

**SEED BANK DEPLETION EFFECTS ON  
POST-FIRE RECRUITMENT OF TWO CO-  
OCCURRING *PROTEA* SPECIES**

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## ABSTRACT

A knowledge of pre-fire seedbank size and post-fire recruitment is vital to our ecological understanding of the Proteaceae as well as to wild flower farming management. To test the relationship between pre-burn seedbank size and post-fire seedling recruitment in *Protea repens* and *P. neriifolia*, the pre-fire seedbanks of twenty 10 x 10m plots were estimated from the number of cones occurring in each plot and mean number of seeds per cone. The number of seedlings that recruited after an autumn burn were counted six months after the burn. A positive linear relationship was found between pre-fire seedbank size and post-fire seedling recruitment for both *P. repens* (seeds:seedlings = 2.7:1) and *P. neriifolia* (seeds:seedlings = 2:1). Overall cone production per plot decreased with increasing parent density. Pre-fire seed predation was high, and post-fire predation was not evident. A small proportion of seedlings was lost to insect predation. A model for optimal flower harvesting is proposed from the relationship between seeds and seedlings. This suggests that current harvesting guidelines may be too low for Autumn burns. Seeds that are not removed by harvesting may otherwise result in density dependant seedling deaths or dense stands of non-reproductive adult plants. Additional data on seedling migration, as well as pre- and post-fire parent counts are discussed.

## INTRODUCTION

There has been much debate over the determinants of post-fire recruitment of serotinous (canopy-stored seed) Proteaceae. Presently there are two arguments; the first is that post-fire factors, such as predation and time until germination, are the major factors determining seedling recruitment numbers; the second is that the pre-fire seed bank size is the primary constraint determining post-fire recruitment. Surprisingly no research to date has directly addressed the relationship between pre-burn seedbanks and post-fire recruitment.

Knowledge of the relationship between pre-burn seedbanks and post-burn recruitment is not only important to our ecological understanding of the Proteaceae, but is vital to wild flower farming management. The harvesting of wild flowers (inflorescences and infructescences (cones)) particularly of serotinous Proteaceae of the fynbos is economically important and is rapidly expanding (Greyling & Davis, 1989). Harvesting of Proteaceae takes place along the southern lowlands, southern mountain foothills, and as far as the Langkloof in the east (Van Wilgen *et al.*, 1992). At present, wild flower farmers are advised to harvest up to 50% of the flower heads of serotinous Cape Proteaceae per year, and there should be no harvesting for at least one year prior to a burn (Cowling & Mustart, 1992; Van Wilgen *et al.*, 1992). Autumn burning is advised and should take place every 12-15 years to allow seed reserves to accumulate and to maintain a vigorous population. Old Proteas produce fewer flowers and eventually senesce (Bond, 1980). These recommendations are proposed to ensure that there is sufficient seed for regeneration after a fire.

However the harvesting recommendations are largely based on speculation since the relationship between pre-fire seedbanks and post-fire seedling recruitment is unknown. The

important question for the wild flower farming industry is; how can adequate seed reserves be maintained with flower harvesting so that populations regenerate adequately? For the conservation manager, the same question applies for determining fire intervals.

To gain insight into this question, the main aim of this project is to quantify the relationship between pre-fire seed bank size and post-fire seedling recruitment by differentially removing part of the seed banks of two *Protea* species, *P. repens* and *P. neriifolia*. From an estimate of seed and seedling loss to various parameters, we can then decide at what stage in the life history the greatest mortality is occurring, and thus whether seed bank size or post-fire factors are more important to seedling recruitment. From this knowledge models for harvesting management can be proposed.

An additional aim is to examine the dispersal abilities of the two species. There is growing interest in the importance of dispersal for the colonization and survival of plant populations (Crawley, 1992). Local extinction appears common in plant populations and survival of *Proteas* in the landscape may depend on effective colonization abilities. Very little is known about the importance of dispersal in plant population dynamics here or anywhere else in the world. For example, is seed immigration proportional to the density of the population or the properties of the seeds? By counting the number of seeds that reach the edges (barrier) of the plots whose seed bank size is known, a basic measure of their dispersal abilities should be possible.

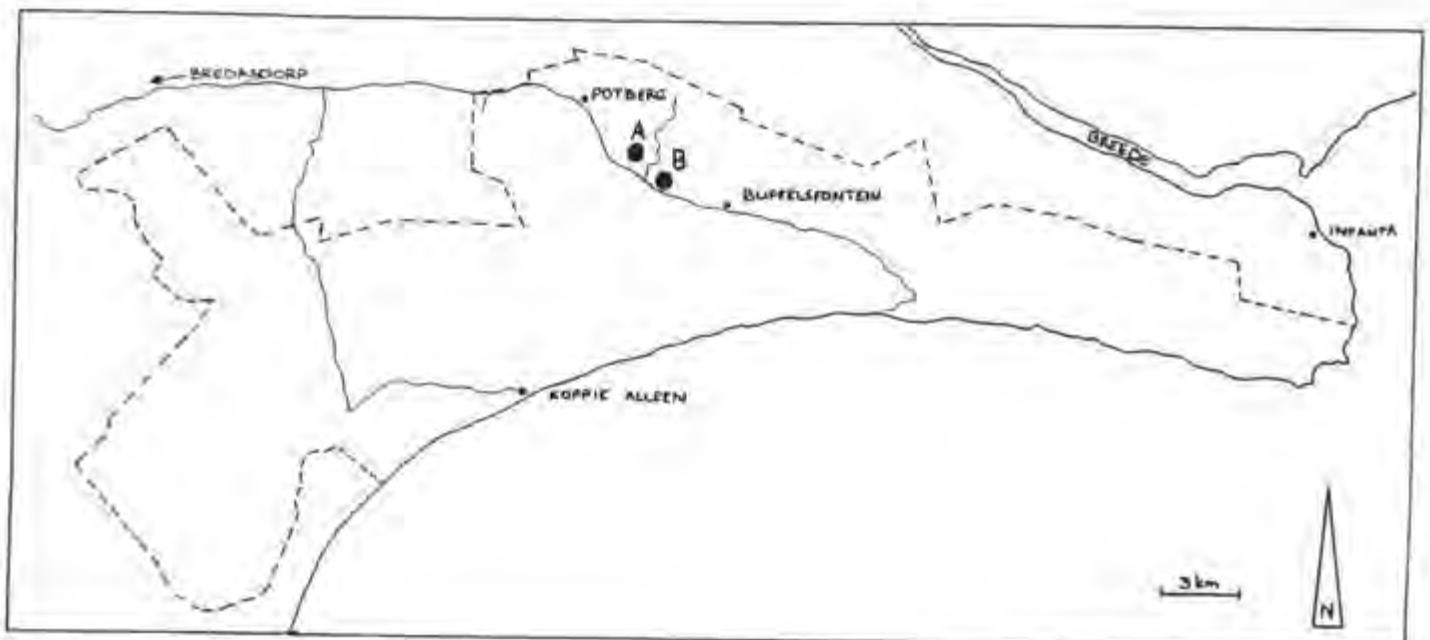
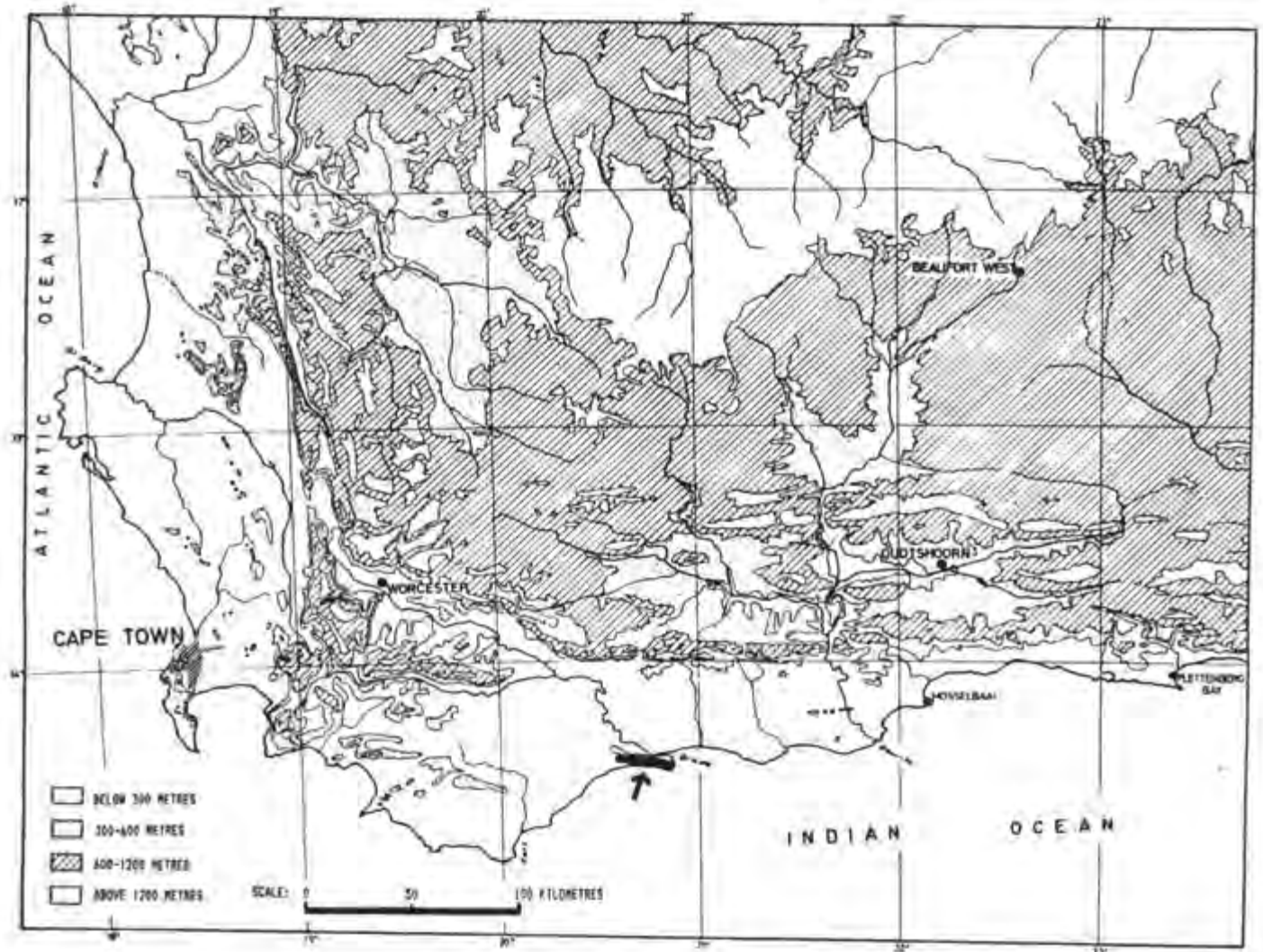


Figure 1. Map of the south western Cape showing the locality of the De Hoop Nature Reserve and below a more detailed map of the Potberg area showing the study site marked A. (The unburnt area where the second data set (Appendix B) was collected at B.)

## METHODS

### Study area

The study area was situated on the flat plains below the Potberg in the De Hoop Nature Reserve (34°24'10"S, 20°33'40"E) (marked A on Figure 1). Sampling was carried out in nine-year-old mixed *P.repens* and *P.neriifolia* fynbos (Plate 1) growing on soils derived from Table Mountain sandstone, silcrete gravel and possibly wind blown sand. The climate of the area is mediterranean in type with 65% of the annual rainfall (mean annual rainfall 409mm) occurring between April and September.



Plate 1. Potberg study site A in February 1993 before a burn.

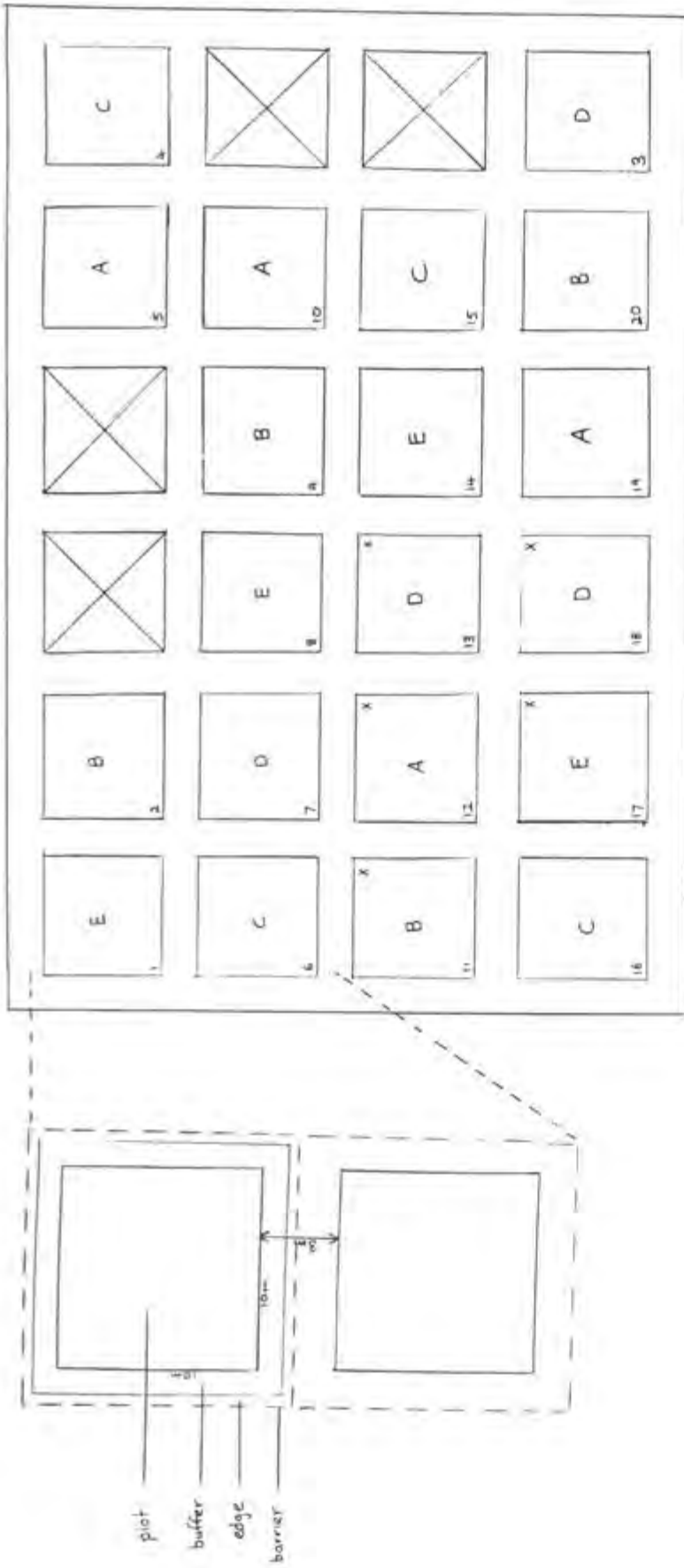
## Species studied

The species studied were *Protea repens* and *Protea neriifolia* which are both serotinous shrubs, that is that the release of mature seed is delayed. The seeds are stored in woody infructescences ("cones") for several years and are only released after a fire, when the plants are killed and the cones open and the seed is released in large numbers. They germinate in the following winter (Kruger, 1983). Serotiny enables the accumulation of seed for dispersal under the appropriate conditions (ie. high post-fire nutrient level and few competitors). The predator food supply may also be saturated so that not all seed is predated.

*P.repens* seeds take seven months to mature (Jordaan, 1944), and with time the seeds rapidly lose viability and many are predated (Coetzee & Gilomee, 1984; Myburgh & Rust, 1975). These factors are important when trying to predict a model for fire management (ie. fire regime and optimal flower harvesting). *P.repens* is an erect, much branched shrub that is common in lower altitude proteoid communities throughout the Cape Fynbos region (Cowling, 1987). The populations in the south-western Cape flower in winter between May and October (Rourke, 1980).

*P.neriifolia* is a serotinous large erect shrub that is distributed at low altitudes, in coastal or immediately adjacent areas from Port Elizabeth to Jonkershoek. The populations in the south-western Cape flower in winter between May and August (Rourke, 1980).

To explain the relationship between pre-burn seedbanks and post-fire recruitment, I divided a dense proteoid stand into subplots for each of which pre-burn seedbanks were estimated. Cones were harvested from each subplot to provide a large range of pre-burn seed densities.



- A - all flower heads removed
- B - 25% flower heads removed
- C - 50% flower heads removed
- D - 100% flower heads removed

Figure 2. Diagrammatic representation of the plot layout showing the edge and buffer zones, the position of the barrier, and the randomly assigned harvesting treatments A - B.

### Pre-fire procedure

1. 24 10 x 10m quadrats were laid out on a grid, with a 3m buffer zone between each plot (Fig. 2). Four of the plots were unsuitable for use as they were disturbed by alien vegetation.

2. For each of the 20 10m x 10m plots, one of four different harvesting treatments was randomly assigned so that there were four plots per treatment (Fig. 2 shows the layout of the plots and their the respective harvesting treatments A-E). The four harvesting levels were:

- A - all flower heads removed
- B - 25% flower heads removed
- C - 50% flower heads removed
- D - 100% flower heads removed

For *P.neriifolia* for each of the harvesting treatments, the harvesting of one year old cones (Plate 2), and two year old and older cones, was carried out separately. The reason for treatment A was to obtain an estimate of dispersal between the plots.

All of the remaining flower heads in each plot for each species were counted (the two cone age groups of *P.neriifolia* were counted separately).

Each plot was separated from its neighbour by a 3m buffer zone in which all of the flower heads were removed from *Protea repens* and *Protea nerifolia* plants (Figure 2). The flower heads of each species and of the different age groups for *P.neriifolia*, were brought back to

the laboratory and heated at 40°C for four days to allow the flower heads to open and the seeds to be released.

A burn took place on the 17 February 1993. (Daily rainfall data from 18 February (day after the fire) to the 31 August are recorded in Appendix C). The burn took place within the natural fire season of the south-western Cape which is from late summer to autumn (Van Wilgen, 1984). At this time, mature seed availability is maximum. Winter and spring burns result in poor seedling recruitment (Bond *et al.* 1984).



Plate 2. A one year old *P. neriifolia* cone.

### Post-fire work immediately after the fire

3. To prevent seed dispersal into adjacent plots, barriers were constructed along the middle of the 3m buffer zones between all plots. They consisted of soil piled up to 30cm above ground level (see Plate 3).
4. To get an estimate of seed and seedling loss to predation, two 2 by 2 by 0.3m wooden exclosures were placed in two randomly chosen areas that were cleared of *Protea* seed. 150 and 102 *P.repens* seeds were planted in each of the two exclosure A and B respectively, and the same number were planted in an adjacent plot of the same size. To prevent seeds dispersing into the plots adjacent to the exclosures, small rocks were placed around the perimeters, which still allowed predator access (Plate 4).
5. To get an estimate of seedling loss to heat from the fire, burnt flower heads were removed from plants in the area immediately adjacent to the plots, and were taken back to the laboratory for viability tests.



Plate 3. Barriers running between the plots to prevent seed dispersal between the plots. These were constructed after the burn.



Plate 4. Rodent enclosure and control plot that were constructed after the fire.

### Seed viability tests

Seed viability was deduced in two ways; by cutting the seeds open and inspecting for embryos, and by germination trials for both the *P.neriifolia* and *P.repens* seeds. The viability of seeds from burnt *P.repens* cones was determined by germination. The average number of viable seeds per flower head was determined by plotting the cumulative mean against the number of samples until the graph levelled off (Fig. 3.1 & 3.2). Pre-dispersal predation was recorded. Some of the flower heads were infected with beetle and moth larvae. The mean number of cones infected and mean number of seeds lost to pre-dispersal seed predators were determined.

An estimate of viable seed number per flower head along with counts of the number of flower heads per plot enables an estimation of the size of the seed bank per plot, before the fire.

### Seedling counts

In June, July and August, seedling counts were carried out in the edge zones of 5 plots (see Figure 2 for zones). The edge is a 50cm band adjacent to the barrier, the number and seedling species were counted on each side of the plot. The edge counts are used as a basic measure of the proportions of seedlings that migrate from the parent plants. The germination times of the two species was noted. Final seedling counts were done in September for all 10 × 10 m plots, as well as edge and buffer counts. The buffer area is the zone between the edge and the 10 × 10 m plot.

The seedlings in the exclosures and the plots adjacent to the exclosures were counted in June, July and August to determine seed as well as seedling loss to predators. This was done by mapping the position of each seedling as it germinated and monitoring its growth.

To measure the efficiency of the barriers between the plots, the number of seedlings in the plots which had all of their cones removed were counted.

Five 1m<sup>2</sup> plots were marked around patches where the seedling density was very high, and similarly five plots were marked around areas where the seedling density was low. The number of seedlings in each of these 1m<sup>2</sup> plots was counted in June, July and August, so as to give a measure of seedling survival in relation to density for the first few months of growth. These plots should be inspected in subsequent years to assess seedling loss to competition.

It is important to follow up this project in later years, as more seedlings may emerge in the second year after the fire, although Bond *et al.* (1984) found this to be negligible. (Some seeds were found in the opened cones in September) (Plate 5).

Most studies of parent and seedling numbers in fynbos rely on the skeletons of the plant after the burn as an indication of pre-fire parent numbers. The number of skeletons of both species were counted after the fire for comparison with pre-fire counts. It is hypothesized that skeleton counts of *P.repens* should be lower after the burn because these plants are thinner and thus burn completely and may not be detected after the fire. However at higher densities higher counts may be expected after a burn due to difficulties in accurate counts

because of the pre-burn vegetation density. Smaller differences are expected for *P.neriifolia* as they are larger plants that are more easily counted before a fire, and are also less likely to be burnt completely.



Plate 5. *P.repens* cones that opened after the fire and did not release all of their seed.

## RESULTS

### Pre-burn seed banks and post-fire recruitment

The average number of viable seeds per cone was determined by the cutting method to be 8 for both *P.repens* and *P.neriifolia* by graphing the cumulative mean number of seeds against the number of cones sampled (Fig. 3.1 & 3.2). From this cumulative average the estimated number of viable seeds per plot was calculated for both species by multiplying the number of cones per plot by the average number of viable seed per cone (Appendix A). The germination method was not successful due to the time and space taken to load seeds from a sufficient number of cones into petri dishes. However all the seeds containing embryos germinated (determined by cutting the seeds that did not germinate), confirming that all of the seeds with embryos are viable.

Seedlings emerged in mid June, approximately 16 weeks after the burn (Plates 6, 7 & 8). The rainfall from the time of the burn to the end of August is recorded in Appendix C. From edge counts in June, July and September, it was evident that *P. repens* germinated about 2 weeks before *P.neriifolia*. The seedling counts for each month and area (ie. edge, buffer and plot) are recorded in Appendix A. The results of the cone and plant counts in the plots are also recorded in Appendix A.

From seedling counts in the plots that had all seed removed, the mean number of seedlings successfully dispersing across the barriers into other plots was calculated to be 40.5 (median = 33) for *P.repens*, and 79.25 (median = 73) for *P.neriifolia*. However plot number A19 (Appendix A) had very high values probably caused by the low eastern barrier over which

seeds could easily disperse. This value was subtracted from the total seedling per plot value to control for dispersal of seed into plots. Similarly for the number of seedlings dispersing into the plot area (10 x 10m) the mean for *P.repens* is 16 (median = 16.5), for *P.neriifolia* the mean is 31 (median = 34).



Plate 6. Vegetation recruitment at Potberg six months after an autumn fire.

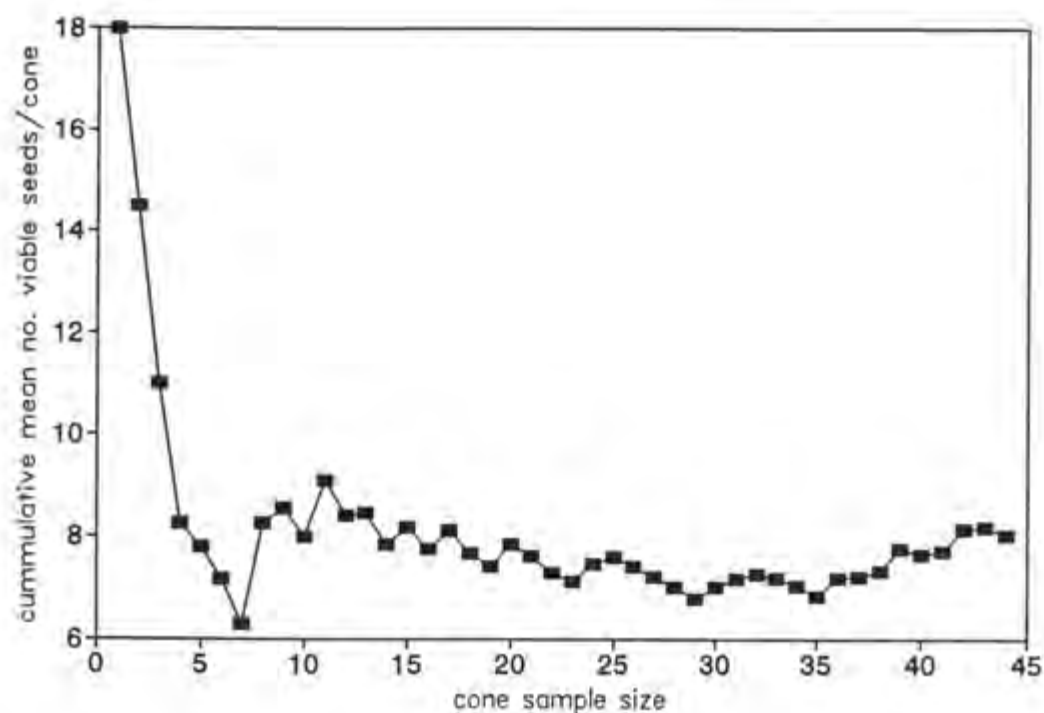


Fig. 3.1. Cumulative mean number of viable *P. repens* seeds versus the number of cones sampled by the cutting method (SD=7.28, SE=1.1, n=44).

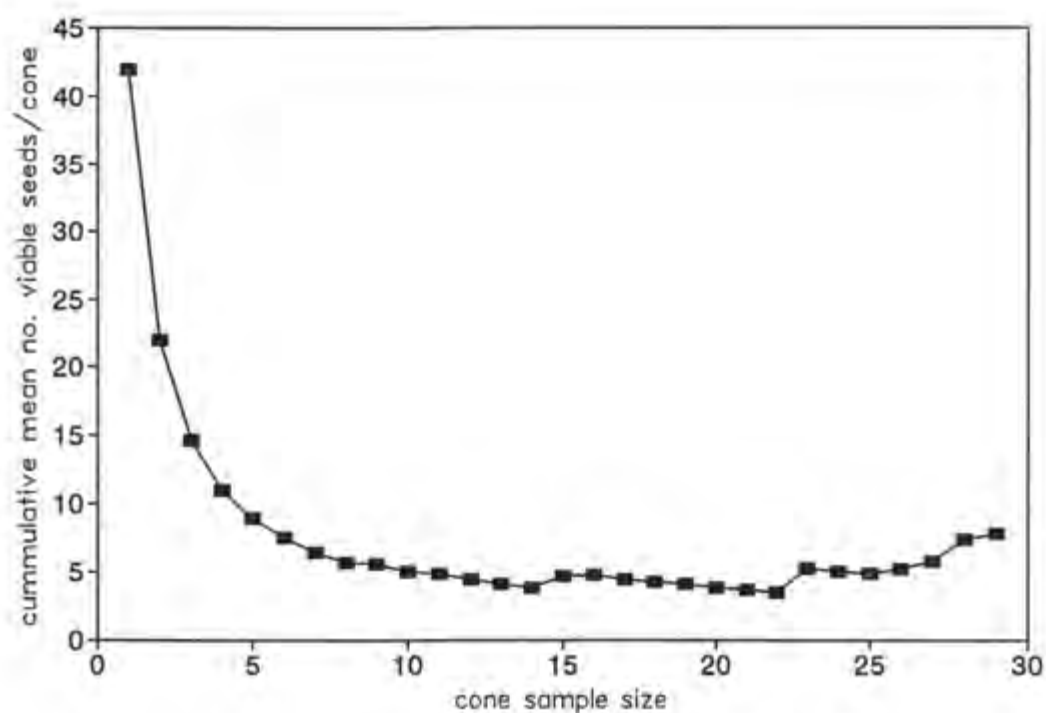


Fig. 3.2. Cumulative mean number of viable *P. nerifolia* seeds versus the number of cones sampled by the cutting method (SD=14.25, SE=2.65, n=29).



Plate 7. Six month old *Protea repens* seedling.



Plate 8. Six month old *Protea neriifolia* seedling.

Additional data was available from a study in an unburnt adjacent site of the same age and composition (Figure 1). The data are presented in Appendix B.

In *P. repens* there is a strong linear relationship between the amount of seed in the plot before the burn and the number of seedlings produced after the burn. This is the case when both the buffer and edge zones are included (Fig. 4.1) or excluded (Fig. 4.2) in the analysis. The regression analyses showed that when the buffer and edge counts are included the relationship is highly significant. From this regression the ratio of seeds to seedlings was calculated to be approximately 2.7:1. When only the resident seedlings (seedlings that have remained within the 10 x 10 m plot) are included in the regression, the relationship is still significant and the ratio of seeds to seedlings is 4.7:1.

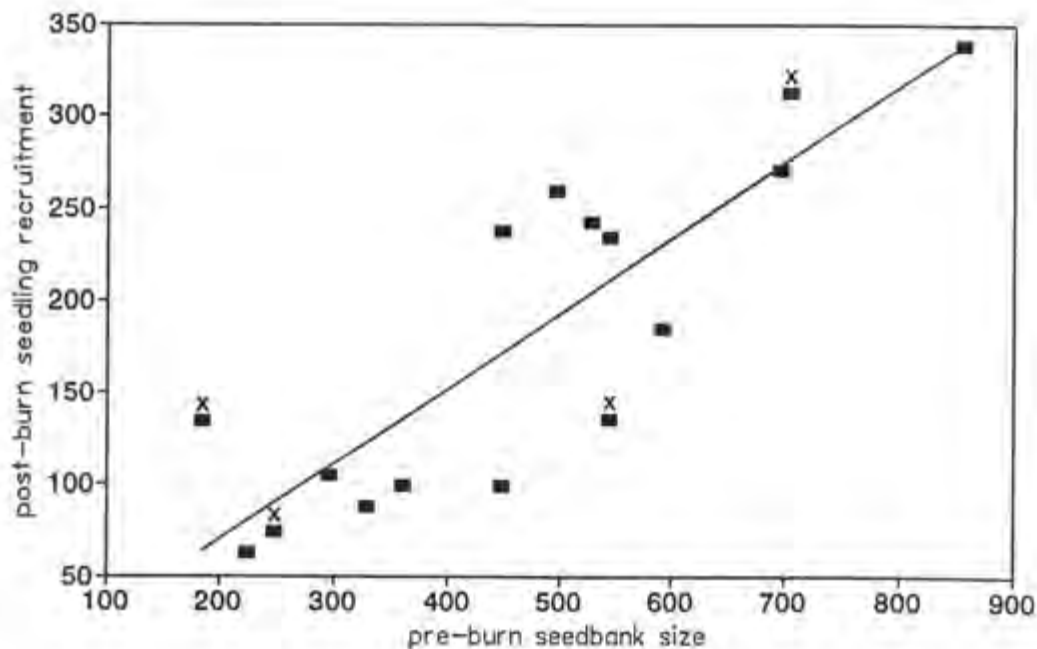


Fig. 4.1. The total number of *P.repens* seedlings recruited versus the pre-fire seedbank size, ( $r^2 = 0.73$ ,  $df=16$ ,  $p < 0.01$ ,  $m = 0.409$  and  $y$ -intercept =  $-12.1$ ).

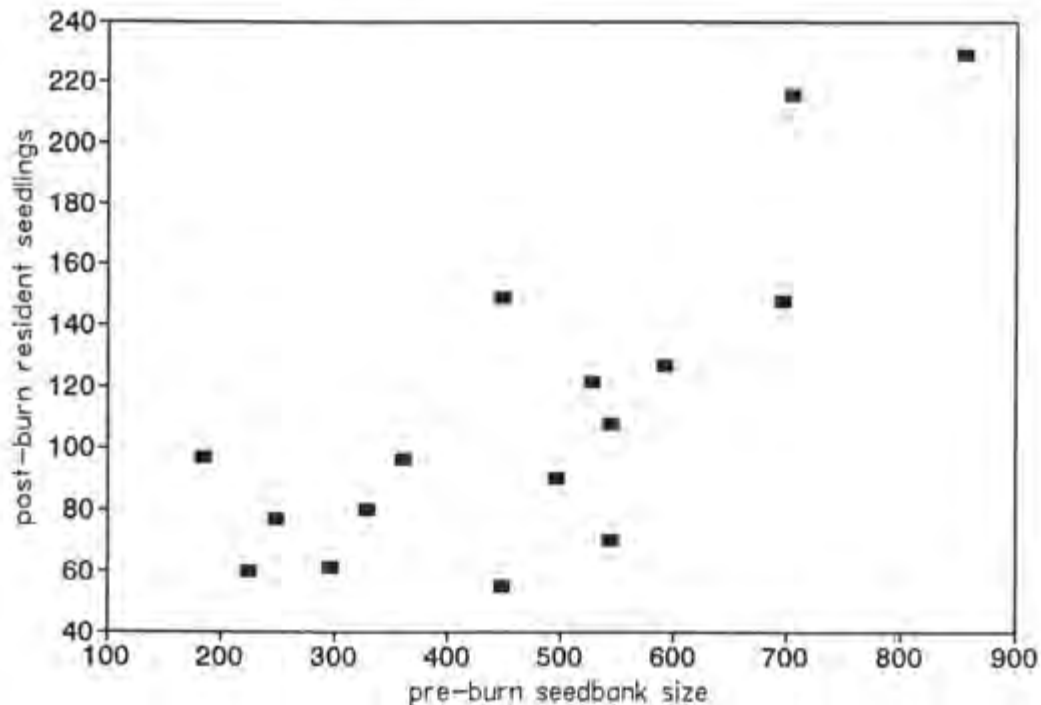


Fig. 4.2 The number of resident *P.repens* seedlings (in plot) recruited versus pre-fire seedbank size ( $r^2=0.61$   $df=16$  The slope = 0.22 and y-intercept = -5.6).

In *P.neriifolia* the linear relationship between the amount of seed per plot before the burn and the number of seedlings produced after the burn is not as strong as for *P.repens*, but the regression is still significant. This is the case when both the buffer and edge zones are included (Fig. 5.1) or excluded (Fig. 5.2) in the analysis. From this regression the ratio of seeds to seedlings was calculated to be approximately 2:1. When only the resident seedlings are included in the analysis the ratio of seeds to seedlings is 3.3:1.

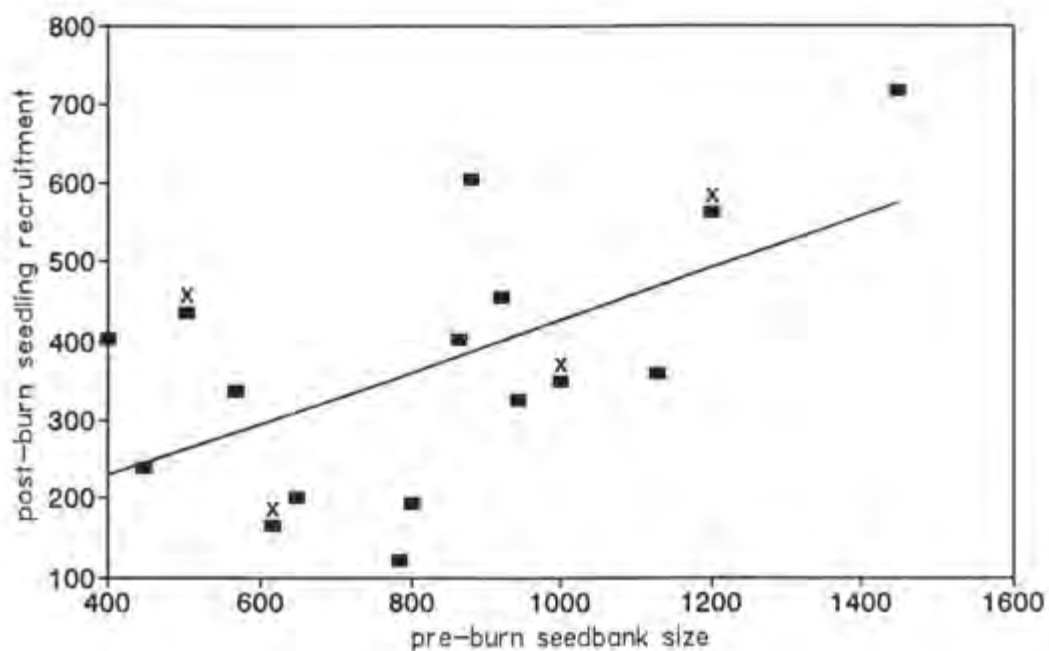


Fig. 5.1. The total number of *P.nerifolia* seedlings recruited versus the pre-fire seedbank sizes. ( $r^2=0.33$ ,  $df=16$ ,  $p<0.01$ ,  $m = 0.33$  and  $y$ -intercept = 97).

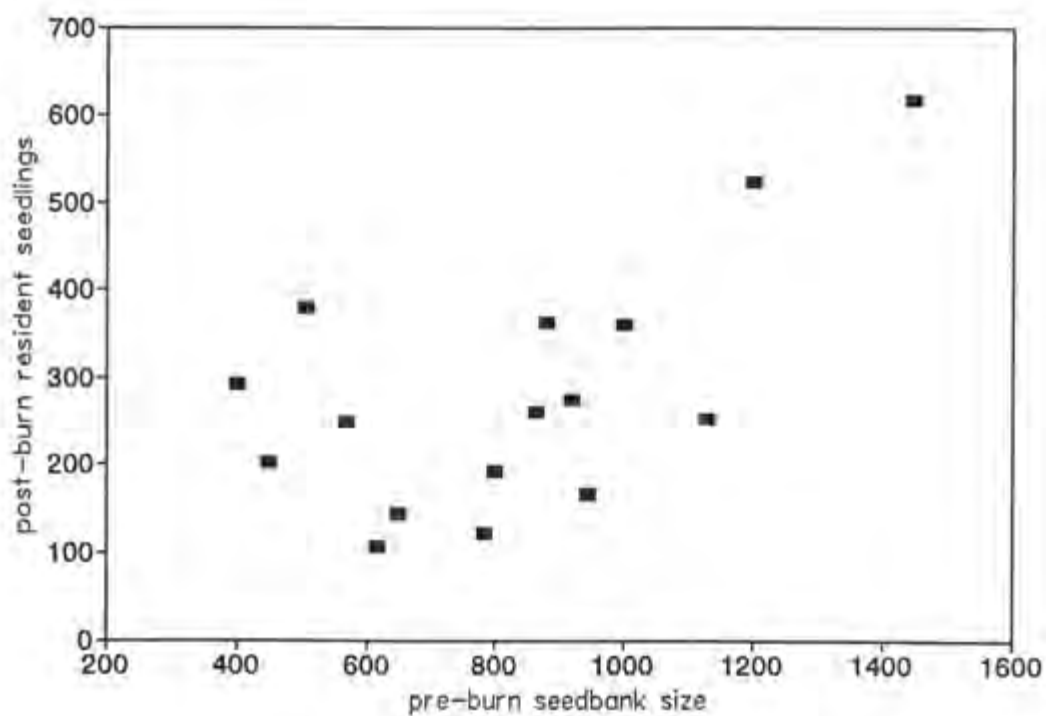


Fig. 5.2. The number of resident *P.nerifolia* seedlings recruited versus the pre-fire seedbank size ( $r^2 = 0.36$ ,  $m = 0.29$  &  $y$ -intercept = 8.7).

## Sources of seed and seedling mortality

### Pre-fire seed predation

Pre-dispersal predation rates were high in both species. Pre-fire seed predation was determined from the cutting experiment and 67% of the *P.repens* cones of 1753 cones examined were found to be infected with parasites (data from the second data set were used). A smaller sample size of *P. nerifolia* showed that 14 out of 47 cones had been predated (ie.30%). In *P.repens* these parasites reduced the average number of viable seeds in the predated cones from 18 (average number of viable seeds in uninfected cones) to 2 (average number of viable seed in predated cones).

### Post-fire seed predation

There were no significant seed losses to post fire seed predation from the exclosure experiments. Results for the rodent exclosure experiments are recorded in Table 1.

### Seeds burnt by fire

The four plots that did not burn with the same intensity as the rest of the study area (evident from unburnt foliage) were marked on the seedling versus seed graphs (4.1 & 5.1) for both species and show that seed germination is not dependent on fire intensity within this range.

Germination tests of the percentage viable seed per cone after fire were unsuccessful due to the number of replicates needed.

Table 1. Factors responsible for attrition of seeds and seedlings of *P.repens* and *P.neriifolia*.

	<i>P. repens</i>	<i>P. neriifolia</i>
pre-fire seed predation (% of total seed)	67% (n=1735) cones predated and had seed reduced to 2	30% (n=42) cones predated and had seed reduced to <1
post-fire seed predation	not evident	not tested
seedling predation	12 of 100 seedlings germinated were predated (from both exclosures and controls)	not evident

### Post emergence seedling death

Insect predation of seedlings was evident but the insect type is not known. The predated seedlings had been cut through at their base, and the leaves and upper parts of the stem were intact. Although eight 1m<sup>2</sup> plots were monitored for density dependent seedling deaths, none were evident in September.

Seedling mortality to either competition or herbivory can be estimated in a very crude way from comparing the number of seedlings to the number of parents. If one assumes that the population size stays the same, the relationship can be used to give an indication of the number seedlings that would become adults.

### Seedling to parent ratios for estimating seedling survival.

The relationship between the estimated number of resident seedlings (remaining in the plot) and number of parents is illustrated graphically for both species in figures 6.1 & 6.2 to explore seedling mortality under the assumption that the population size stays the same. Because a proportion of the cones had been harvested for this study, true parent to seedling ratios could only be established by estimating from the percentage of cones harvested, how many seedlings there would have been if there had been no harvesting. This estimate is feasible because there is a linear relationship between seed bank size (a function of cone number) and the number seedlings recruited (cf. Figs. 3.1 & 3.2). (Note that in these graphs the number of parents (adults) are dependent on the number of seedlings, as the assumption is that the number of adults will be determined by the number of seedlings.)

In *P.repens*, as the number of seedlings increase there appears to be no increase in the number of parents for seedling numbers over about 170 when 110 parents are found (Fig. 6.1). Thus with seedling numbers over 170 up to 400 there is no expected increase in parent (adult) density, therefore density dependent mortality could be expected to be occurring amongst those seedlings that do not become adults. However from the additional data set available for *P.repens*, much higher parent densities (ie. 561 per 10m x 10m area, see Appendix B) have been found.

In *P.nertifolia* the situation appears quite different. For seedling numbers up to 600 there is a linear relationship, that is that number of parents (adults) increase with increasing numbers of seedlings (Fig. 6.2). The two distant data points at high seedling density (ie. >1100 seedlings) suggest that the more seedlings produced the higher the chance of

variation in the chance that a seedling will become an adult. That is that the more seedlings produced the more chance of their density dependent mortality.

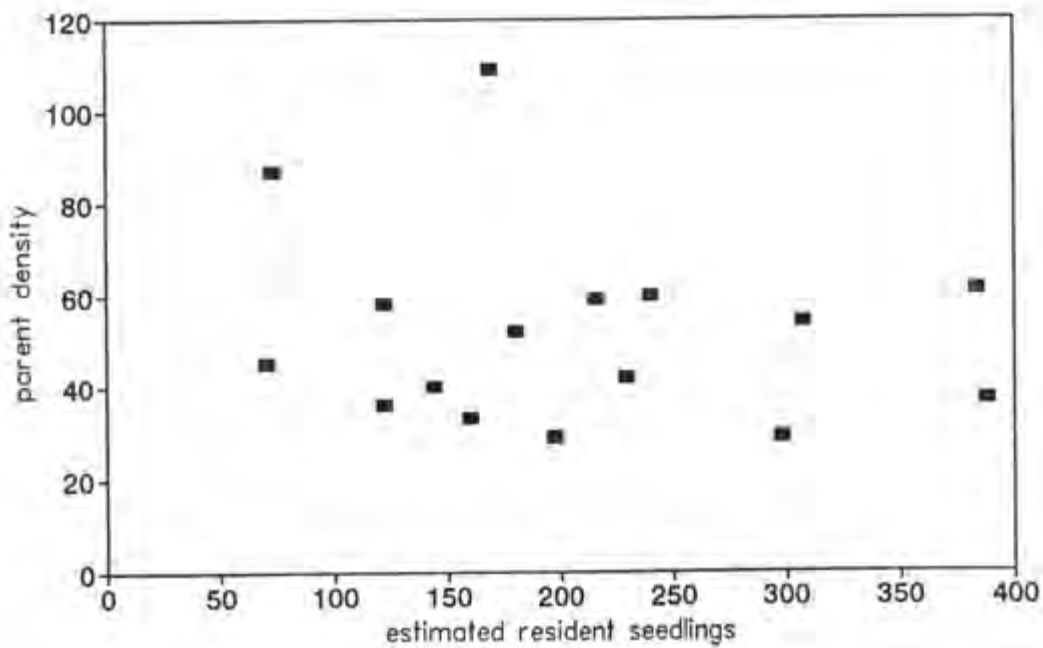


Fig. 6.1. The number of pre-fire *P.repens* parents versus the estimated number of resident (in plot) *P.repens* seedlings for 16 10m x 10m plots.

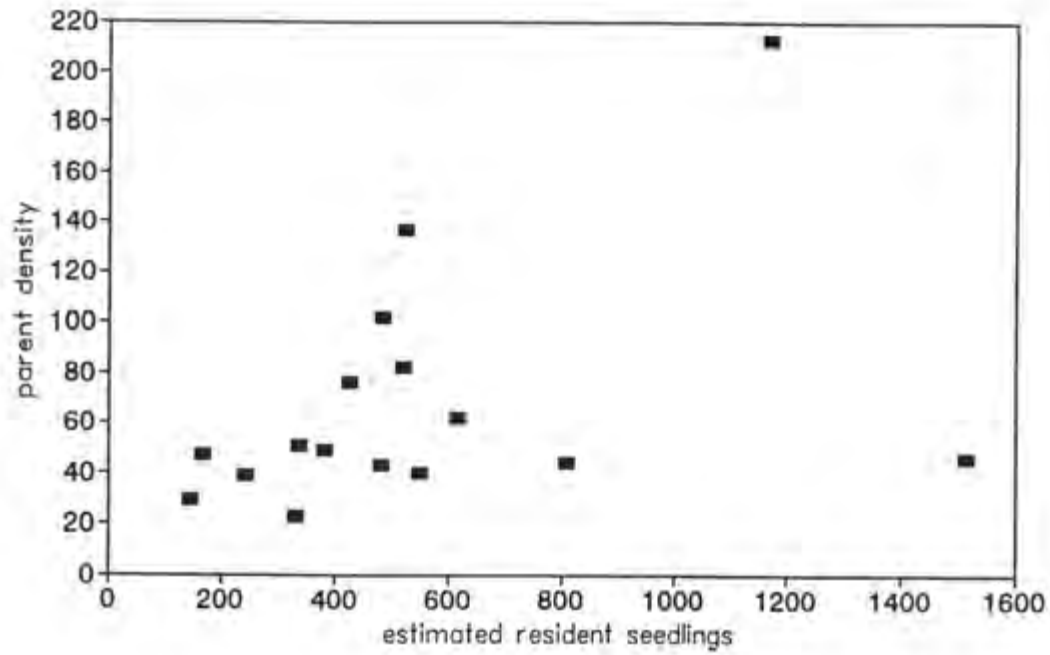


Fig. 6.2: The number of pre-fire *P.neriifolia* parents versus the estimated number of resident (in plot) *P.neriifolia* seedlings for 16 10m x 10m plots.

## PREDICTING HARVESTING LEVELS

The above data can be used to produce the information necessary for exploring the impacts of flower harvesting.

### Parent density and cone production per parent

Data from the additional 20 plots for *P.repens*, in an adjacent unburnt area of the same age was collected and pooled with the burnt site *P.repens* data. The relationship for the pooled data sets between the number of *P.repens* cones produced per plant and the total plant density per plot is shown in Fig. 7. Total plants or plant density (*P.repens* + *P.neriifolia*) is used as it is assumed that the two species would require similar resources and thus influence each others performance. (When parent densities are used a similar relation ship is found).

Additional data was not available for *P.neriifolia*, a graph of cones per plant and total plants was produced using the burnt data set only. The relationship was not as clear as was for *P.repens*, however there was a significant decrease in the number of cones produced per plant at densities of over 200 plants per plot (Fig. 8).

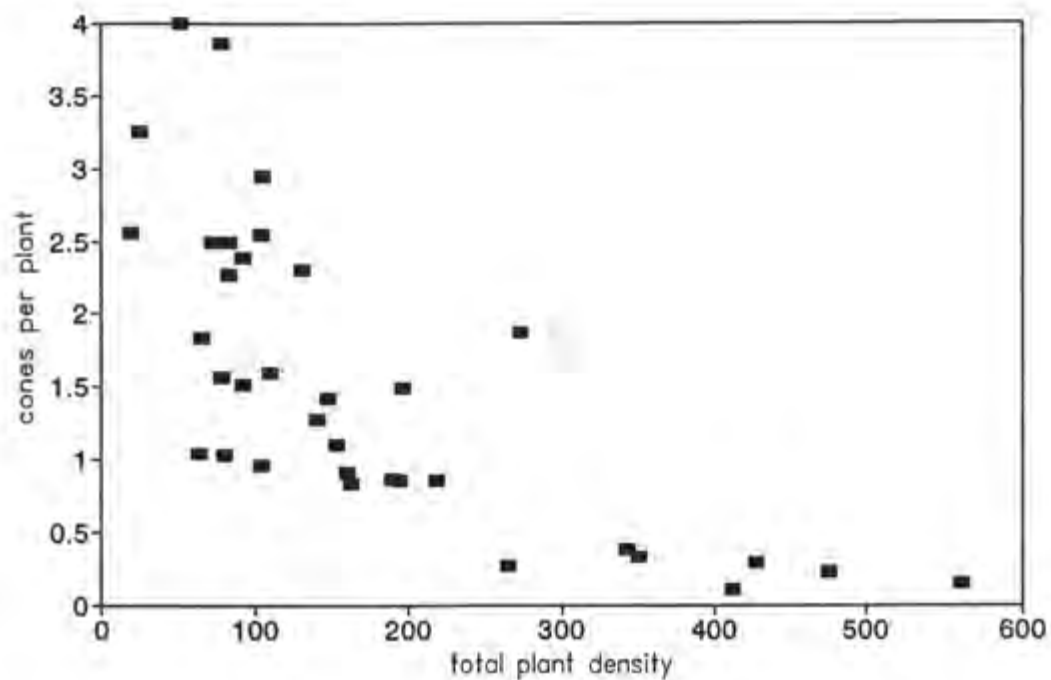


Fig. 7. The number of cones produced per *P. repens* plant versus the total plant density (*P. repens* + *P. nerifolia*) for 16 10m x 10m plots.

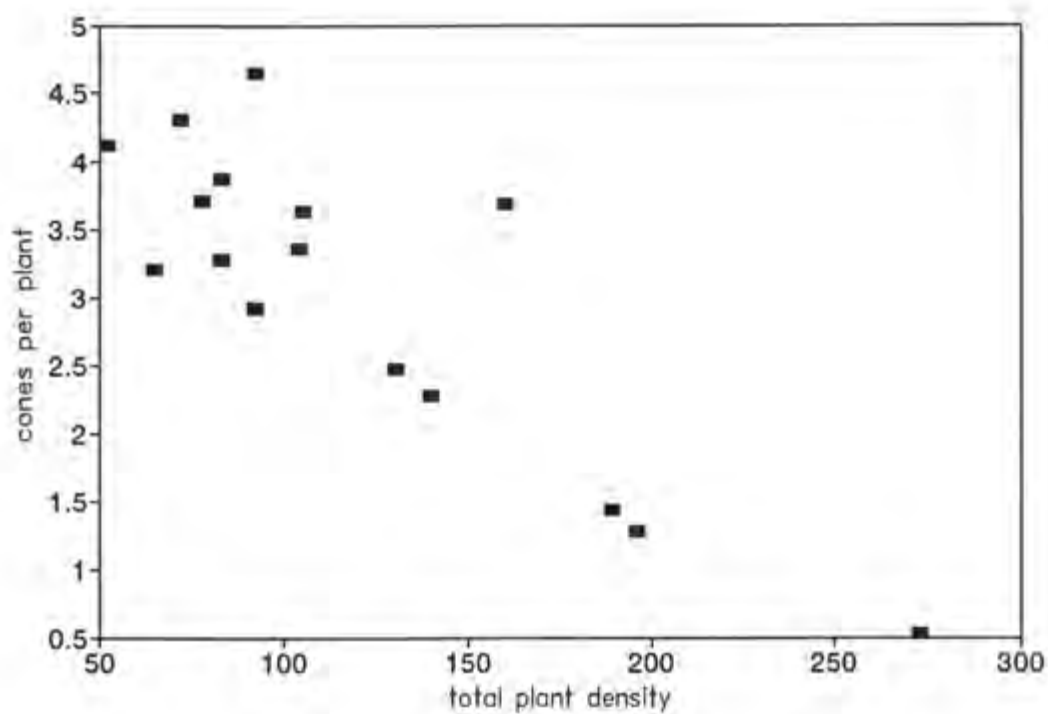


Fig. 8. The number of cones produced per *P. nerifolia* plant versus the total plant density (*P. repens* + *P. nerifolia*) for 16 10m x 10m plots.

### Parent density and overall cone production

Using the burnt data set only the relationship between total *P.repens* cone production per 10 x 10m versus the number of parents in the plot, is not very clear (Fig. 9.1). The unburnt data set was included to give the graph in Fig. 9.2 which shows more clearly the relationship between overall cone production and parent density. At parent densities below 50, less than 70 cones are produced per 10 x 10m area. Above parent plant densities of about 150, cone production is maximised (about 250 cones per 10 x 10m plot) and there appears to be a weak tailing of in cone production when parent numbers exceed 250.

From a frequency distribution (Fig 9.3) of cones produced per plant versus number of individuals (for the unburnt data set), it is apparent that out of 3628 plants in an area of 1900m<sup>2</sup>, 2718 plants are non-reproductive (ie. bear no cones).

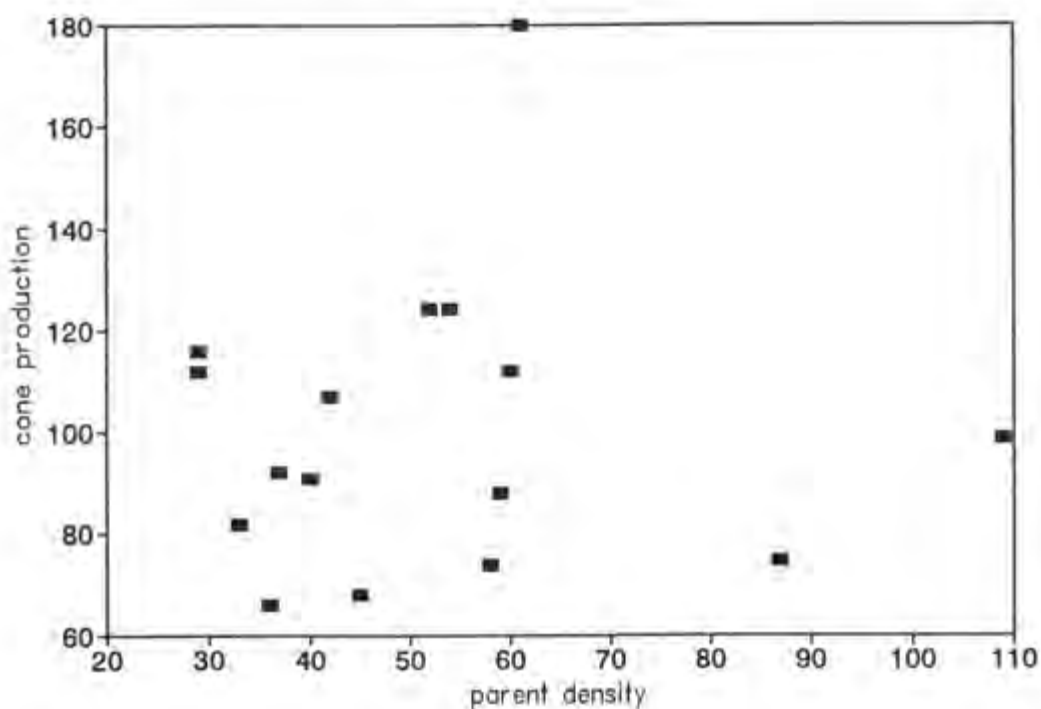


Fig. 9.1 Overall cone production of *P.repens* versus *P.repens* parent density for 16 10m x 10m plots.

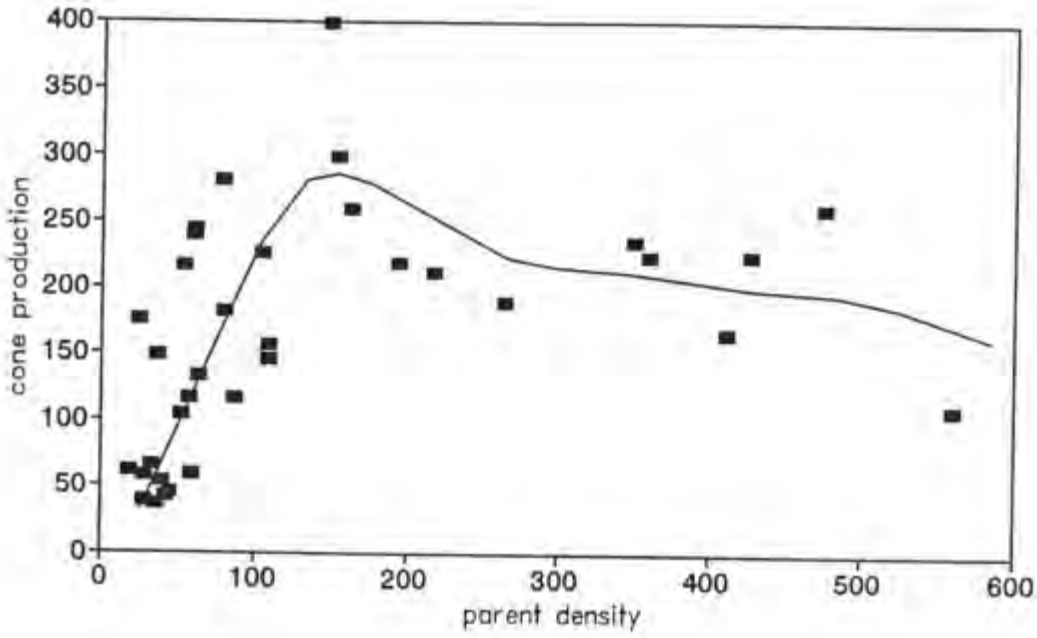


Fig. 9.2 Overall cone production of *P. repens* versus parent density for the combined data set.

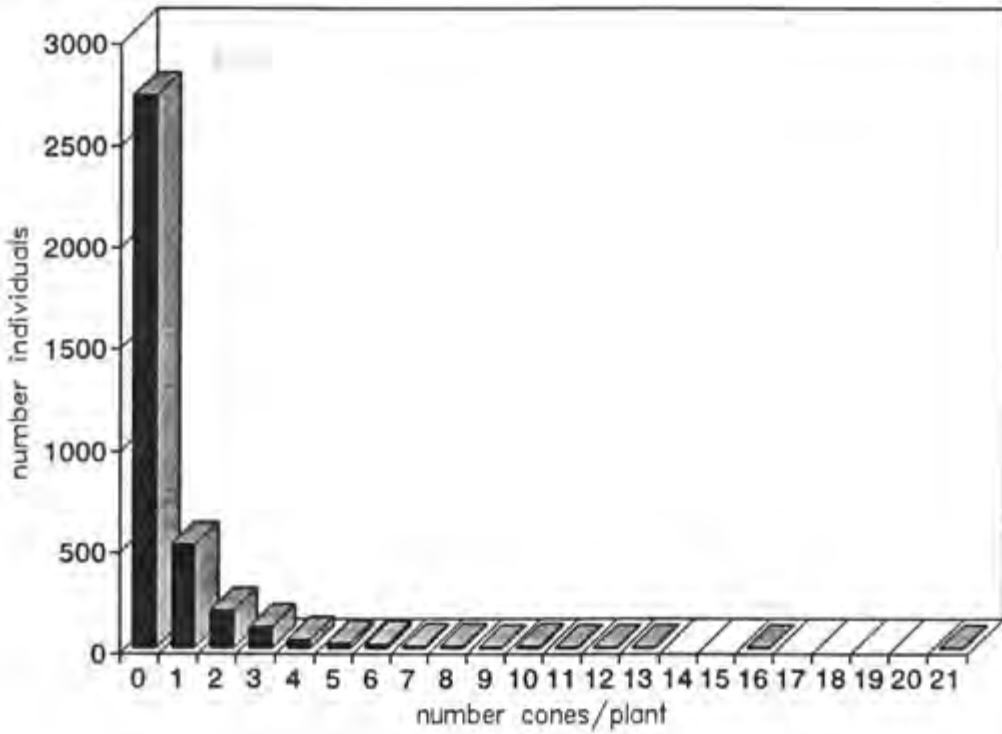


Fig. 9.3 Frequency distribution of *P. repens* number of flowers per parent from the second data set. See appendix B).

In *P. nerifolia* at parent densities below 40 and above 200, total cone production is relatively low (ie. fewer than 120 cones are produced per 10 x 10m plot) (Fig.10). Between 70 and 80 parents per plot, the maximum number of cones are produced (ie. about 180 per 10 x 10m plot).

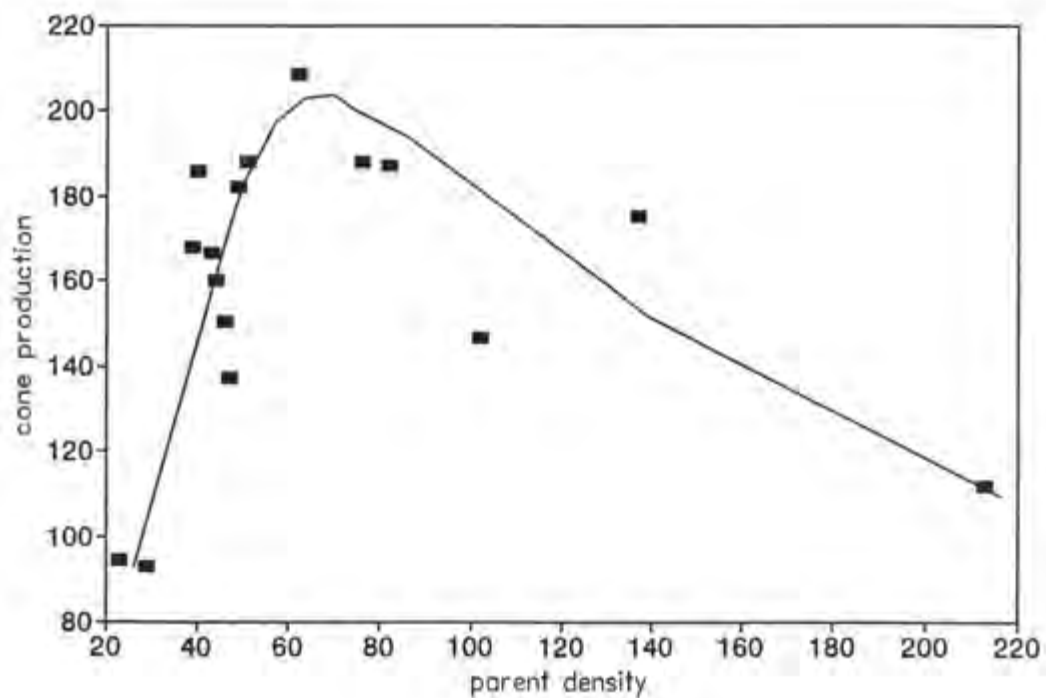


Fig. 10 Overall cone production of *P. nerifolia* versus *P. nerifolia* plant density for 16 10m x 10m plots.

## ADDITIONAL INFORMATION

### Dispersal out of the plot

The number of migrant seedlings (edge counts only) was plotted against the number of viable seeds produced per plot for each species. A weak positive linear relationship was found for *P.repens* (Fig. 11). For *P.neriifolia* (Fig. 12) there was no linear relationship.

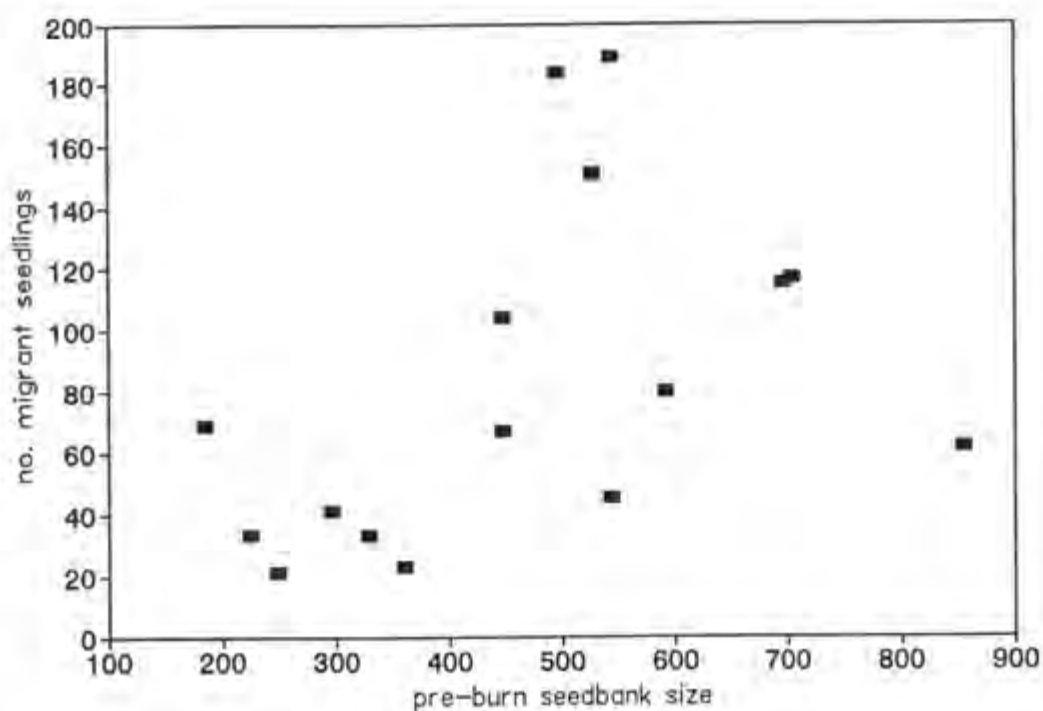


Fig. 11. The number of *P.repens* migrant seedlings (edge) versus the number of *P.repens* seeds for 16 10m x 10m plots. ( $r^2=0.19$ ,  $m=0.13$ ,  $y\text{-intercept}=23.2$ )

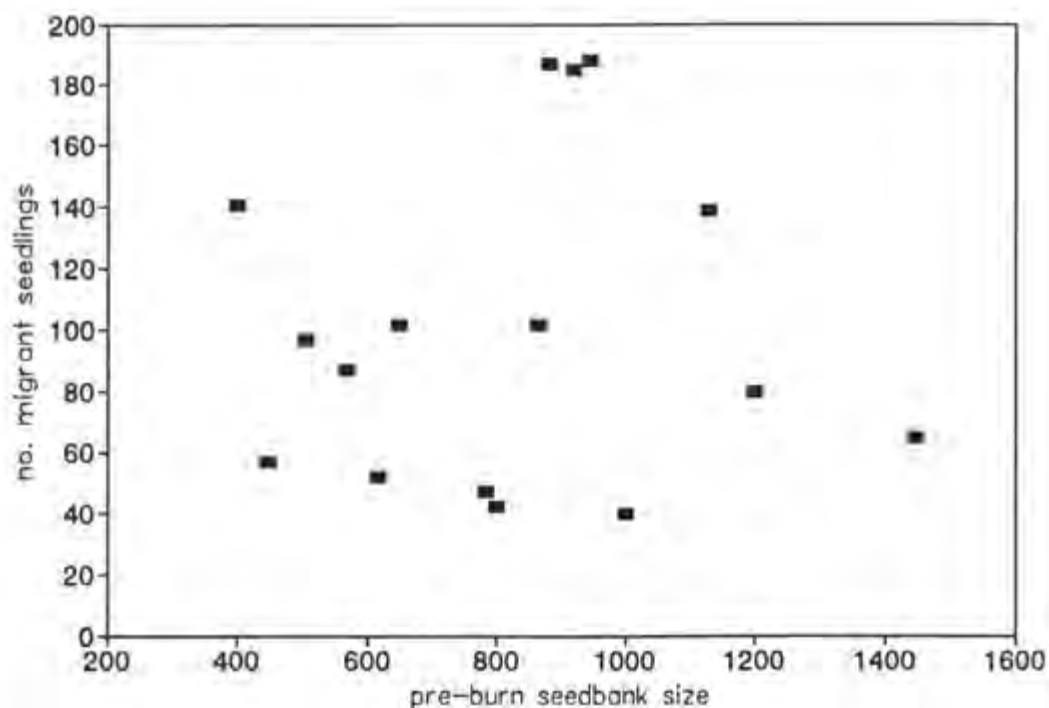


Fig. 12. The number of *P.nerifolia* migrant seedlings (edge) versus the number of *P.nerifolia* seeds for 16 10m x 10m plots. ( $r^2=0.003$ ,  $m=0.01$ ,  $y$ -intercept=93)

To give a better estimate of the proportion of dispersed individuals, the number of migrant seedlings was plotted against the total number of seedlings (as opposed to seeds) in the plot (Fig. 13 & 14). This gives a more accurate measure of the proportion of migrants, as the actual number of seeds per plot was an estimation based on the average number of seeds per cone. A positive linear relationship was found for *P.repens*, with about 1 seedling in every 4 leaving the source area. For *P.nerifolia* the relationship appears asymptotic with a levelling off of migrants at high densities (> 500 seedlings). Although there is more scatter, fewer *P.nerifolia* seedlings (approximately 1 in 6) migrate relative to *P.repens*. When 150 seedlings are produced, 55 migrate, when 350 seedlings are produced 140 migrate. Therefore at high seedling densities more seedlings migrate.

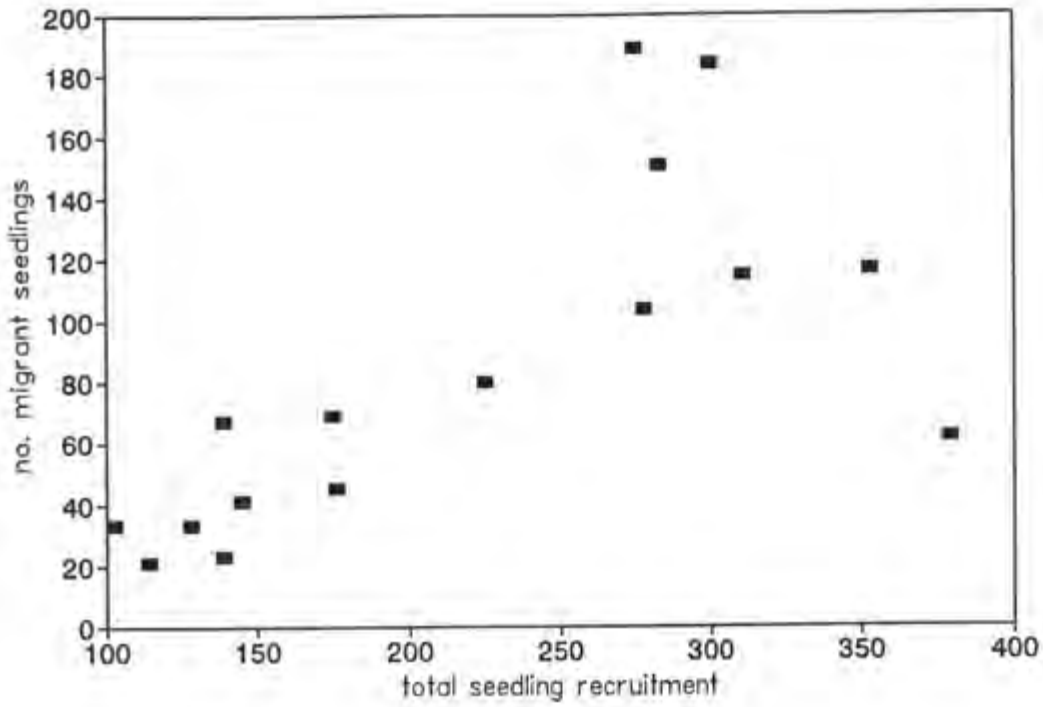


Fig. 13. The number of migrant *P. repens* seedlings (edge) versus the total number of *P. repens* seedlings (edge+buffer+plot) for 16 10m x 10m plots. ( $r^2=0.48$ ,  $m=0.42$ ,  $y=-9.1$ )

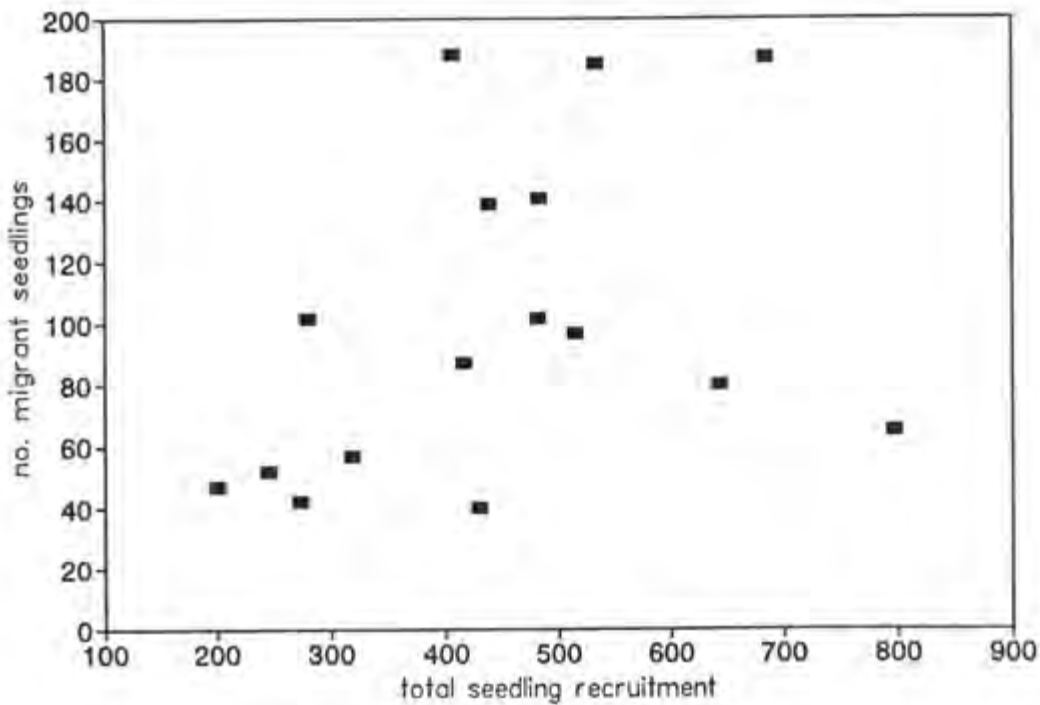


Fig. 14. The number of migrant *P. neriifolia* seedlings (edge) versus the total number of *P. neriifolia* seedlings (edge+buffer+plot) for 16 10m x 10m plots. ( $r^2=0.14$ ,  $m=0.19$ ,  $y$ -intercept = 47.7).

The results of a two-way anova of seedling dispersal and direction of dispersal showed that dispersal of seed to the west edge of the plot is significantly greater than to the other sides as would be expected from the southeasterly winds following the burn.

### **Counts of parents before and after the fire**

The skeleton counts and pre-fire plants numbers are shown in Appendix A. For *P.neriifolia* the counts are very similar, but for *P.repens* there are some plots in which substantial differences, both higher and lower than the pre-fire counts, were found. More parents of *P.repens* were counted after the burn in plots of high density (eg. plot D3) and fewer in some plots of lower density.

## DISCUSSION

### Relationship between seeds and seedlings

In general plants are known to produce far more seed than the number that grow into seedlings. It is therefore surprising to find that such high proportions of viable seed in both *P.repens* and *P.neriifolia* germinate to seedlings. In the case of *P.repens*, it takes approximately 2.7 seeds to produce 1 seedling. In the case of *P.neriifolia*, it takes approximately 2 seeds to produce 1 seedling. The fact that the  $r^2$  value is lower in *P.neriifolia* may be explained by the higher standard deviation of the mean number of viable seeds per cone when compared with *P.repens*.

The linear relationships between seeds and seedlings indicate that a constant proportion of seeds germinate and that seedling recruitment in this study is seed limited not microsite limited. Perhaps the fact that the rainfall was high could mean that there was ample moisture available for recruitment. However, when very high numbers of seedlings are produced, it is likely that due to the aggregation properties of the seeds that they will grow in clumps (Midgley, 1990) and thus suffer density dependent deaths due to competition. Possible reasons for such high recruitment will be discussed below.

### **Sources of seed mortality pre- and post-burn**

A large proportion of the seed bank is lost to pre-fire predation by a number of insects in both *P.repens* and *P.nerifolia*. Similar percentages of infestation were found in this study as was found in a more extensive study of infestation in *P.repens* cones (Coetzee & Gilomee, 1987). I found larvae of some of coleopteran (beetle) and Lepidopteran (moth) species. In Coetzee & Gilomee's study, 84% of *P.repens* seeds were damaged by insects within 102 weeks after flowering. Thus canopy stored seed in *P.repens* is highly vulnerable to insect predation. The low seed set in these two species makes the predators search for food more difficult especially in *P.repens* where viable and non-viable seeds look the same. Pollinator limitation has not been tested.

These insects are a serious detriment to the wild flower industry not only because they decrease the seed set but mainly because they destroy other parts of the flower, such as the florets, to such an extent that the flowers cannot be marketed (Coetzee & Gilomee, 1987).

### **Post-fire seed predation**

A negligible amount of post-fire seed predation was found as the seedling counts in the enclosure and control did not differ much. In other studies by Van Hensbergen *et al.* (1992) and Bond (1984) low amounts of post-fire seed predation were found following Autumn burns. One aspect that may decrease post-fire predation of seed is the fact that a large proportion of seed dispersed is non-viable and thus predators are fooled. Little is known about the degree to which seed predators influence the population dynamics of plants in the long term.

In this area I think that post-fire seed predation is minimal as the exposed environment is particularly dangerous for rodent seed predators (Midgley & Clayton, 1990) especially with a large raptor element in the area (pers obs) possibly a result of high rodent concentrations in the wheat fields a few km away. A further factor limiting the number of rodents in the area is that the closest unburnt vegetation was approximately 300m away from the study site.

It has been hypothesised that high seed densities lead to higher predation rates (Root, 1973) because the predator has to search for less time to find more seed. In this study a constant proportion of the total seedbank germinates into seedlings, thus there is no increase in predation at high seed densities. This confirms the fact that post-fire seed predation was minimal in this study.

Thus the proportion of seeds that did not germinate is attributed to germination failure. Post-fire seed predation is expected to be higher following a spring burn, which results in seeds being exposed to predators for a longer period (Bond, 1984).

### **The effects of fire on seed viability**

It has been proposed (Midgley & Viviers, 1991) that fire intensity may affect the germination of seeds. Cooler fires are expected to result in poorer seedling recruitment than hot fires, but very hot fires may burn the seed completely. From four adjacent plots in this study that were not burnt as intensely as the rest of the site, there was no difference in the germination percentages of viable seed. Thus fire intensity, at least within this range, may have no bearing on seed germination other than if it is very hot, where seeds may be burnt completely. This is contrary to what has been found in two myrmecochorous species (ie.

*Mimetes fimbriifolius* and *Leucospermum conocarpodendron*) where an increase in fire intensity leads to an increase in seedling recruitment per parent (fire intensity was measured as classes of canopy damage as was done in this study) (Bond *et al.*, 1990). To test this idea further, one could compare very hot with cooler burns to see whether fewer seedlings than expected recruit after a hot burn.

### Seedling mortality

Predicting seedling mortality is difficult at such an early stage in seedling development. The risk of seedling death may be highly variable due to factors such as summer drought either this year or the following year, seedling density, seedling predation, or other environmental factors such as unfavourable site. However, according to the literature there is no evidence to suggest that seedlings undergo self thinning (Midgley, 1988).

In the current study at this stage the only evidence of seedling mortality is due to insect predation but this seems minimal. Knowledge of fynbos insect herbivores is poorly understood. Plant herbivores are few in fynbos in general because of the low palatability of the foliage (Marloth, 1913), however the seedling stage is possibly more palatable. Other studies in both mountain (Midgley, 1988; Bond, 1984; van Hensbergen *et al.*, 1992) and lowland fynbos (Mustart & Cowling, 1993) have examined seedling mortality in years after a burn. In mountain fynbos seedling mortality up to three years after a burn is minimal (<7% in the Swartberg, (Midgley, 1988)) for a moderate summer, but is higher for severe summers (25% at Swartboskloof, (van Hensbergen, 1992)). In lowland fynbos seedling mortality has been shown to be high (25%) especially in the second summer after a burn.

In the lowland fynbos the summer drought was not particularly severe. The mountain fynbos study involved an average summer. How would this compare to a very hot summer?

Mustart & Cowling's study showed that seedlings are dependent on moisture availability as there was higher seedling survival on limestone soils that have a significantly higher soil-moisture content than colluvial sands. It is important to understand how soil type and summer drought interact in determining seedling survival.

Season of burn has been shown to be an important factor for seedling recruitment (Jordaan, 1981; Bond *et al.*, 1984; Van Wilgen & Viviers, 1985; Midgley, 1989). However seedling survival appears to be <sup>high?</sup> low and constant over all seasons of burn (Midgley, 1989).

### Density dependent mortality

There is no published data on density dependent seedling mortality for Proteaceae. It has been suggested (Midgley, 1988) that seedling mortality due to density dependence is unlikely. The 1m x 1m plots in this study should give an indication of this in the years to follow. I would disagree with the prediction that density related mortality would not occur, but rather that there will be some degree of density dependent mortality. It is hard to imagine that 30 seedlings in a 30cm x 30cm area will grow to adults (see Plate 9). In the plots in this study it was particularly evident that seedlings are often found growing in dense patches, a result of the seeds being trapped by some obstacle such as a fallen branch or a rock. It may also be probable that the seeds adhere to one another occasionally and thus germinate in clumps. Perhaps in other areas in Fynbos seeds do not grow in dense clumps due to the nature of the



Plate 9. *Protea repens* and *Protea neriifolia* seedlings growing in a dense clump.

terrain which may be unencumbered by trapping materials.

Using the Clark-Evans measure of aggregation, Midgley & Von Maltitz (1990) showed for several serotinous Proteaceae species that as the number of seeds in an area increases, so does the tendency for the seeds to clump. The seed hairs along with wind are probably important for the aggregation of the seeds.

One way to obtain an estimate of the number of seedlings that die is to compare seedling to parent ratios for a number of different sites. The assumption that the population size stays the same is then more justified. However this would only be useful for evolutionary studies of the species and not for harvesting management in a relatively small area. Le Maitre & Midgley (1992 book) produced seedling survival curves and found that although there is a decrease in survivorship over time, this is gradual.

The graphs of seedlings versus parents do not appear to be useful for predicting how many seedlings will survive to adults, as it is evident from the high plant densities found in this study (ie. 561 *P.repens* in 10 x 10 m) that plants can survive at much higher densities than is suggested by the graphs. Very low levels of adult mortality due to overcrowding has only been demonstrated in very old *Protea* stands (Le Maitre, 1992). However although the *P.repens* plants can survive in very dense stands, only a small proportion are reproductive (Fig. 9.3).

Evident from this study is the fact that there is a large gap in our knowledge of the causes and magnitude of seedling mortality. It is uncertain whether seedling mortality is density dependent or independent, and how important drought is as a mortality factor. The fact that

the number of seedlings far exceeds the number of parents in this study suggests that if the population size stays roughly the same then seedling mortality must be high. If density dependent death is an important factor then harvesting can be seen as removing seedlings that would otherwise die due to seedling competition. If density independent factors, such as herbivory, are more important causes of seedlings deaths, then predicting suitable harvesting levels is more tricky.

### **Predicting harvesting levels**

The following model is proposed for predicting the number of cones needed for optimal parent recruitment. The excess cones can then be harvested. The reasoning behind the model is discussed below.

$$\text{Required number of cones} = \frac{(N \times r)}{(S \times g)}$$

- where
- N = optimal parent density for flower production
  - r = number of seeds needed to make one seedling
  - S = number of seeds per cone
  - g = fraction of seedlings that survive to adults

Variation in parent plant densities may lead to variations in yield and mortality in the component plants, due to the consumption of resources in limited supply, the reduction of toxins or changes in conditions such as protection from wind and influences on the behaviour (Harper, 1977). One such variation in this study was that the overall number of cones and viable seed set was reduced in stands of high density (Fig. 9.2 & 10). With an increase in parent plant density there is a decrease in overall cone production as well as seed production per plant.

This is contrary to Esler & Cowling's findings (1990) who found that overall seed production increased with density in *P.lepidocarpodendron*. However these results are from comparisons of three different areas that differed from each other in parent density. A sparse site occurred on granite and the denser sites on sandstone. Therefore comparisons of total seed production between different density stands at different sites are affected by site specific factors such as soil type and nutrient availability and their effects on reproductive output.

The optimal population density for flower production is desirable for flower farming. Many plants are too crowded to produce flowers. This can be attributed to within-species competition (Bond *et al.*, 1984). Therefore from the graphs for each species, of flower production versus parent density, the optimal density for flower production can be determined.

For *P.neriifolia*

$N = 70$

$r = 2$

$S = 8$

When

$g = 0.8$  (20% mortality)

Then the number of cones needed to produce 70 adults is 22. This value is compared to the number of cones produced at the optimal parent density in this study which is 180. Therefore flower heads in excess of this amount can be harvested (ie. harvest up to 88%). When  $g = 0.2$  (very high mortality) the number of cones needed to produce 70 adults is 88. This leaves 50% of the cones for harvesting.

In *P.repens* the situation differs and problems arise with this model because from the second data set it is evident that 3 year old *P.repens* cones contain virtually no viable seed. Therefore there may be little point to leaving cones of the plants for more than three years before a burn. If for *P.repens* the optimal parent density for cone production is 100, then the number of cones needed to produce this many adults is 42 assuming 20% seedling mortality (ie. harvest up to 85%). If 80 % mortality is assumed, then 169 cones are needed.

The above harvesting levels are higher than the current guidelines. However few farmers harvest below 70%. The fact that despite scientific community warning, the farmers tend to harvest up to 75% of each year's flowers, is viewed negatively by some members of the scientific public. These high harvesting levels may not be as detrimental to seedling recruitment as was previously thought to be the case.

It should be borne in mind that a general management model of this nature cannot be produced until many more studies of seed bank size in relation to seedling recruitment have been done in other areas, for other species and for other fire regimes. This model is not extended for other fire regimes, such as the influence of fire season or age of burn. However from this study it is evident that nine years is long enough for sufficient seeds to accumulate for regeneration after an Autumn burn.

### Other factors necessary for a more complete model

Factors necessary for a more complete harvesting model that have not been tested here are the accumulation rate of cones with time and the decrease of seed viability and number in older cones with time. Some studies concerning this have been done for other species (Mustart 1991).

It is important to note that different areas may also respond differently to different fire regimes (eg. Bond *et al.*, 1984 found that serotinous Proteaceae are more sensitive to season of burn on the northern slopes of the Swartberg than on the southern slopes.)

### Dispersal

Although questions concerning dispersal are a side issue in this study, some interesting aspects have been found. In *P.repens* dispersal appears to be density dependent. That is that the more seedlings that are produced, the more they disperse elsewhere. However it is unclear how the relationship would look at very high seedling densities and also how this would look with increasing distance from the parents. For *P.neriifolia* where the seedling densities are twice as high as *P.repens* there is a levelling off of migration over seedling densities of about 500 which suggests that seeds are hindered in some way from dispersing. A linear relationship for seed production and seed migration is not known from any other study.

The hairs of the seeds appear to enable seed dispersal by rolling along the ground, this has been suggested by Bond (1985). The fact that the majority of seeds are dispersed in the direction of the strongest wind shows that wind significantly affects the dispersal of both *P. repens* and *P. neriifolia* seeds. If the seeds migrated to the edge of the plots then they could have travelled from as little as 1.5m or 11.5m. Judging from the high proportions of migrant seedlings in *P. repens* and *P. neriifolia* it may be possible that the seeds could have dispersed much further if they had not been stopped by the barriers. Manders (1986) showed that dispersal distances for non-myrmecochorous fynbos species is less than 10m.

#### **Parent counts before and after the fire**

As previously mentioned, *Protea* skeleton counts are used in many population studies in the Fynbos. The differences in parent counts before and after the fire raises some doubt about using post-fire parent counts particularly in the case of *P. repens* where higher counts after the fire resulted for very dense plots, and some lower counts resulted for less dense plots.

Lower counts result probably because *P. repens* branches are thin and easily burnt. In many cases a *P. repens* plant before the fire was a single stemmed 60 cm high plant. Higher counts could have resulted after the fire either because they were missed in the pre-fire counts, or that they were mistaken for different species such as *Aulax* species after the fire. A bare thin stem is easily misidentified.

## CONCLUSION

Studies of seedbank size in relation to recruitment are non-existent in plants other than a few annuals let alone fire adapted species. For most plants this is because many decades must pass (due to the generation time) before the effects on populations are known. The life-cycles of *Protea* species are adapted to fire such that fire kills the plants and canopy-stored seed is released. Thus in serotinous Proteaceae there are discrete generations making them suitable for demographic studies.

Plants are considered to produce far more seeds relative to the number of seedlings produced (Harper, 1977; Crawley, 1992) but few studies demonstrate the relationship between seeds and seedlings. It is therefore surprising to find that high proportions of seed germinates to seedlings in *P.repens* and *P.neriifolia*.

Up until now there has been much speculation on how seed bank depletion affects post-fire seedling recruitment of Proteaceous species. The study by Mustart & Cowling (1992) is not supported by enough data to conclude that harvesting of current inflorescences should not exceed 50%. The number of seeds required for post-fire regeneration is now better understood in *P.repens* and *P.neriifolia*, from the positive linear relationship between pre-fire seed bank size and post-fire regeneration following an Autumn burn. Thus for this Autumn burn, seedling recruitment does not appear to be dependent on post fire factors, but rather seed availability. From the constant proportion of seeds that germinate to seedlings, germination failure can be invoked to explain the proportion of seeds that do not germinate.

Mustart & Cowling's (1992) estimates of annual harvesting of 70% leading to a depletion of the seed bank appear to be too low for Autumn burns as cones that are not harvested may result in non-reproductive adults or density dependent seedling deaths due to seedling clumping (Midgley & Von Maltitz, 1990).

Seedling mortality has not been demonstrated to be higher than 25% from other studies in Fynbos, therefore even with a more conservative estimate of seedling mortality of 50%, harvesting levels well above 70% result in sufficient seedling recruitment after an Autumn burn in a nine year old stand. However for a rule of thumb to be proposed for the wild flower farmer, it is necessary to take into account unseasonable fires which may mean that farmers should leave more flowers on the parents.

The conservation manager of unharvested areas may not want to maximise recruitment as this leads to very dense parent populations and many of these plants may be non-reproductive. Clearly important results from this study will come in the years ahead when the adult plant numbers stabilize. Ultimately studies similar to this should be replicated to get a per seed probability of recruitment for the same species over time in a variety of habitats.

Dispersal could be more important in non-myrmecochorous Protea population dynamics than was previously thought. Seedling migration in *P.repens* appears to be density dependent. The proportion of migrant seedlings increases with seed production. Perhaps at very high seed densities fewer seeds would be dispersed due to pre-germination seed aggregation, which is possibly facilitated through the seed hairs and wind. In fynbos habitats that are less encumbered by seed trapping materials seedling clumping may be less likely.

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## APPENDIX A.

Raw data collected from the burnt site (site A on map) at Potberg.

*Protea repens*

Plot No.	cones	orig plants cones		skel	estim seeds	seedlings			tot
						plot	edge	buffer	
A5	0				0	19	11	12	42
A10	0				0	12	3	1	16
A12	0				0	14	9	1	24
A19	0				0	19	58	3	80
B2	74	99	109	51	592	127	80	18	225
B9	87	116	29	32	696	148	115	48	311
B11	68	91	40		544	108	45	23	176
B20	56	75	87	79	448	55	67	17	139
C4	62	2	52	80	496	90	184	26	300
C6	41	82	33	46	328	80	33	15	128
C15	37	74	58		296	61	41	43	145
C16	56	112	29		448	149	104	25	278
D7	45	180	61		360	96	23	20	139
D13	31	124	54		248	77	21	16	114
D18	23	92	37	50	184	97	69	9	175
D3	28	112	60	215	224	60	33	10	103
E1	66	66	36	32	528	122	151	10	283
E8	107	107	42	41	856	229	62	88	379
E14	68	68	45		544	70	189	16	275
E17	88	88	59	57	704	216	117	20	353

*Protea neriifolia*

PLOT NO.	cones	orig cones	plants	skel	estimated seedbank	seedlings			
						plot	edge	buffer	tot
A5	0				0	42	30	14	86
A10	0				0	26	8	26	60
A12	0				0	14	12	9	35
A19	0				0	42	68	26	136
B2	141	188	51	49	1128	252	139	48	439
B9	71	95	23	28	568	248	87	81	416
B11	125	167	43		1000	361	40	28	429
B20	110	147	102	136	880	363	187	135	685
C4	115	186	40	70	920	274	185	75	534
C6	98	168	39	62	784	121	47	32	200
C15	108	187	82		864	260	102	120	482
C16	100	182	49		800	191	42	39	272
D7	56	160	44		448	202	57	59	318
D13	77	188	76		616	106	52	87	245
D18	63	151	46	91	504	379	97	39	515
D3	50	112	213	251	400	292	141	50	483
E1	81	93	29	36	648	144	102	33	279
E8	181	208	62	65	1448	617	65	115	797
E14	118	137	47		944	166	188	52	406
E17	150	175	137	146	1200	524	80	39	643

## APPENDIX B

Raw data collected from the unburnt site (site B on map) at Potberg.

PLOT NO	cones	estimated	repens	total
		seed	plants	plants
1	399	1777.89	135	147
2	156	260	73	109
3	175	424.18	24	25
4	109	512.04	426	561
6	261	685.67	438	476
7	133	762.19	56	64
8	226	626.26	88	104
9	211	835.38	170	218
10	225	1687.5	407	427
12	224	392.86	317	360
13	61	287.95	16	19
14	281	2498.45	64	78
15	181	358.76	70	80
16	219	991.94	127	194
17	299	723.25	138	153
18	189	413.88	254	265
20	166	819.83	347	412

## APPENDIX C

Rainfall data for Potberg 1993.

Date	rainfall (mm)	Date	rainfall (mm)
Jan 8	1.5	May 3	44
12	5	6	3.5
23	1	7	2
31	5	14	6
		22	7
Feb 3	2	26	7
7	5	27	4
15	7	28	5
16	1	29	5
22	34	June 3	9
March 2	1	11	5
3	10	12	14
4	12	13	4
21	8	29	7
April 2	4	July 8	9
3	7	9	5
5	17	11	28
6	10	15	5
8	11	17	6
9	4	18	3
11	6	27	10
12	70	28	4
13	31	Aug 4	15
18	1	8	10
27	2	11	5
30	6	20	7
		22	7
		29	1
		31	5