesperantha falcata Ker-Gawl.	F
Senecio pterophorus DC.	F
S. gramineus Harv.	F
March 8 1981	
Diascia capsularis Benth.	F
Myrica brevifolia E. Mey. ex A.DC.	Fy
March 29 1981	
Helichrysum petiolare Hilliard & Burtt.	F
April 14 1981	
Helichrysum felinum (Thunb.) Less.	F
Oxalis smithiana Eckl. & Zeyh	F
Pimpinella stadensis (Eckl. & Zeyh.) Harv.	F
April 20 1981	
Hermannia flammea Jacq.	F
Neodregea glassii C.H.Wr.	F
Tagetes minuta L.	F
May 16 1981	
Chaetacanthus setiger (Pers.) Lindl.	F
Erica curviflora L.	Fy
Gnidia nodiflora Meissn.	F
Podalyria velutina Burch.	Fy
Rapanea melanophloeos (L.) Mez.	S
Sebaea hymenosepala Gilg.	F
Senecio lineatus DC.	F
Sutera campanulata (Benth.) Kuntze	F
Teedia lucida Rudolphi	F
June 21 1981	
Erica glumiflora Klotzsch ex Benth.	Fy
Senecio pinifolius Lam.	F
July 30 1981	
Buchenroedera multiflora Eckl. & Zeyh.	F
Chasmanthe aethiopica (L.) N.E. Br.	F
Plantago remota Lam.	F