

## Effects of seed and seedling predation by small mammals on seedling recruitment of *Protea neriifolia* in Swartboskloof, Cape Province

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Seed and seedling predation by small mammals, thought to be significant factors controlling the recruitment of Proteaceae in fynbos shrublands, were studied in a fynbos shrubland before and after a fire in March 1987. Seeds of *Protea neriifolia* R.Br. were planted inside and outside 14 mm mesh exclosures. The abundance of small mammals was recorded at two fynbos and five forest sites before the fire and at an additional forest and fynbos site after the fire. Seed predation reduced seedling recruitment from seeds planted in March 1986 in mature fynbos, but the reduction was significant only at the site with the highest abundance of small mammals. Seed predation did not significantly reduce seedling recruitment from seed planted in July, August and September 1986 in mature fynbos. The primary cause of seedling mortality before the fire was wilting, presumably owing to moisture stress. After the fire small mammal abundance decreased in burnt fynbos and increased in unburnt forest refuges until eight months after the fire when it increased again in the fynbos to a maximum of 41 animals per 100 trapnights two years after the fire. Seedling predation by small mammals had a limited impact after the fire probably because their numbers dropped soon after the fire. The effects of seed predation did not decrease with increasing distance from a forest refuge. Fungal pathogens and herbivory by insects were the primary causes of seedling mortality after the fire. Small mammal abundance in mature fynbos 25–30 years after a fire may have been too low to prevent the recruitment of a second cohort of *P. neriifolia* seedlings.

Saad- en saailing-predasie deur kleinsoogdiere, wat as belangrike faktore in die bepaling van die verjonging en struktuur van serotiene Proteaceae gemeenskappe in fynbos-plantegroei beskou word, is bestudeer in 'n fynbos-struikveld voor en na 'n brand in Maart 1987. Sade van *Protea neriifolia* R.Br. is binne en buite 14 mm-maas uitsluitingshokkies geplant. Kleinsoogdierdigtheid is bepaal vir twee fynbos- en vyf woud-persele voor die brand en by 'n bykomende woud- en fynbos-perseel na die brand. Saadpredasie het saailing-opkoms, vanaf sade wat in Maart 1986 in volgroeiende fynbos geplant is, betekenisvol verminder, maar die vermindering was net betekenisvol by die perseel met die hoogste digtheid van kleinsoogdiere. Saadpredasie het nie saailing-opkoms vanaf sade wat in Julie, Augustus en September 1986 in volgroeiende fynbos geplant is, betekenisvol verminder nie. Die primêre oorsaak van saailingsterftes in volgroeiende fynbos was verwelking, waarskynlik te wyte aan waterspanning. Na die brand het kleinsoogdierdigtheid afgeneem in die gebrande fynbos en toegeneem in die ongebrande woudrefugia tot agt maande na die brand, waarna dit in die fynbos toegeneem het tot 'n maksimum van 41 diere per 100 valnagte, twee jaar na die brand. Saailing-predasie deur kleinsoogdiere het 'n beperkte impak gehad na die brand, waarskynlik omdat hul getalle kort na die brand afgeneem het. Die invloed van saadpredasie het nie afgeneem met toenemende afstand vanaf 'n woudrefugium nie. Swampatogene en skade deur herbivoor insekte was die primêre oorsake van saailingsterfte na die brand. Kleinsoogdierdigtheid in volwasse fynbos 25–30 jaar na 'n brand was dalk te laag gewees om die verjonging van 'n tweede kohort van *Protea neriifolia*-saailinge te verhoed.

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Serotinous Proteaceae regenerate from seeds within the first year after a fire (Kruger & Bigalke 1984). The period between seed dispersal and completion of seedling establishment is an extremely vulnerable stage in the life-cycle of a plant (Grubb 1977; Harper 1977) and predation of seeds and seedlings during this period can affect the subsequent composition and structure of the plant community (Bond 1984; Bond, Vlok & Viviers 1984; Botha 1989; Manders & Botha 1989). Three different, but not necessarily mutually exclusive, hypotheses have been advanced to explain why seedling recruitment of serotinous Proteaceae was significantly higher after fires in mid-summer to mid-autumn (January to

April) than after winter and spring fires (Bond *et al.* 1984; van Wilgen & Viviers 1985; Midgley 1989). Firstly, variation in seedling recruitment is inversely proportional to the amount of time during which the seeds are exposed to rodent predation (Bond 1984). Seed germination is confined largely to autumn and winter (Bond 1984; Midgley, Hoekstra & Bartholomew 1989) so that seeds released after late-winter or spring fires are exposed to granivores for a longer period than after summer or autumn fires, and losses of seeds are correspondingly greater (Bond 1984). Secondly, variation in recruitment is linked to seasonal variations in the size of the seed store at the time of the fire (Jordaan

1949; Midgley 1989). Thirdly, variation in seedling recruitment is linked to the loss of seed viability or seed decay during prolonged exposure (e.g. after spring fires) (Midgley 1989).

Seed and seedling predation by small mammals are considered the primary factors limiting the recruitment of serotinous Proteaceae in mature fynbos and thus maintaining even-aged stands (Breytenbach 1984; Bond & Breytenbach 1985). Long-term studies of populations of *Protea neriifolia* R.Br. have shown, however, that it is able to regenerate successfully in the absence of fire, probably in gaps created by the death of senescent *P. neriifolia* plants (Kruger & Bigalke 1984; K.B. Higgins & P.T. Manders unpublished). These findings are not necessarily contradictory, as the abundance of rodents in mature fynbos more than 20 years post-fire is low (Willan & Bigalke 1982; Kruger & Bigalke 1984). These low densities may reduce seed and seedling predation levels, allowing *P. neriifolia* to establish seedlings.

Small mammal abundance declines rapidly following fires, presumably because the lack of cover in burnt areas exposes the animals, especially the diurnal species, to predators (Fox, Quinn & Breytenbach 1985; Breytenbach 1987; Midgley & Clayton 1990). As the vegetation cover increases the abundance of small mammals increases (Willan & Bigalke 1982; Fox *et al.* 1985). Little is known about the extent to which small mammals use unburnt refuges inside a burnt area. If seed and seedling predation have a significant impact on seedling recruitment then the size and availability of refuges could affect the recruitment success of serotinous Proteaceae. The impact should decrease with increasing distance from refuges because of the limited distance a small mammal can cover and because of increasing exposure of small mammals to predators with increasing distance from a refuge.

The effects of seed and seedling predation on the seedling recruitment of *Protea neriifolia* R.Br. were studied in the Swartboskloof valley near Stellenbosch before and after a fire. The area was burnt in a controlled fire on 17 and 18 March 1987. The dominant vegetation before the fire was a tall (2–3 m), 29-year-old shrubland dominated by *P. neriifolia*. Many of the mature *P. neriifolia* shrubs had died or begun to senesce and seedling recruitment of the second generation had already begun (K.B. Higgins & P.T. Manders unpublished). This study was designed to answer the following questions:

- (i) Is seedling recruitment in mature fynbos dependent on the abundance of small mammals?
- (ii) Is seedling recruitment after fires reduced by small mammals?
- (iii) Do small mammals use refuges after a fire and, if so, does the extent of seed and seedling predation decrease with increasing distance from a refuge area?

## Methods

Seed predation and seedling recruitment in mature fynbos

### Mammal abundance

Small mammals were trapped at two permanently marked sites (Sites 1 and 2) in Swartboskloof near Stellenbosch in a

29-year-old fynbos shrubland. Site 1 was located on a flat area with a slight northerly aspect on loamy soils derived from Cape granites and no exposed rocks or boulders. The vegetation was a tall (> 2 m) shrubland with a closed canopy dominated by *Protea neriifolia*. Site 2 was located on a rock and boulder-strewn, north-facing slope on sandy soils derived from Table Mountain sandstone. The vegetation was a tall shrubland with an open canopy dominated by *P. neriifolia* and *P. repens* (L.)L. and scattered clumps of *Widdringtonia nodiflora* (L.) Powrie (Cupressaceae).

At each site a small-mammal trapping grid (48 m × 48 m) was set out comprising 49 trap stations (7 × 7 grid) at 8-m intervals. One live Elliot folding trap was set at each station on four consecutive days and nights. Traps were baited with a mixture of peanut butter, lard and candle wax (1:1:1 by mass) melted together and mixed with rolled oats (2 parts by mass) (Willan 1986). No pre-baiting was done. Traps were visited daily and small mammals were permanently marked on first capture to track individuals and movements between trapping sites.

### Seed and seedling survival

*Seed source.* Seeds (technically fruit [achenes]) of *P. neriifolia* were extracted from freshly picked, sun-dried inflorescences and hand-sorted to separate the plump seeds, those with a firm, white embryo. About 90% of these sorted seeds will germinate in controlled conditions (Le Maitre 1990).

*Germination and mortality.* At each site three sets (replicates) of four large exclosures (1 m × 1 m and 0,20 m high of 14 mm diamond mesh) were set out in autumn (21 March 1986). Two exclosures in each replicate were open at the base, allowing small mammals in, and two were closed to ground level. Leaf litter may inhibit seed germination (McPherson & Muller 1969; Manders 1987) or hinder seed imbibition, so the litter in one open and one closed exclosure in each replicate was removed. As seeds left on the surface may be washed or blown out of exclosures (see Bond 1988), seed planting was used as a general practice in this study. Seed planting may, however, influence germination patterns in proteas (Lombaard 1971; Le Maitre 1990) so the effects of planting were tested as follows. Ten plump seeds of *Protea neriifolia* were sown on the soil surface in one half, and ten were pushed 3–5 mm into the soil, radicle end downwards, in the other half of each exclosure. The number of seeds which germinated and the fate of seedlings was monitored at monthly intervals. Seedling mortality was recorded as owing to either herbivory (either the shoots were removed below the cotyledons or the complete plant was consumed) or drought (where the leaves and stem had wilted).

*Seasonal predation.* In order to determine whether seedling predation varied seasonally, ten small exclosures (150 mm diameter and 250 mm high) were set out at each site on 9 July (mid-winter), 21 August (late-winter) and 17 September 1986 (spring). Four seeds were planted inside each exclosure and four seeds were also planted outside five of these exclosures when they were set out.

## Use of refuges and seed and seedling predation after fire

### Mammal abundance

Small mammals were trapped in five potential refuges two months before the fire. Four refuges were in tall forest (canopy > 10 m) along perennial streams and one in low forest on a boulder scree. Twenty live traps were set at random about 5 m apart in each locality on four consecutive days and visited daily. The bait was prepared and dispensed as described above and no pre-baiting was done. Small mammals were permanently marked on first capture. Trapping as described above, was carried out at these localities again immediately after the burn, one month later, thereafter bimonthly on three occasions, and quarterly on two occasions two and a half years after the burn. After the fire an additional refuge in a strip of tall forest along a perennial stream was selected and trapping began one month after the fire.

A third permanent small-mammal trapping grid, identical to those at Sites 1 and 2 was set out in the burnt area shortly after the fire. Before the fire the vegetation at this site (Site 3) was a tall open shrubland similar to that at Site 2 but with a low density of protea shrubs. The traplines were parallel to the ecotone between the burnt area and the additional forest refuge and 60 m from it (Figure 1). The trapping procedure was identical to that used before the fire. Trapping began at all three sites immediately after the fire, again one month later and thereafter bimonthly on five occasions, and 3–4 monthly on seven further occasions.

### Seed and seedling survival

**Germination and mortality.** Ten small exclosures were placed at 5-m intervals on each of seven parallel lines 20 m apart (Figure 1). The first line traversed the forest refuge 18 m from the ecotone between the forest and the burnt shrubland. The remaining lines were all situated in the burnt shrubland at increasing distances from the refuge, with the last three lines traversing Site 3. Four seeds were planted inside and outside each exclosure on 8 April 1987. Causes

of seedling mortality were classified into three categories: (i) herbivory, (ii) fungal attack (young seedlings showing typical symptoms of damping off, i.e. wilting and falling over, and older seedlings, which were killed by a form of the fungus *Colletotrichum gloeosporioides* (Penz.) Sacc., typically showing die-back and blackening of leaves and stems) and (iii) other causes (mainly from drought but including seedlings which disappeared in the period between visits).

**Seasonal predation.** Additional exclosures were set out to test for variation in seed and seedling predation during the first winter after the fire. Ten large (1 × 1 m) exclosures were set out at each pre-fire trapping site on 29 April at Sites 1 and 2 and on 8 May at Site 3. Five of these exclosures were open at the base, to allow small mammals in, and five were fully enclosed to ground level. Twelve seeds were planted in one half of each exclosure at establishment. Twelve seeds were planted in the other half of each of these exclosures on 29 May 1987 at Sites 1 and 2 and on 8 May at Site 3. On 30 June further sets of large exclosures were set out at all three sites and seeds were planted as described above. Seeds were planted in the other half of these exclosures on 30 July 1987.

In addition, five small exclosures (150 mm diam.) were set out at each site on 21 May, 19 June, 15 July, 19 August, 10 September and 22 October 1987. Four seeds were planted inside and outside each of these exclosures when they were set out.

### Statistical analyses

**Seed germination and predation and seedling survival.** The pre-fire large exclosure data was analysed as a balanced design with site (replicates), open versus closed exclosures ('plots') and with and without litter removal (treatments). Seed sowing and planting were interpreted as split-plot treatments. The small exclosure data were analysed using an unbalanced analysis of variance including site, date of establishment and site of planting as treatments. The post-fire data were treated in a similar fashion. The number of seeds which germinated in each treatment was analysed using an analysis of variance (GLM Procedure SAS 1985) of the log<sub>10</sub> transformed data except where otherwise specified.

### Mammal abundance

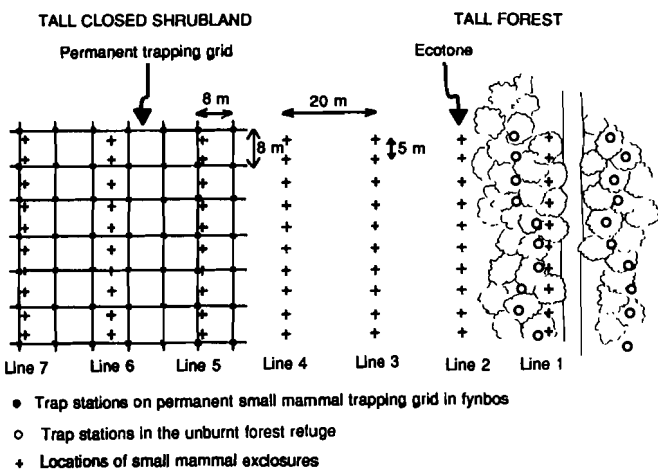
Mammal abundance is expressed as the total number of animals captured per 100 trapnights, a widely used density index. Mammal species nomenclature follows Meester, Rautenbach, Dippenaar & Baker (1986).

## Results

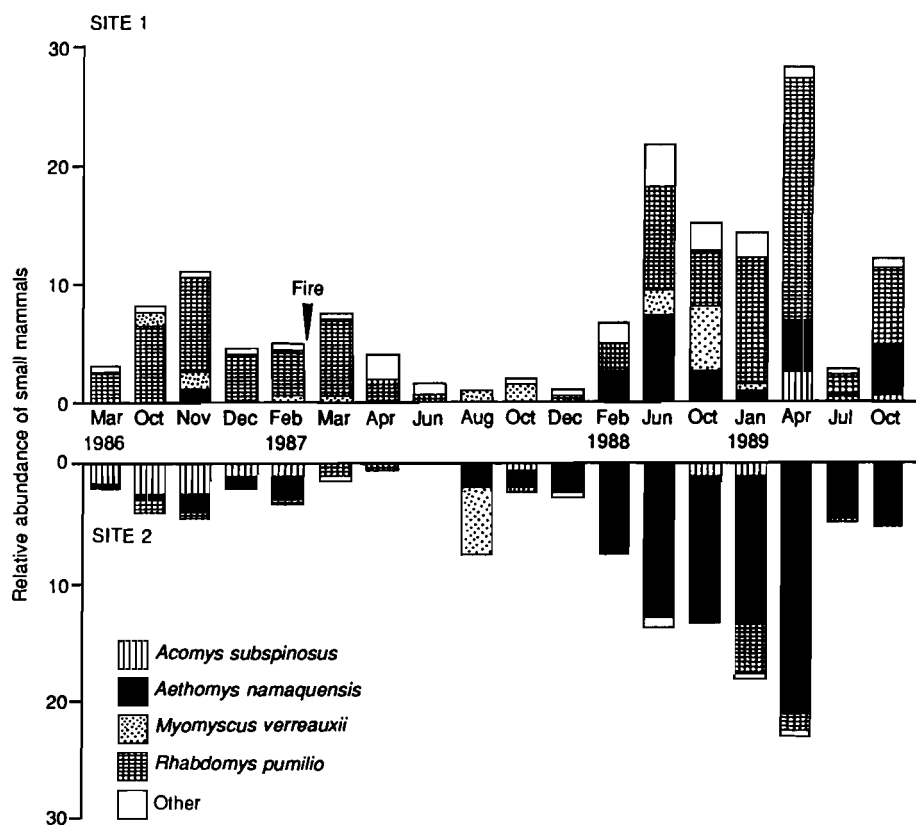
### Seed predation and seedling recruitment in mature fynbos

#### Mammal abundance

The mean abundance of small mammals during the trapping sessions in the year before the fire at Site 1 was twice as high as that at Site 2 (6,5 vs 3,3). *Rhabdomys pumilio* was the dominant species at Site 1, and *Acomys subspinosus* and *Aethomys namaquensis* were co-dominants at Site 2 (Figure 2). The numbers fluctuated seasonally reaching a maximum



**Figure 1** A diagram of the layout of trap stations in the forest refuge and the trapping grid at Site 3 showing the lines of small mammal exclosures, the extent of the forest and the burnt fynbos.



**Figure 2** The relative abundance (number of captures / 100 trapnights) of small mammal species on two permanent sampling sites in fynbos in Swartboskloof. Other species captured at Site 1 were *Crociodura flavescens*, *Myosorex varius*, *Mus minutoides* (only found after the fire at both sites) and an *Otomys* species. *Otomys* and *Myosorex* were not captured at Site 2. A fire occurred in March 1987.

of 11,2 and 4,6 at Sites 1 and 2, respectively, in November 1986.

#### Seed and seedling survival

**Germination and mortality.** Seed germination was not affected by the sowing method or the removal of litter (Tables 1 and 2). Significantly more seeds germinated in closed exclosures than in open ones at both sites and this accounted for most of the variance. There was a significant difference between the sites largely because all the seeds were removed from the open exclosures only at Site 1, which also had a greater abundance of small mammals (Figure 2). The effect of rodent exclusion differed significantly between sites (site  $\times$  rodent interaction, Table 2) because there was recruitment in the open exclosures at Site 2 but not at Site 1 (Table 1). The only other significant interaction was between site and seed planting method (Table 2), primarily owing to the higher recruitment from planted seeds at Site 2 compared with Site 1, but this accounted for only a small part of the total variance.

One hundred-and-sixteen (55,2%) of the 210 seedlings which germinated and survived predation inside the large exclosures on Sites 1 and 2, survived the first summer drought. Seedling survival after establishment was independent of rodent exclusion ( $0,5 > p > 0,1$ ; Chi-square test of independence), with an overall survival of 56% in treatments excluding rodents, compared with 50% in treatments not excluding rodents. Wilting of leaves and stems, presumably owing to water stress, was the primary cause of morta-

**Table 1** Seed germination (mean  $\pm$  standard deviation) in mature fynbos at two sites. Each treatment was replicated three times at each site. Ten seeds were planted in each treatment (20 per exclosure) in March 1986

Site	Substrate	Exclosure type			
		Open		Closed	
		Planting method		Planting method	
		sown	planted	sown	planted
1	Litter removed	6,0 $\pm$ 1,4	6,0 $\pm$ 3,0	0,0	0,0
	Litter left	8,0 $\pm$ 1,5	8,0 $\pm$ 0,8	0,0	0,0
	Mean germination (%)	70,0		0,0	
2	Litter removed	6,7 $\pm$ 1,5	7,2 $\pm$ 1,1	1,0 $\pm$ 0,8	6,7 $\pm$ 2,1
	Litter left	6,6 $\pm$ 1,3	7,5 $\pm$ 0,6	2,7 $\pm$ 2,4	3,0 $\pm$ 1,4
	Mean germination (%)	70,0		33,5	

lity (70 to 90% of the dead seedlings) and herbivory accounted for the remainder. Some of the wilted seedlings may have been killed by pathogenic fungi, but no damping off or discolouration of stems and leaves was observed.

**Seasonal predation.** Exclusion of small mammals did not have a significant effect on the germination of seeds planted later on during winter and spring 1986 (Table 3a, b) although the abundance of small mammals increased at both sites during the winter (Figure 2). At Site 1 slightly more of

**Table 2** The results of an analysis of variance on the  $\log_{10}$  transformed data summarized in Table 1. The higher level interactions were all non-significant and have been omitted

Source	Sum of squares	Degrees of freedom	F -ratio	Significance
Full model	30,14	4	54,69	**
Site	5,07	1	36,80	**
Litter removal	0,04	1	0,33	ns
Rodent exclusion	24,51	1	177,93	**
Planting	0,51	1	3,72	ns
Two way interactions				
Site $\times$ litter	0,11	1	0,79	ns
Site $\times$ rodent	4,35	1	31,60	**
Litter $\times$ rodent	0,14	1	0,99	ns
Site $\times$ planting	0,63	1	4,54	*
Litter $\times$ planting	0,18	1	1,30	ns
Rodent $\times$ planting	0,44	1	3,20	ns

ns = non significant; \* =  $p < 0,05$ ; \*\* =  $p < 0,01$ .

the seeds planted in July and August germinated inside than outside the exclosures, but at Site 2, where small mammal densities were lower, the differences were negligible. Germination success also decreased from July to September at both sites (Table 3a), and was lower than the 71% germination of seeds planted in March 1986 (Table 1).

#### Use of refuges and seed and seedling predation after fire

##### Mammal abundance

The overall mean abundance of small mammals in all the refuges before the fire was low (1,0 animals per 100 trap-nights). The dominant small mammal in the forest refuges before the fire was *Myosorex varius* (mean = 0,5) followed by *Myomyscus verreauxii* (0,3) and *Rhabdomys pumilio* (0,2). The fire did not burn through any of the refuges and only the forest fringes were scorched. Although the fire burned through all the fynbos sites, Site 1 was burnt in the early morning when conditions were moist and cool and it did not burn cleanly. The patches which did not burn were relit later in the day but Site 1 was not burnt as cleanly as Sites 2 and 3. The abundance of small mammals increased shortly after the burn in the refuge adjacent to Site 3 (Figure 3). Small mammal abundance decreased rapidly in the cleanly burnt fynbos at Site 2 (Figure 2) and was low at Site 3 in April 1987 (Figure 3) but remained relatively high at Site 1 (Figure 2). The mean abundance up to seven months after the fire was 5,2 in refuges compared to 2,5 in the burnt fynbos sites. By October 1987, seven months after the fire, small mammal abundance in the refuges and the burnt fynbos sites was essentially the same (Figures 2 and 3).

Only three small mammal species were captured in five forest sites before the fire. In the forest refuge adjacent to Site 3 the species richness increased to four species shortly after the fire and a total of six small mammal species were trapped in the forest refuges in March and April 1987. The number of species captured on the fynbos sites decreased after the fire, from six to four species, and only returned to pre-fire levels in August 1987 at Site 2 and February 1988

**Table 3** Results of an experiment to determine seasonal variation in seed predation in mature fynbos.

(a) Mean number of seeds ( $\pm$  the standard deviation) that germinated inside and outside small exclosures (150 mm diam.) by 22 October 1986. Five seeds were planted inside each of the 10 exclosures and outside five of the exclosures on each date

Site	Date of planting	Mean of number of seeds germinated	
		Inside	Outside
1	9 July 1986	3,2 $\pm$ 1,1	2,6 $\pm$ 0,5
	21 August 1986	3,3 $\pm$ 1,1	2,6 $\pm$ 1,3
	17 September 1986	1,5 $\pm$ 1,4	2,4 $\pm$ 1,5
	Mean germination (%)	53,3	50,7
2	9 July 1986	4,4 $\pm$ 0,7	4,2 $\pm$ 1,1
	21 August 1986	2,7 $\pm$ 1,3	2,8 $\pm$ 2,2
	17 September 1986	0,0 *	0,0 *
	Mean germination (%)	47,3	46,7

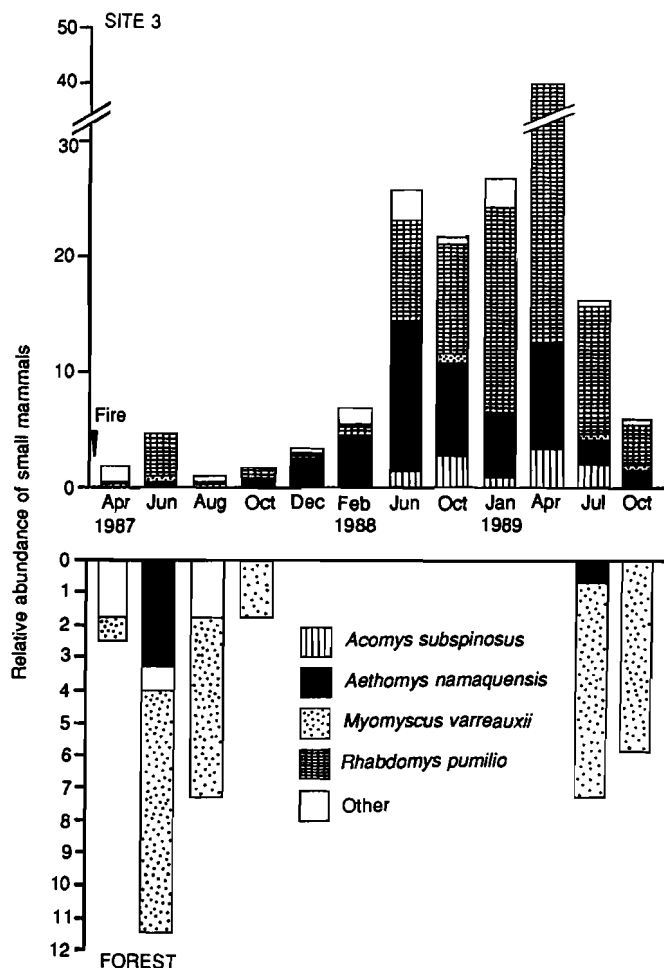
\* — no seeds had germinated by 22 October 1986.

(b) Results of an analysis of variance of the  $\log_{10}$  transformed germination data

Source	Sum of squares	Degrees of freedom	F -ratio	Significance
Full model	5,03	9	19,27	**
Site	0,23	1	7,96	**
Rodent exclusion	0,00	1	0,00	ns
Date of planting	3,04	2	52,41	**
Two way interactions				
Site $\times$ rodent excl.	0,01	1	0,30	ns
Site $\times$ date of planting	0,92	2	15,81	**
Rodent $\times$ date	0,09	2	1,57	ns

ns = non significant; \* =  $p < 0,05$ ; \*\* =  $p < 0,01$ .

at Sites 1 and 3. *Aethomys namaquensis*, *Myomyscus verreauxii* and *Acomys subspinosus* utilized the forest refuges effectively at a stage when conditions were unfavourable on the burnt fynbos sites. Their mean abundance in forest refuges declined abruptly to 3,9 in August and 3,2 in October 1987 (Figure 3) whereas their abundance in fynbos increased, at least on Site 3 (Figure 3). Our recapture data were generally disappointing, very few animals were trapped for more than one trapping session and only a handful moved between sites. Nevertheless, the data provide some support for emigration into forest refuges and subsequent recolonization of the burnt fynbos as the vegetation recovered. A *Rhabdomys pumilio* was trapped in fynbos in April and a forest refuge in July. A *Myomyscus verreauxii* was trapped in fynbos in March and a forest refuge in June. Movements from forest to fynbos were recorded for *Myomyscus*, *Rhabdomys* and *Acomys* in July and October 1987. Most of the recorded movements were, however, between fynbos sites and no small mammals moved between the trapping grid and the forest refuge at Site 3, a distance of 50–100 m. *Rhabdomys pumilio*, one of the dominant small mammals on the fynbos sites, was captured continuously in the burnt fynbos but only rarely in the forest refuges. It was



**Figure 3** The relative abundance (number of captures / 100 trap-nights) of small mammal species after a fire in March 1987 in burnt fynbos at Site 3 and in the adjacent forest refuge (see Figure 1 for the layout). Other species captured in the burnt fynbos were *Crocidura flavescens*, *Myosorex varius*, *Mus minuoides* (only after the fire at both sites) and an *Otomys* species. *Crocidura* and *Myosorex* were the only other species captured in the forest refuge.

not trapped at all in the forest refuge adjacent to Site 3 despite being abundant at this site after the fire (Figure 3).

**Seed and seedling survival**

**Germination and mortality.** *Protea neriifolia* seeds planted in the tall forest adjacent to Site 3 (see Figure 1) began germinating on the 8th of April 1987, long before those planted in small exclosures in the burnt fynbos (Figure 4). Four hundred and three seeds germinated in this experiment, which represented a germination success of 72%. The average germination success inside exclosures at fixed distances from the forest-fynbos ecotone was not significantly higher than that outside ( $p > 0,05$ ; Wilcoxon paired sample test). The survival of these seedlings during the first year after germination is summarized in Table 4. The overall seedling mortality was significantly higher outside than inside the rodent exclosures ( $P < 0,05$ ; Chi-square test of independence) but the number of seedlings killed by herbivory was independent of protection by exclosures (eight inside and 13

**Table 4** Percentage germination and mortality of *Protea neriifolia* seedlings during the first year following germination inside and outside small exclosures (150 mm diam.). Four seeds were planted inside and outside each of the 70 exclosures on 8 April 1987; 10 of the exclosures were located in an unburnt forest refuge, 10 in a partially burnt forest-fynbos ecotone and the remainder in fynbos burnt on 17 March 1987

	Percentage surviving	Percentage dead	Total seedlings	Percentage germination
Inside	56	44	214	76
Outside	46	54	189	68
Total seedlings	206	197	403	72

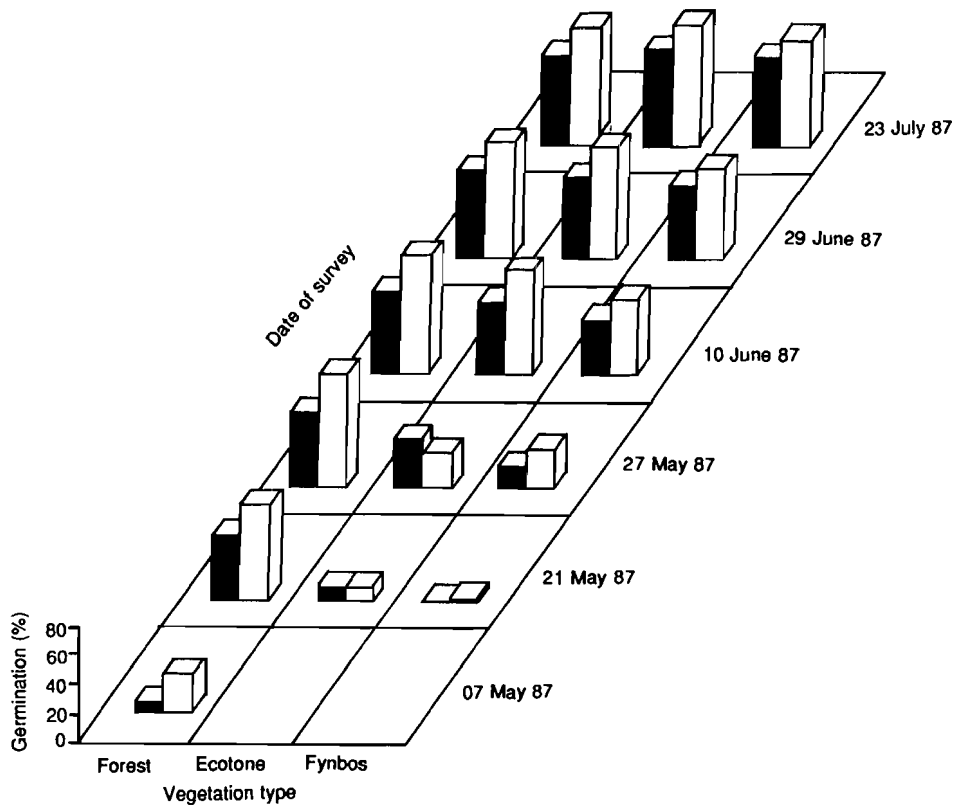
outside  $p > 0,05$ ; Chi-square test of independence). This suggests that invertebrate herbivores small enough to enter the exclosures were responsible for some seedling mortality in the first year.

Although seed germination in the forest was relatively high (Figure 4), none of the seedlings survived the winter. Herbivory and 'other' causes accounted for a greater percentage of seedling mortality in the forest than in the fynbos where pathogenic fungi were the major factor (Figure 5). Fungal diseases were the most significant known cause of seedling mortality in both the fynbos and the forest sites after the fire. The remaining pre-fire mortality was due to herbivory, indicating that herbivory by invertebrates was more important at this stage.

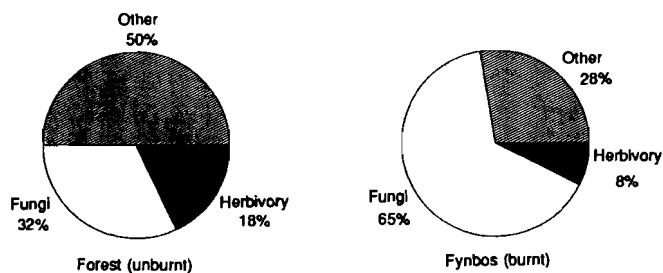
**Seasonal predation.** The germination success of seeds planted in large (1 × 1 m) and small (150 mm diam.) exclosures on different dates is summarized in Tables 5 and 6. Seed germination was slightly higher in open than in closed large exclosures after the fire (Table 5a) but not significantly so (Table 5b). Seed germination differed significantly between the sites, being significantly lower at Site 3 (mean = 8,65 seeds per exclosure) than Sites 1 and 2 (mean = 9,90 and 9,75 respectively,  $p < 0,05$  Tukey test GLM Procedure SAS 1985, Table 5b). In the parallel small exclosure experiment seed germination was significantly lower outside than inside the exclosures (mean = 2,56 and 2,92 respectively, Table 6a,b). The greatest differences between outside and inside were found at Site 3 but there was virtually no difference at Site 1 (Table 6a). At Sites 2 and 3 the difference increased with planting date to a maximum after the September plantings. In both experiments there was a significant decline in seed germination from a maximum of about 80% in April (Table 5a,b) to about 32% after planting in September. These patterns were not strongly related to small mammal abundance although the smallest reduction in seed germination was at Site 1 (Table 5a) where the mean small mammal abundance from April to October 1987 was 1,80 compared with 2,69 at Site 2 and 2,19 at Site 3.

**Discussion**

Seedling regeneration in mature stands of serotinous Proteaceae appears to be limited to a large extent by granivory and



**Figure 4** Cumulative germination (percent) of *Protea neriifolia* seeds planted in three different habitats: a forest refuge, the forest-fynbos ecotone and in burnt fynbos. Seeds were planted outside (shaded bars) and inside (unshaded bars) small mammal exclosures.



**Figure 5** Causes of mortality of *Protea neriifolia* seedlings in an unburnt forest and a burnt fynbos community.

herbivory by small mammals, as hypothesized by Breytenbach (1984), but only when small mammal abundance is relatively high. In this study, for example, there was no germination and seedling establishment under the open large exclosures at Site 1 before the fire (Table 1). Here *Rhodomys*, an omnivore, was dominant and occurred in relatively high numbers (Figure 2). At Site 2 *Acomys*, a granivore, and *Aethomys*, an omnivore, occurred in lower numbers (Figure 2) and significantly fewer seeds germinated in the open than in the closed large exclosures (Table 2). Seed predation had only a small, non-significant impact on seeds planted later that winter at Sites 1 and 2 (Table 3), despite an increase in small mammal abundance during this period (Figure 2). The most likely explanation for this discrepancy is that seeds planted in March were exposed for about 50 days before germination began, compared with 20 to 25 days in seeds planted later (Le Maitre unpublished data). The longer

exposure could have resulted in the predation of a greater proportion of the seeds. An alternative explanation is that the dietary preferences of small mammals vary over time depending on food availability. *Acomys* ate more seeds in March than at other times in studies in the Cedarberg (Botha 1989). The germination of *Protea neriifolia* seeds was not inhibited by a litter layer on the soil or allelopathic chemicals in the litter, unlike *Widdringtonia cedarbergensis* (Manders 1987).

After the fire small mammal densities declined rapidly as found at other sites burnt in the same fire (Van Hendsbergen, Botha, Forsyth & Le Maitre, in press) and in the southern Cape (Midgley & Clayton 1990). The proteas released large quantities of seeds with *Protea neriifolia* releasing its seeds over a period of several months. About 50% and 85% of the inflorescences on the shrubs had released all their seeds by the end of April and May 1987, respectively (Le Maitre, unpublished data). The mean density of seeds of serotinous Proteaceae (primarily *P. neriifolia*) on the soil surface at the three trapping sites one and three weeks after the fire was about 340 seeds per square metre. More than 97% of these seeds contained no embryo (Le Maitre, unpublished data).

Full and empty seeds of *P. neriifolia* can be reliably sorted by feel and, to some extent, colour (Le Maitre 1990). If small mammals are unable to distinguish between full and empty seeds without manipulating them, their efficiency as granivores would be markedly reduced by the large proportion of empty seeds. Bond & Breytenbach (1985) found that rodents could locate buried *P. repens* seeds by smell, but they may not be able to separate full from empty seeds in

**Table 5** Results of an experiment to determine seasonal variation in seed predation after a fire on 18 March 1987. (a) Mean number of seeds ( $\pm$  standard deviation) which had germinated by 22 October 1987 in large (1  $\times$  1 m) exclosures. Twelve seeds were planted in each exclosure on each date

Site	Date of planting	Number of seeds germinated	
		Inside	Outside
1	29 April 1987	11,4 $\pm$ 0,8	11,4 $\pm$ 0,9
	29 May 1987	9,4 $\pm$ 3,2	8,8 $\pm$ 1,3
	30 June 1987	10,0 $\pm$ 1,4	10,4 $\pm$ 2,5
	30 July 1987	7,8 $\pm$ 1,6	10,0 $\pm$ 1,2
	Mean germination (%)	80,4	84,6
2	29 April 1987	10,0 $\pm$ 1,9	10,8 $\pm$ 0,4
	29 May 1987	8,8 $\pm$ 2,5	11,0 $\pm$ 0,7
	30 June 1987	9,8 $\pm$ 1,6	9,4 $\pm$ 2,7
	30 July 1987	8,8 $\pm$ 2,0	9,2 $\pm$ 1,3
	Mean germination (%)	77,9	84,2
3	8 May 1987	10,0 $\pm$ 1,4	11,0 $\pm$ 1,0
	29 May 1987	8,2 $\pm$ 2,9	9,8 $\pm$ 2,5
	30 June 1987	8,8 $\pm$ 1,5	10,4 $\pm$ 1,1
	30 July 1987	5,6 $\pm$ 1,8	4,8 $\pm$ 1,9
	Mean germination (%)	69,2	75,0

(b) Results of an analysis of variance of the log<sub>10</sub> transformed germination data

Source	Sum of squares	Degrees of freedom	F-ratio	Significance
Full model	0,74	18	4,65	**
Site	0,14	2	7,84	**
Rodent exclusion	0,02	1	1,79	ns
Date of planting	0,40	4	11,36	**
Two way interactions				
Site $\times$ rodent excl.	0,00	2	0,03	ns
Site $\times$ date of planting	0,20	5	4,54	**
Rodent $\times$ date	0,01	4	0,23	ns

ns = non significant; \* =  $p < 0,05$ ; \*\* =  $p < 0,01$ .

this fashion. The data from this study suggest that mass dispersal of *P. neriifolia* seeds after the fire and the high densities of empty seeds resulted in the satiation of the few resident granivores so that the degree of predation did not decrease with increasing distance from the refuges. These findings support the hypothesis that selective pressure to reduce seed predation has been an important factor in the evolution of serotiny (O'Dowd & Gill 1984).

By the time small mammal abundance recovered again in late 1987 and early 1988 (Figures 2 and 3, Van Hendsbergen *et al.*, in press) seed germination had ended. Herbivory seems to be a relatively minor cause of seedling mortality (Figure 5), supporting Bond's (1984) finding that seed germination is an effective escape from herbivory. Granivory by small mammals was more important before than after the fire in the exclosure studies, largely because the few granivores remaining after the fire were effectively satiated by

**Table 6(a)** Mean number of seeds ( $\pm$  standard deviation) which had germinated by 22 October 1987 inside and outside small exclosures (150 mm diam.). Four seeds were planted inside and outside each exclosure and five exclosures were set out on each date at each site

Site	Date of planting	Number of seeds that germinated	
		Inside	Outside
1	21 May 1987	3,0 $\pm$ 1,7	3,0 $\pm$ 1,4
	19 June 1987	3,4 $\pm$ 0,5	3,0 $\pm$ 0,0
	15 July 1987	2,8 $\pm$ 0,8	2,8 $\pm$ 1,3
	19 August 1987	2,8 $\pm$ 1,1	2,8 $\pm$ 0,8
	10 September 1987	1,2 $\pm$ 1,3	1,2 $\pm$ 1,3
Mean germination (%)		66,0	64,0
2	21 May 1987	3,6 $\pm$ 0,5	3,8 $\pm$ 0,4
	19 June 1987	3,4 $\pm$ 0,5	3,8 $\pm$ 0,4
	15 July 1987	3,4 $\pm$ 0,9	3,6 $\pm$ 0,9
	19 August 1987	3,0 $\pm$ 0,7	2,4 $\pm$ 0,5
	10 September 1987	2,0 $\pm$ 1,4	0,8 $\pm$ 0,4
Mean germination (%)		77,0	72,0
3	21 May 1987	3,8 $\pm$ 0,4	3,4 $\pm$ 0,5
	19 June 1987	3,8 $\pm$ 0,4	3,4 $\pm$ 0,9
	15 July 1987	3,2 $\pm$ 1,1	2,6 $\pm$ 1,3
	19 August 1987	2,6 $\pm$ 0,9	1,2 $\pm$ 1,1
	10 September 1987	1,8 $\pm$ 1,6	0,6 $\pm$ 0,9
Mean germination (%)		76,0	56,0

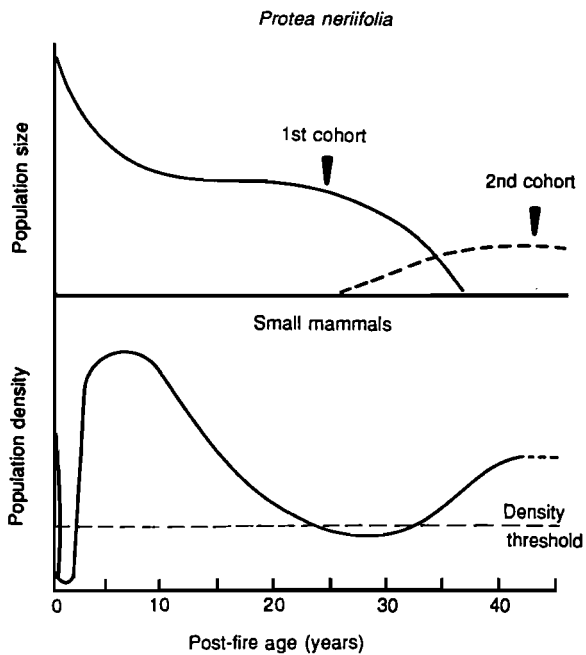
(b) Results of an analysis of variance of the log<sub>10</sub> transformed germination data

Source	Sum of squares	Degrees of freedom	F-ratio	Significance
Full model	3,20	21	6,70	**
Site	0,10	2	2,18	*
Rodent exclusion	0,10	1	4,40	**
Date of planting	2,61	4	28,62	**
Two way interactions				
Site $\times$ rodent excl.	0,08	2	1,82	ns
Site $\times$ date of planting	0,20	8	1,10	ns
Rodent $\times$ date	0,12	4	1,27	ns

ns = non significant; \* =  $p < 0,05$ ; \*\* =  $p < 0,01$ .

the large numbers of *Protea neriifolia* seeds. Water-stress induced wilting and death was the most important cause of seedling mortality in mature fynbos, but about half the seedlings survived the summer drought. Fungal pathogens, notably *Colletotrichum gloeosporoides*, were more important after the fire. This same fungus is known to kill adult *Hakea sericea* Schrad. (Proteaceae), an invasive alien plant (Richardson & Manders 1985) and *H. sericea* seedlings are apparently highly susceptible (M. Morris, pers. comm. 1990). More studies are needed to determine the significance of fungal pathogens in seedling mortality of indigenous Proteaceae after and between fires before any conclusions about the general importance of fungal pathogens can be reached. Stomach contents of *Rhodomys*, *Aethomys* and *Myomyscus* trapped after the Swartboskloof fire comprised





**Figure 6** A simplified model of the changes in the populations of *Protea neriifolia* (adapted from K.B. Higgins and P.T. Manders unpublished) and small mammal abundance in Swartboskloof: (a) the mortality of the first post-fire cohort and the recruitment of a second cohort of seedlings of *P. neriifolia*, and (b) the successional changes in small mammal abundance after fire. The density threshold above which small mammals limit seedling recruitment is also shown.

45% seeds (largely from *Protea* spp.), 50% plant material and insects and unidentified remnants the remainder (Botha, unpublished data), confirming that seeds form a relatively large part of the diet of fynbos rodents after fires (Breytenbach 1982; Bond 1984).

We suggest the following model for the seedling recruitment patterns observed in *Protea neriifolia* populations at Jonkershoek (Figure 6): After the initial post-fire seedling recruitment there is no more recruitment before the plants mature. Small mammal abundance peaks during this period and then declines as found by Toes (1974) and Willan & Bigalke (1982). This decline continues until *P. neriifolia* reaches maturity and maximum fecundity, (between 15 and 25 years of age) but small mammal densities remain high enough to prevent recruitment from seeds released from the inflorescences of dying shrubs. At about 25 years of age *P. neriifolia* shrubs in the study area began to senesce. Gaps were created in the canopy and the dying shrubs released their seeds. At this stage small mammal densities were too low to prevent seedling recruitment. This proposition is supported by successful seedling recruitment which was observed in a population of *P. neriifolia* near Site 1 between 28 and 35 years of age (Figure 6a, K.B. Higgins & P.T. Manders unpublished data). As a result of the gaps formed in the canopy, the understory community recovers (Van Wilgen 1981) and the availability of seeds and palatable plant material allows small mammal abundance to increase again (Willan & Bigalke 1982), limiting any further recruitment.

## Conclusions

This study has shown that small mammals, pathogenic fungi, and moisture stress during summer are important determinants of the recruitment of *Protea neriifolia* and thus the structure of both the mature and the regenerating stand. The impact of small mammals depended on their abundance; where densities were low seed predation by small mammals had little effect on seedling recruitment. The large quantities of seeds released after the fire also appeared to reduce predation levels by satiating the few small mammals remaining after the fire. This study has also shown that fire patchiness and the distribution of refuges for granivores and herbivores may not be important. These conclusions are based, however, on a fire in March. Granivores and herbivores could have a much more significant impact after a fire in spring, for example, when the prolonged exposure of the seeds would have resulted in greater seed predation and herbivory levels. Studies of the impact of granivores and other biotic factors influencing plant regeneration should be an integral part of any study of plant population dynamics.

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