BIOTIC RESISTANCE TO THE INVASION OF *PINUS RADIATA* INTO MOUNTAIN FYNBOS

BOTANY HONOURS PROJECT

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ABSTRACT

Pinus radiata is a serious invader of mountain fynbos. This study aimed to answer the following questions: a) is there a post-fire age at which fynbos is no longer susceptible to invasion by *P. radiata*? and b) what role do natural seed and seedling predators play in inhibiting invasion by this species? The age structure of *P. radiata* populations invading mature fynbos was determined at three plots in the Jonkershoek State Forest. Predation studies on seed and week-old seedlings were performed at a four-month burn and an adjacent stand of mature fynbos on the Cape Peninsula.

Age structure data showed that the invading populations were essentially even-aged but that recruitment generally occurred between fires. Differences between this and similar studies are ascribed to clearing practices. Fynbos appears to be open to invasion by *Pinus radiata* only when in the mature phase (10 - 30 years) and undisturbed.

Minimal predation on seed or seedlings was observed in the burnt site. This is ascribed to the absence of rodents here. Rodents removed all accessible seeds within a week at the mature site. Mortality of unprotected seedlings was very high (>80%) at this site after 7 weeks, mostly due to predation by rodents, probably *Otomys sp.*. Although limited by not considering the effects of seasonal water stress, this study shows that rodents potentially provide a major biotic resistance to the recruitment of *Pinus radiata* into fynbos.

INTRODUCTION

Effective control of invasive alien plants requires an understanding of their patterns of invasion and the processes responsible for these patterns. The need for a better comprehension of patterns of invasion in the fynbos biome, which is severely threatened by over 30 invasive species (MacDonald & Jarman 1984) has frequently been acknowledged. This study was undertaken to explore some of the patterns and processes involved in the invasion of mountain fynbos by *Pinus radiata*.

Pinus radiata, which is native to small areas on the Californian coast (Vogl *et al*. 1977), has been used in afforestation in South Africa since about 1910 (Poynton 1960 in Richardson & Brown 1986) and is presently the chief commercial softwood species in the southern and western Cape (Grey 1989). It has also become naturalised in mountain fynbos where it is recognised as a major weed (eg. MacDonald & Jarman 1984, Richardson & Brown 1986). Dense stands of *P. radiata* may have highly detrimental effects on natural vegetation (Richardson & Van Wilgen 1986), streamflow and soil properties; they also increase the fire hazard (Kruger 1977).

In terms of its life history traits (see McCune 1988), this is potentially the most threatening of the invasive pine species in the fynbos biome (Richardson, Cowling & Le Maitre submitted). *Pinus radiata* attains reproductive maturity by the age of about 8 years and is serotinous, releasing large quantities of highly dispersible seeds (Van Wilgen & Siegfried 1986) after fire. The cones also open in hot, dry conditions (Bannister 1965; Dean, Holmes & Weiss 1986) so that natural vegetation within a wide radius of mature *P. radiata* plantations is susceptible to a constant, if erratic, seed-rain.

In recent years the determination of population age structure has been an effective means of describing the pattern of invasion of several pine species into the fynbos (Richardson & Brown 1986; Richardson 1988; Richardson, Cowling & Le Maitre submitted) and elsewhere (Van der Sommen 1986). In general, the pattern observed is that the majority of trees recruit in the immediate post-fire period, so that the populations tend towards even-agedness, but that recruitment is not limited to this period.

The phenomenon that the natural vegetation of the fire-disturbed Mediterranean-type heathlands of the world is even-aged,is frequently noted (Christensen & Muller 1975a,b; Kruger 1979; Bond 1984; Cowling & Lamont 1987). Reasons proposed for the failure of establishment in mature vegetation include competition with already-established plants for water or light (Miles 1973; Christensen & Muller 1975a) and allelopathic effects (Christensen & Muller 1975a, 1975b), although the evidence for the role of seed and seedling predation is the most convincing (Christensen & Muller 1975a, 1975b; Bond 1984; Breytenbach 1984; Bond & Breytenbach 1985; see also references in Quinn 1986).

Much has been written, both in South Africa (eg. Grut 1965; Donald 1969; Bigalke 1980) and elsewhere (eg. Smith & Aldous 1947; Sullivan & Sullivan 1982) on the way that predators retard afforestation with pines. No quantitative studies have, however, been performed on the potential role of predators in restricting the invasion of natural fynbos habitats by pines.

This study therefore aimed to answer the following two questions:

i) Given that the recruitment of *Pinus radiata* into fynbos is not limited to the period immediately after a fire, is there nevertheless some post-fire age at which fynbos is no longer susceptible to invasion by this species? Previous studies have not considered specifically the relationship between age structure of pines and the corresponding age of the fynbos.

ii) What potential role do seed and seedling predators play in controlling the invasion of *P. radiata* into mature fynbos?

The study consisted of two parts. Firstly, the age structure of three self-sown *Pinus radiata* populations was determined and related to the age of natural vegetation invaded. Secondly, a comparison was made between predation on seed and seedlings of *P. radiata* in a four-month old summer burn and that in an adjacent 12-year-old stand of fynbos. The first part of the study was performed at Jonkershoek near Stellenbosch, the second at Scarborough on the Cape Peninsula.

METHODS

Age structure of invading *Pinus radiata* populations

In order to show the pattern of *Pinus radiata* invasion into fynbos in the years following a fire, the ages of all self-sown *Pinus radiata* trees invading fynbos of over ten years was ascertained at three plots; the plots were also surveyed for pine seedlings. Other pine species were noted but not aged for the purpose of this study.

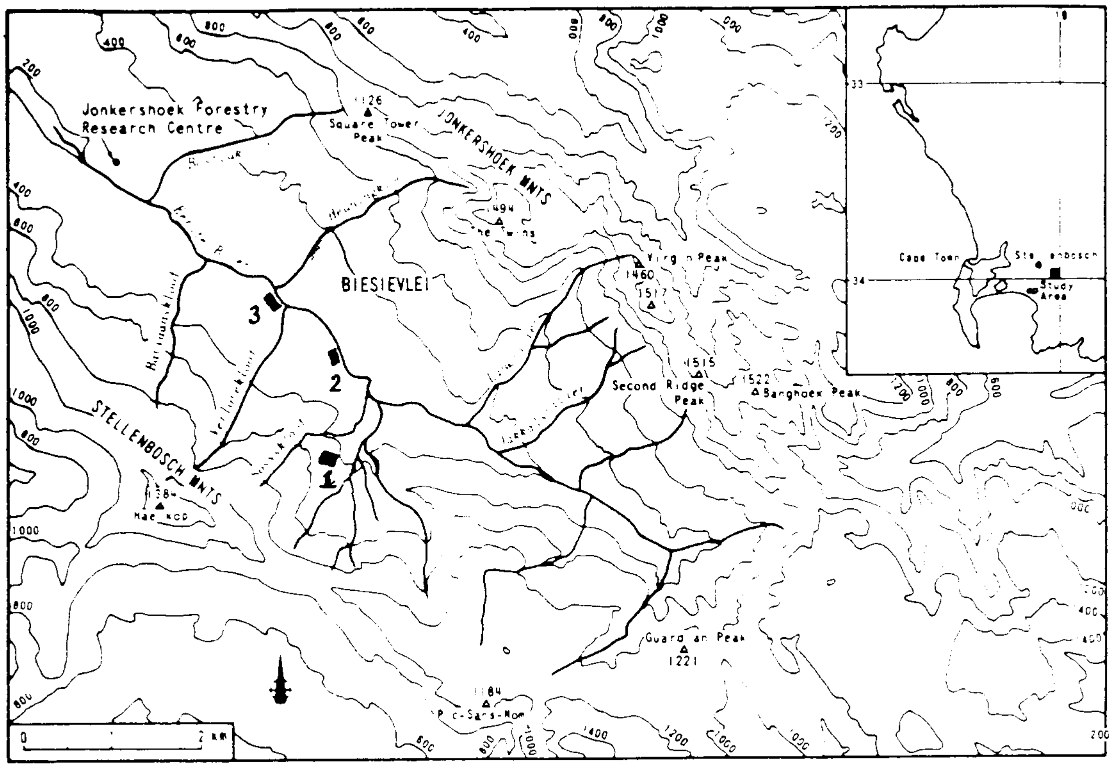

Figure 1 Part of the Jonkershoek State Forest, south-western Cape, showing the position of the plots used for age structure determination of *Pinus radiata*. After Richardson & Van Wilgen (1986).

The plots were all located in the Jonkershoek State Forest in the south-western Cape (33°57′S, 18°55′E). The climate, geology and soils of this area have been described elsewhere (Heth & Donald 1978). Figure 1 shows the position of the plots; all were within 200m of a plantation of *Pinus radiata* and differed in size according to the size of invaded area which was found. Fire records were available for the first plot only; the age since fire was determined by counting the nodes of *Protea repens* and *P. neriifolia* at plots 2 and 3 respectively. A number of independent counts were made and an average obtained.

Age structuring was performed following the method of Arno and Sneck (1977 in Richardson, Cowling & Le Maitre (submitted). All pines were felled below 60cm height except for a few which were too large; core samples were taken from these using an increment borer. A section was cut from the base of each felled tree, oven-dried at 90° C for 24-48 hours and then sanded using a belt sander. Ages were determined by counting growth rings; this was done by two or three people to reduce error. Some problems of this method have been discussed by McBride (1983) but estimates should be accurate to within a year or two (P. Brown pers. comm.).

From the estimated ages it could be determined in which year since the last fire the pines had recruited. The percentage number of pines which recruited in each year was converted to a cumulative percentage. This was plotted against age of fynbos to see whether there was any consistent pattern.

Seed predation and seedling survival study

Study site

The aim of this part of the study was to compare predation rates on pine seed and seedlings in recently burnt and mature fynbos. The site chosen was an approximately 12-year-old community and an adjacent area which had been burnt in February 1989. This is situated beyond Scarborough on the Cape Peninsula on land belonging to the Four Ways Nursery (34°15′S, 18°25′E). The site is at an elevation of about 90m, faces west and is gently sloping. Soil is highly infertile, ~~covered with~~ leached, white sand. The vegetation of the mature area may be described as ericaceous fynbos with cover ranging from total (100%) to very sparse (20%) in patches. Cover at the burnt site was very low at the commencement of the study (5%), provided mostly by resprouting Proteaceae and geophytes.

There was substantial evidence of rodent presence (burrow entrances, runs and faeces) in the mature area but not in the burnt area.

Pinus halepensis appears to be an important invader in the vicinity (pers.obs.) and some burnt individuals of *P.pinaster* were found in the burnt area. A dense stand of *Acacia saligna* was situated approximately 50m from the plot in the mature fynbos.

Seed predation study

The experiment was set up on 7 June 1989. In each area (burnt and mature), twenty-seven replicates were set up at five-metre intervals in a rectangular grid design (nine by three replicates). The corner replicates were at least 30m from the road separating the two areas, in order that any rodents from the mature site would not enter the burnt site or vice versa (rodent runs are unlikely to exceed 30m, S.Botha pers. comm.). Each replicate consisted of two petri dishes buried 20-40cm apart with the rims just protruding. Four *Pinus radiata* seeds (wings removed) were pressed lightly into the soil in the dishes. One dish ("protected") was covered with a chicken wire exclosure (14mm diamond mesh, 150mm basal diameter and 250mm high) secured firmly with pegs to exclude vertebrate seed predators. The uncovered dish ("open") was marked with a plastic nursery stick for easy location. In the mature site the replicates were generally located in small clearings.

The site was revisited two and nine days after setting up and seed loss determined by inspection or by sieving the soil where necessary. By the ninth day, however, rodents had entered the exclosures in the mature site (rodent faeces and seed husks were found inside them), apparently through the holes, not by burrowing underneath the wire. This part of the study was then discontinued.

Seedling predation and survival

As most seeds in the mature site had been predated, germination in the field could not be studied; instead seedlings germinated in a nursery were used. "Improved" seed was soaked in Kelpak for 24 hours to separate viable from unviable seed; one percent of the seed weight of Kaptan (a fungus inhibitor) was then added. Seeds were stratified for 46 days at 2-3°C, following which they were sown in vermiculite and kept in a growth chamber (12 daylight hours, 25°C day temperature, 15°C night). They were planted at the site at an age of about one week and watered at the same time.

The design was similar to that of the seed study although several changes were made. Firstly, owing to a limited number of "healthy" seedlings available, only fifteen replicates could be set up at each site. In general, the groups of seedlings consisted of three "unhealthy" and one "healthy" seedling. Secondly, the exclosures were covered with 40% shade-cloth from the base to 15cm height in order to exclude rodents, yet keep shading to a minimum. As this was nevertheless expected to alter the microclimate, a second control ("exposed") was added by propping up one side of another cage just enough to allow rodent entry (about 5cm) but imitate the microclimatic conditions of the experiment. Each replicate thus consisted of two controls ("exposed" and "open") and the experiment ("protected").

The seedlings were censused on five occasions from planting to about seven weeks and probable causes of mortality were recorded at the same time. Owing to time constraints, however, the "open" seedlings were planted only on the 2-day census of the others and were thus censused on four occasions.

RESULTS

Age structure of invading *Pinus radiata* populations

Table 1 Size and post-fire age of three plots in the Jonkershoek State Forest, south-western Cape, and descriptive statistics of the *Pinus radiata* populations invading these plots.

Plot	Extent (ha)	Age since fire	No. of trees	Age structure of invading *P. radiata* populations				
				Mean (s.d.)	Median	Mode	Min	Max
1	2	12	87	7.8 (1.5)	8	8	5	11
2	1	16	75	9.0 (1.8)	9	10	4	13
3	0.4	23	43	7.7 (1.7)	8	8	4	12

The size and post-fire age of each plot, as well as statistical information about the invading *Pinus radiata* populations, is given in Table 1. Fynbos in all plots was mature (10-30 years) (*sensu* Kruger & Bigalke 1984). From the maximum pine ages it is clear that all the trees in these sites have recruited since the last fire, while the minimum ages reflect the fact that no seedlings were found at any of the sites. The closeness in mean, median and modal ages indicates that the populations are essentially even-aged, but the spread of ages shows that recruitment was not limited to the immediate post-fire period.

Figure 2 shows the pattern of invasion of *P.radiata* at the three plots in relation to the age of fynbos.

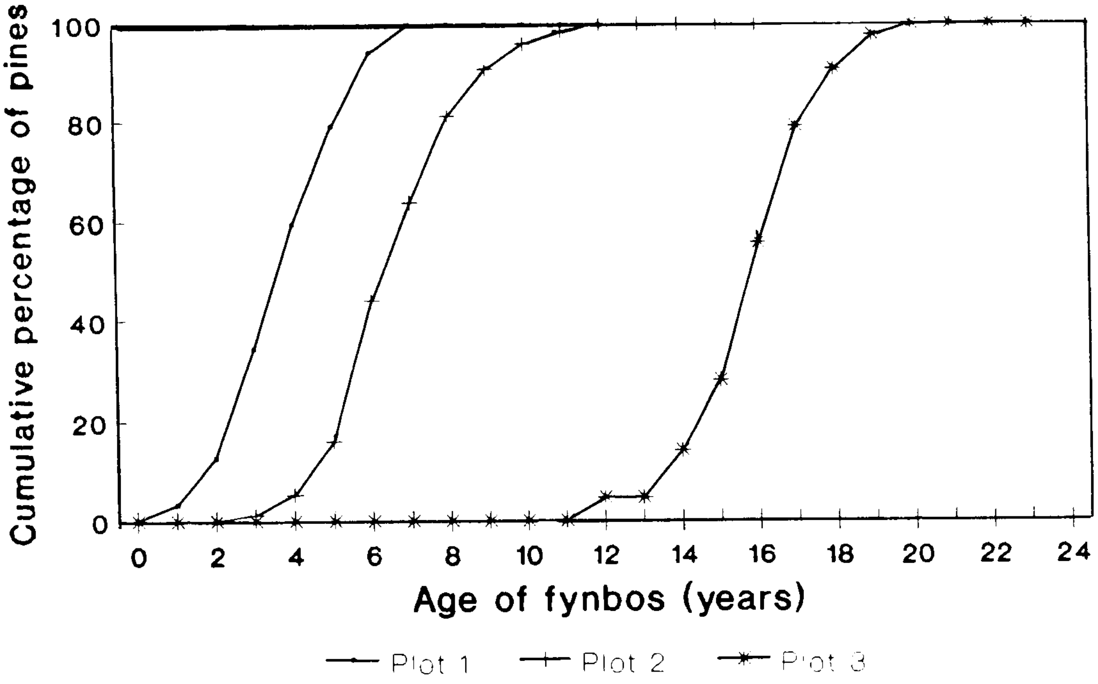

Figure 2 The pattern of invasion of *Pinus radiata* into mature fynbos at three plots in the Jonkershoek State Forest. See text for explanation of how the graphs were derived.

In each case a similarly-shaped curve was obtained : there was an initial one to three year period of low recruitment followed by a six to nine year period of major recruitment, with very little to no recruitment in the past three to five years. The difference between the graphs is seen in their starting points, particularly in the third plot in which recruitment appeared to be initiated only when the fynbos was eleven years old. From the slopes of that part of each graph representing one year's recruitment it can be seen that most trees surviving to the present recruited in the fourth, sixth and sixteenth year in plots 1, 2 and 3 respectively.

One *Pinus pinaster* tree and one tree of an unidentified pine species were found at plots 1 and 2 respectively.

Seed predation

The results of the seed predation study are given in Table 2. In the burnt site, there was no significant difference between number of seeds present in the exclosures and that in the open after either two (p=0.208) or nine days (p=0.083, one-tailed Fisher exact test). In the mature site, the difference between number of seeds in the exclosure and open after two days was clearly significant (one-tailed Fisher exact test, $p < 0.001$); the low value inside the exclosures after nine days reflects seed predation by rodents small enough to climb through the mesh.

Table 2 Results of predation study on seed of *Pinus radiata* in a four-month summer burn and an adjacent 12-year-old fynbos stand at Scarborough, Cape Peninsula. Total numbers of seeds (out of a possible 108) remaining after 2 and 9 days are given.

	Burnt site		Mature site	
No. of days	Protected	Open	Protected	Open
2	103	99	105	56
9	101	94	21	0

In the burnt site the loss of seeds appeared to be due primarily to wind as the seeds were generally found displaced a short distance from the dishes. Three seed husks and one partially-chewed seed were also found, however, suggesting predation, but the predator could not be determined. The causes of seed loss in the mature site is assumed to be predominantly or exclusively due to rodent predators because of the circumstantial evidence of fresh rodent faeces, seed husks *in situ* or nearby (see Bond & Breytenbach 1985) and signs of digging which had displaced some of the dishes. All four seeds had been removed in each case of obvious predation by rodents.

Seedling survival

The cumulative percentage decrease in seedling survivorship over time at both sites (all replicates in each treatment combined) is shown in Figures 3 a) and b). The data for one replicate in the mature site was discarded as it was set up a few days after the others. Although in the burnt site there appears to be a slightly better survival of seedlings in the "open", application of the Kolmogorov-Smirnov two-sample test to the data in pairs showed no significant difference between any of the comparisons ("protected" vs "exposed" : KD = 1; "protected" vs "open" : KD = 2; "exposed" vs "open" : KD = 2). Neither was there any significant difference between "exposed" and "open" in the mature site (KD = 3). The results for "exposed" were significantly lower than those for "protected", however (KD = 5, $\alpha < 0.01$), and thus those for the "open" as well.

The causes of seedling mortality in the burnt area appeared to be primarily physical - many seedlings wilted and shrivelled, suggesting water stress. Some seedlings had chlorotic or red needles, while strong winds and rain buried others in sand. Small pieces of seedling material which were sometimes found next to damaged or destroyed seedlings in each treatment type may be evidence of insect predation. Insect numbers at the site increased during the course of the study and a caterpillar was found on one seedling. What appeared to be rodent faeces were found on four occasions but there was no clear evidence of seedling predation by rodents.

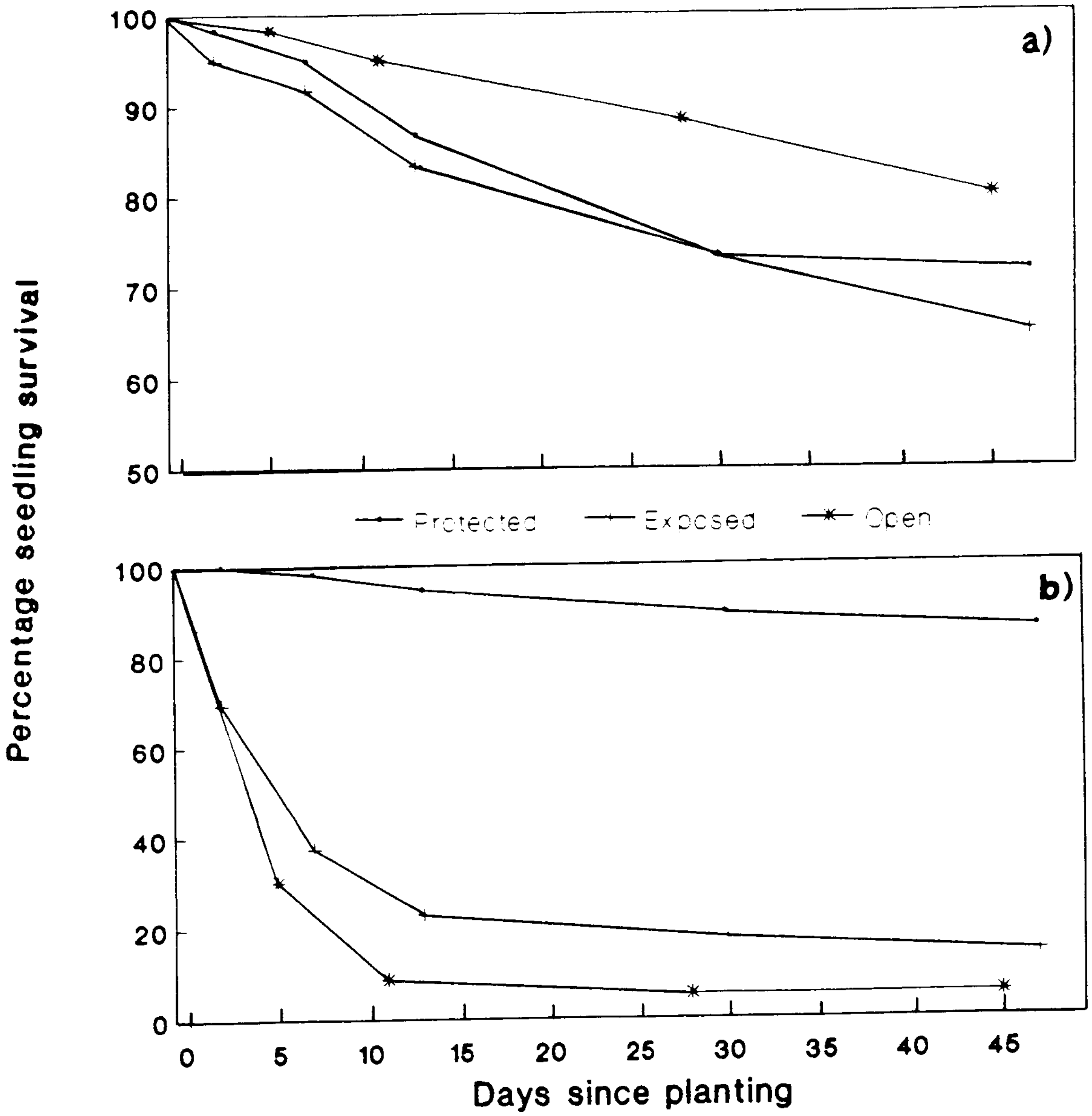

Figure 3 The percentage decrease in seedling survivorship of *Pinus radiata* seedlings in a) a 4-month burn and b) a stand of 12-year-old fynbos, at Scarborough, Cape Peninsula. Note difference in scaling of y-axis.

In the mature site, physical stress caused the death of a small percentage of seedlings but rodents were presumably responsible for most mortality in the two controls. Seedlings were either removed completely or severed at the stalks; pieces of seedling and faecal pellets were frequently found nearby. The only seedlings remaining at the two controls after seven weeks were at replicates situated in very sparsely vegetated patches, which are probably avoided by rodents as unsafe. Only eight seedlings died within all the "protected" treatments. Half the cases were clearly due to physical stress; faeces were found inside two cages but death by predation was not obvious in either case.

DISCUSSION

Is there a post-fire age at which mountain fynbos is no longer open to invasion by Pinus radiata ?

The pattern of *Pinus radiata* establishment into fynbos detected by this study agrees in general with that found in similar studies (Richardson & Brown 1986; Richardson 1988; Richardson, Cowling & Le Maitre submitted). The invading populations at each plot are largely even-aged (Table 1) and recruitment was not restricted to the immediate post-fire phase.

Several differences are found, however, when the results of this study are compared with those of Richardson & Brown (1986) for *Pinus radiata* at four 16-year-old plots in the Jonkershoek Valley (outside the State Forest). Firstly, in their study several of the trees had recruited prior to the last fire, while in this study all had recruited since the last fire. Secondly, a more gradual increase in recruitment was found at these plots in comparison with the rapid and abundant post-fire recruitment flushes, more typical of population regeneration of *P. radiata* (McCune 1988), found by the above authors. The greatest discrepancy is seen at plot 3 of my study in which recruitment appeared to occur entirely between 11 and 20 years. Lastly, tree densities at my plots were considerably lower than in the other study (0.4 to 1.1 trees $100m^{-2}$ as opposed to 1.4 to 27.7 trees $100m^{-2}$).

The most probable explanation for these differences is that my plots, being situated within the State Forest, had previously been cleared of pines, while there was no evidence of clearing at any plots in the other study (D.M. Richardson pers.comm.). Clearing normally involves felling and subsequent burning within 18 months to destroy any invasive seedlings which may have germinated since felling (MacDonald & Jarman 1984). Pre-burn felling would directly explain the absence of trees older than the stand in plots 1 and 2, and to some extent the differences in densities. It must be assumed that trees were felled 12 to 15 years ago in the third plot without subsequent burning (presence of 23-year-old *Protea neriifolia* individuals which do not survive fire). This facilitated the successful invasion by *Pinus radiata* into mature fynbos. As the plot does not lie within a zoned area, no management records are available to check this assumption.

In Richardson & Brown's (1986) plots, fire facilitated recruitment by stimulating the release of large amounts of seed from the pines already present in the stand. In my study the fire would have succeeded seed release and thus limited recruitment by destroying the young seedlings. Many of the recruits may have been derived from seed released from the adjacent plantations; this is a less abundant and more erratic propagule source than seed released after fire. Clearing of trees would thus also explain the apparently slower rate of recruitment at my plots, and the lower densities.

Despite the differences, the results of both studies (with the exception of those for my third plot) have shown that the invasion of *Pinus radiata* into mountain fynbos burnt within the past three decades is limited to about the first ten years (the immediate post-fire, youth and transitional phases of fynbos *sensu* Kruger & Bigalke 1984).

As fynbos enters the senescent phase (30+ years, Kruger & Bigalke 1984), the mortality of canopy species creates gaps facilitating the recruitment of some plants. This appears to include *Pinus radiata*. In a fifth plot of Richardson & Brown's (1986) study which was senescent (no evidence of fire in at least the last 30 years), 10% of all *P.radiata* trees found were saplings (about 2 years old).

It appears, therefore, that mountain fynbos is closed to invasion by *Pinus radiata* only when in the mature phase and undisturbed.

What potential role do seed and seedling predators play in controlling the invasion of Pinus radiata into mature fynbos?

The results of the experimental study suggest that invasion by *Pinus radiata*, in this site at least, would be severely restricted by seed and seedling predation.

At the mature site, the removal within a week of all seeds in the open and over 80% of those inside exclosures shows that *Pinus radiata* seeds are clearly very desirable foods for rodents. As conifer seeds are particularly nutrient-rich (Smith 1970) and most granivorous rodents of the fynbos are unspecialised feeders (Willan 1980a), this is not surprising.

The possible role of non-rodent predators here is unlikely. The non-significant differences between seed removal in treatment and control in the burnt site belie any granivory by birds (see also Bond, 1984 ; Bond & Breytenbach, 1985). Ants did not appear interested in the seeds (pers. obs.) which lack any subsidiary ant-attractive bodies.

The lack of any certain seed predation in the burnt site presumably shows that rodents have not yet recolonised this site. Small mammal recolonisation after disturbance is slow in fynbos relative to other South African biomes (Willan & Bigalke 1981). At a site in Stellenbosch, for example, no rodent species were found until 11 months after the fire (Bigalke & Pepler (unpubl.) in Willan & Bigalke 1981). This is probably due to the slow regeneration of the vegetation which rodents require for food and protection from predators (Willan & Bigalke 1981). Bond (1984) has performed a similar study on the predation of *Protea spp.* seed and seedlings in a five-month burn in the Southern Cape. In contrast with my results, he found that the greatest seed predation was in the burnt site (81.7% seeds compared with 38.5% the mature site, control values after 15 weeks). He ascribes this to the lower probability of seed being found by rodents in the "food-rich, structurally diverse, mature fynbos" than in the post-fire environment. Mature fynbos is typically unproductive, however (Willan 1980b), and the results of my study suggest that, at this site at least, there is a very high probability of seed being found.

Several factors may explain the differences in patterns of seed predation between the two studies. They may be due the slight difference in post-fire age of burns (seed counts were made in the ninth and fourth months respectively). Fynbos may recover from fire more rapidly in the Outeniqua Mountains (Bond, Ferguson & Forsyth 1980) thus providing adequate food and cover for rodents earlier than in the south-western Cape. It also appears that rodent densities are much higher in the southern Cape than in the western Cape (Bigalke 1979 in Bond 1984). This serves to highlight the point stressed by Janzen (1971), that post-dispersal seed predation must be considered in the context of the particular habitat.

Seed predation *per se* is unlikely to preclude invasion entirely. Richardson (1985) reported extremely high levels of post-dispersal predation by rodents on *Hakea sericea*, which is the most important invader of mountain fynbos (MacDonald & Jarman 1984). Even under such heavy predation, some seeds will escape to pioneer a new population (Kruger, Richardson & Van Wilgen 1986). Granivory may be high for natural vegetation without preventing re-establishment (eg. Manders & Botha 1989). Factors limiting population regeneration may be far more important at the more vulnerable seedling stage (eg. Janzen 1971; Harper 1977; Louda 1983).

In this study seedling predation was very high in the mature site and negligible in the burnt site. Again this indicates the absence of seedling predators in the burn. The young, unprotected seedlings were clearly a favourable food source in the otherwise unproductive mature environment (cf. Willan 1980b).

The abundance of well-defined runways through the vegetation, the way the seedlings were severed close to the ground and the characteristic seedling debris all point to the herbivore *Otomys sp.* as the likely seedling predator (Davis 1972). This rodent was found only in areas of more than 75% shrub cover in the southern Cape (Bond, Ferguson & Forsyth 1980). This corroborates my observation that the only seedlings not predated in the mature site were in very open areas (<40% cover).

CONCLUSIONS

It is tempting to draw a correlation between the apparent absence of *Pinus radiata* invasion into mature fynbos and the high levels of seed and seedling predation found in mature vegetation at Scarborough. Caution must be exercised here for a number of reasons, however. Firstly, the study was limited by its short duration and the fact that relative survival over summer could not be monitored. In serotinous species which release seeds between fires, drought-induced mortality over summer may be a more important factor in preventing establishment in mature vegetation than seed and seedling predation (Cowling & Lamont 1987). Although pines are relatively tolerant of competition, drought due to competition may be very important in limiting establishment in some sites (Donald 1986).

Secondly, the apparent predation levels found here are probably not typical for mature fynbos. Seed and seedlings were grouped and the study site was small; these together may have had a baiting effect on the rodents. Seeds entering from plantations and the seedlings which establish would presumably be more scattered. This would reduce predation as some would escape detection. A low seedling density would render predation uneconomic for the predator (Janzen 1970).

Thirdly, rodent densities may be higher than usual here due to the infestation of *Acacia saligna* in the vicinity (cf. David 1980,1981 in MacDonald & Richardson 1986). Rodent population densities also fluctuate with season and age of fynbos (Cody *et* *al.* 1983) and are typically lowest in "middle-aged fynbos" (10-14 years) (Willan 1980b).

Nevertheless, the results of this study may have some application for the control of *Pinus radiata* in mountain fynbos. Fire is the major management tool for fynbos in mountain catchments (Richardson 1985). Clearing of woody aliens by felling and burning may have detrimental effects on fire frequency, season and in particular intensity. The practice of felling and encouraging rodent predation of seeds, instead of or before burning has therefore been proposed (MacDonald & Jarman 1984). This study suggests that such a method has potential,as rodent populations of mountain fynbos can provide a powerful biotic resistance to *Pinus radiata* in its earliest life history stages.

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