SEED AND SEEDLING ECOLOGY OF TWO CO-OCCURRING ERICOID FYNBOS SHRUB SPECIES

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ABSTRACT

The seed and seedling ecology of the ericoid fynbos shrubs *Passerina paleacea* and *Phylica ericoides* were studied. These species co-occur in dune fynbos and are dependent on soil seed banks for regeneration after recurrent fynbos fires. ~~Ericoid shrubs comprise most of the 8500 fynbos species, but have been poorly studied. Similarly, soil seed banks have been poorly studied in fynbos. Thus, this study aimed to better our understanding of the adaptions of these species for regeneration in their fire-prone environment. Their seed bank dynamics and germination ecology were the focus, but were placed in the context of their whole life cycles.~~

~~The germination of both species was linked to fire~~. *Phylica* was stimulated by the heat effect of fire. The precise germination cue for *Passerina* could not be determined, although circumstantial evidence pointed to the role of an indirect fire effect associated with the removal of vegetation. The seed banks of both species were seasonally persistent, and were not substantially depleted during the year following seed input. Seed bank estimates for *Passerina* from direct seed counts varied from 441 ± 620 ($\bar{x}$ ± sd) seeds per m^2 before seed dispersal to 737 ± 919 seeds per m^2 after dispersal. The seed bank of *Phylica* was exceptionally stable at 278 ± 450 seeds per m^2. Seed bank estimates from germination were lower. Fire appeared not to kill significant numbers of seeds, but seed banks were largely, although not completely depleted during the winter following fire. *Phylica* appeared to lose little seed after dispersal and most seed appeared to survive for at least several years in the soil. This allowed *Phylica* to build up seed banks larger than the seed input in one year. *Passerina* produced much larger amounts of smaller seeds, most of which were lost before incorporation into the soil seed bank. These large losses were not limiting on population recruitment of *Passerina* after fire, which was apparently limited by seedling mortality during summer drought. The recruitment of *Phylica*, in contrast, appeared to be limited by poor seedling establishment during the first winter after fire. This was possible largely due to germination failure, which is probably affected by the intensity of fire. Recruitment in mature vegetation was severely limited for both species, although *Phylica* appeared to have more potential than *Passerina* for recruitment in this environment.

The implications of results for burning of fynbos and for commercial flower harvesting of *Phylica* are discussed. Differences between the species are also used for suggesting possible means of non-equilibrium coexistence.

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CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

RATIONALE

In the fire-prone fynbos shrublands of the Cape, the survival and expansion of plant populations is dependent on their ability to regenerate after fire. Thus, as in other mediterranean regions, fire is one of the most important selective agents in the evolution of life history traits (Naveh 1975; Gill 1981; Cowling 1987). There is a need for explanations of the adaptions of fynbos species to fire, and for predictions of fynbos community structure and population dynamics in response to fire (Kruger 1983). This knowledge is of more than academic relevance as it may be used in fynbos management, particularly in the manipulation of fire regimes by prescribed burning (Mooney and Conrad 1977; Ford 1985; Cowling *et al* 1987). Commercial harvesting of fynbos species has also become an increasingly important disturbance factor in certain areas, and knowledge of the dynamics of harvested populations may help formulate conservation-minded guidlines for flower pickers (Greyling and Davis 1989). Current management policies have been influenced by previous research which has concentrated on the conspicuous Proteaceae, especially those with canopy-stored seeds (e.g. Bond 1984; 1985; Bond *et al* 1984; Cowling *et al* 1987; Midgely 1988). It has been emphasized, however, that fynbos management practices should aim to conserve as many species as possible and thus a wide range of species need to be studied (Cowling 1987). The small-leaved (ericoid) fynbos species, which comprise most of the 8500 fynbos species (Bond and Goldblatt 1984), have been largely neglected. The only extensive population study of this group has been that of Pierce (1990). Most ericoid species are non-sprouters and are thought to depend on soil seed banks for recruitment after fire (Kruger 1984). Soil seed banks have also been poorly studied in fynbos. Manders (1990) and Pierce (1990) are the only two detailed studies on soil seed banks in fynbos.

This study investigated the seed and seedling ecology of two non-sprouting ericoid fynbos shrub species, *Passerina paleacea* and *Phylica ericoides* (Hereafter referred to by their generic names). These species co-occur in dune fynbos and regenerate after fire from seeds stored in the soil. The dynamics of their seed banks and their germination ecology were the focus, but were placed in the context of their whole life cycles. The importance of population level studies has been emphasized as a requirement for gaining a predictive understanding of the mechanics of community dynamics in fynbos (Manders and Cunliffe 1987). The importance of studying various life history stages in plants, as opposed to isolated components only, has also been emphasized (e.g. Harper and White 1974; Auld 1987; Price and Jenkins 1987; Parker *et al* 1989).

This study was largely inspired by the pioneering work of Pierce (1990) on six ericoid species in eastern Cape dune fynbos. Also of interest were investigations in other fire-prone mediterranean shrublands, viz. European *Calluna* heath (e.g. Mallik *et al* 1984; Willems 1988), Australian heath (e.g. Auld 1986a, b; 1987; Auld and Myerscough 1986; Andersen 1989), and Californian chaparral (e.g. Christensen and Muller 1975; Keeley 1977; 1987a, b; Kelly 1986; Zammit and Zedler 1988).

SPECIFIC AIMS

Germination

Germination studies investigated the adaptions of seeds of *Phylica* and *Passerina* to recurrent fynbos fires. It has been argued that interfire conditions in fynbos do not favour germination (Kruger 1984; Brits 1986a), and indeed it is reasonable to predict that seeds have well developed dormancy broken by fire-related cues. Thus the extent to which germination of *Passerina* and *Phylica* is linked to fire was investigated and efforts were made to determine the nature of possible fire-related germination cues. In Californian chaparral the fire-related effects of heat and charred wood were found to promote seed germination (Keeley 1987a; 1990; Keeley and Keeley 1987; Parker 1987). The indirect fire-effects of increased light reaching the soil (Christensen and Muller 1975), higher diurnal temperature fluctuations in soil (Brits 1986a; 1987; Pierce 1990) and the removal of allelopathic substances produced by adult plants (Christensen and Muller 1975), have also been proposed, but their precise role is less certain.

Seed banks

Soil seed banks have been recognized since Darwin's time (Darwin 1857), but have only been intensively studied in the last two decades (e.g. Heydecker 1973; Harper 1977; Thompson and Grime 1979; Roberts 1981; Fenner 1985; Leck *et al* 1989). For *Passerina* and *Phylica*, recruitment after fire is dependent primarily on the availability of soil-stored seed at the time of fire. The dynamics of the seed banks are thus important as they ultimately guarantee the ability of the populations of these species to maintain themselves (Parker *et al* 1989). This study sought to determine the sizes of the seed banks of *Passerina* and *Phylica* and to determine whether the seed banks were seasonally persistent. Persistence of seeds is selected when it is needed to maintain the population through a period of risk (Parker *et al* 1989). Thus, for these obligate reseeders, seasonally persistent seed banks may be expected in order to protect against the risk of fire in all seasons, and against fire in seasons of extremely low seed production.

Life cycle dynamics

The life history of a plant consists of all stages through which it passes from fertilization to death. These stages may be divided into the following processes: a) seed production, b) seed dispersal, c) seed storage, d) germination, e) seedling establishment, and f) passage of seedling to adult. Life history traits of *Passerina* and *Phylica* during their seed and seedling stages were compared. The amount of seed produced was determined and the pattern of subsequent seed and seedling losses through the life cycle was noted. Attempts were made to identify the processes limiting population recruitment after fire.

In fynbos recruitment of most species is thought to be limited to the few years after fire (Kruger 1984). This was tested for the study species by assessing their potential to recruit in mature vegetation. The emergence and survival of seedlings in mature vegetation was noted.

Cowling *et al* 1987 have suggested that a rewarding area of research is in the study of factors promoting coexistence in species-rich fynbos. Thus, differences between *Passerina* and *Phylica* were used to propose possible mechanisms of non-equilibrium coexistence (Caswell 1982) of these species.

Coexistence may be predicted from differential recruitment of the different species in response to stochastically variable fire regimes or environmental conditions associated with different fires (Cowling 1987).

Practical significance

The implications of germination cues and the dynamics of seed banks for fire in different seasons are discussed. Attempts were also made to predict some effects of extremely long and extremely short interfire periods. The concept of an optimal fire regime was viewed in the light of coexistence hypotheses made. Results were also used to interpret the effects of different harvesting strategies in the commercial exploitation of *Phylica*. The effects of removing large amounts of seed by harvesting were discussed in relation to the dynamics of seed banks. Experiments were also done to examine the effects of different harvesting intensities on the recovery of harvested *Phylica* plants.

METHODS

Many methods at different levels were used to answer the questions posed. Field studies were used to compare seedling recruitment in mature fynbos with that in burnt areas, and to monitor seedling survival in both environments. Germination studies included germination of seeds in soil samples in an open nursery. Seeds collected from plants were germinated under controlled laboratory conditions after the seeds had received various treatments in attempts to break dormancy. Seed banks were studied in a number of ways. Estimates of seed bank sizes were made at intervals using two methods - sorting and counting of seeds from soil samples and germinating seeds in soil samples. These estimates were used, together with seed burial in mesh bags and a harvest experiment, to asses the persistence of seed banks. The harvest experiment involved removing the current years seed crop from in and around plots by harvesting, and comparing subsequent post-fire germination in these plots to that in controls. Such an experimental approach has not often been used to study seed banks (Leck *et al* 1989). Seed bank estimates were also made before and after fire and following recruitment during the first winter after fire. To place the germination and seed bank studies in context relative to other life history phases, and to asses the limits to population recruitment after fire, a "seed budget" (Mallik *et al* 1984; Andersen 1989) was constructed. This involved determining the amounts of seed produced, the number of seeds in the seed bank, the number of seedlings establishing during the first winter after fire, and the number of seedlings surviving their first summer drought.

Statistical analyses included parametric methods (*t*-tests and ANOVA) and log-linear analyses. The approaches to data collection and experimental design often allowed multi-factorial analyses to be made. These enabled the determination of the effects of different sub-sites within the general study area, and the effects of the different species, on seed and seedling counts. Data collected in the seed bank studies were composed of counts and included many zeros, and thus provided some dilemma as to the appropriate statistical methods needed for analysis. Initially parametric statistics (ANOVA), conventional non-parametric statistics (e. g. Kruskal-Wallis and Mann-Whitney tests) and log-linear methods were used. All methods gave similar results. The log-linear analysis results were reported as they were theoretically most appropriate for the type of data.

STUDY SITE

Passerina and *Phylica* (Table 1) are co-dominants at the study site (Fig. 1), which is located on the farm Groot Hagelkraal (34°40'S, 19°30'E), 45 km west of Cape Agulhas. It is a 2 ha area in vegetated dunes, 100 m to 200 m from the sea. It is situated on relatively shallow (0.25 to 0.5 m), but well drained calcareous dune sands overlying Pleistocene calcrete (Die Dam land system) (Thwaites and Cowling 1988). The vegetation is Dune Asteraceous Fynbos (Cowling *et al* 1988) and comprises a fine leaved shrubland with a field layer of evergreen hemicryptophytes (e.g. *Ischyrolepis eleocharis, Calopsis fruticosus, Chondropetalum mucronatum* and *Ficinia lateralis*). Proteoid species are absent and the species diversity is lower than in most fynbos communities. Other common shrubs at the site include *Erica coccinia, Agathosma collina* and *Metalasia muricata.* Patches of thicket occur on the periphery of the site and include species such as *Euclea racemosa, Myrica Quecifolium, Pterocelastrus tricuspidatus* and *Rhus* species. Dune fynbos occurs in a narrow belt on coastal dunes throughout the fynbos biome from Port Elizabeth to Langebaan (Cowling 1984). It is increasingly threatened by invasive alien species, coastal development, the wildflower industry, and generally poor management.

Passerina and *Phylica* had similarly and consistently high cover over the study site, which generally appeared to be very homogeneous. The vegetation is relatively low (0.4-0.8 cm). The site is subject to recurrent fynbos fires and was last burnt 25 to 30 years previously. The vegetation also appeared to be very even-aged, as expected from recruitment being limited almost exclusively to the immediate post-fire period (Kruger 1984).

The site has a mean annual rainfall of approximately 450 mm, with over 65% falling in the winter months from May to October. In summer the site is wind swept and dry. The average annual temperature is 15-16°C. According to the UNESCO-FAO bioclimatic classification, the area has an attenuated mesomediterranean climate (Milewski 1979).

THESIS STRUCTURE

This chapter comprises a brief introduction to the study. It is not intended to provide an extensive literature review. The main findings are presented and discussed in Chapters 2, 3 and 4. These chapters are written in a format and style which is intended to make them easily reduced for scientific publication. This has meant that some details are repeated in more than one chapter. These chapters are, however, somewhat longer than would be required for primary publication, largely due to the more extensive literature review and discussion required for a thesis. Chapter 5 reemphasizes the main conclusions and highlights shortcomings of the study. Two appendices are short reports of more limited studies.

Table 1. Characteristics of *Passerina paleacea* and *Phylica ericoides*.

Characteristic	*Phylica ericoides*	*Passerina paleacea*
Family	Rhamnaceae	Thymelaeaceae
No. spp. in genus in Cape flora[a]	150	18
Distribution[a]	Cape Pennininsula to Port Elizabeth	Cape Penninsula to Bredasdorp
Habitat[a]	Dunes to lower slopes	Sandy flats to lower slopes
Shrub height[ab]	0.15-0.9m (0.45m)	0.3-1.0m (0.5m)
Pollination	Insect	Wind
Dispersal	Ballistic and ant	Unspecialised
Seed mass[c] ($\bar{x}$±sd)	2.5 ± 0.4 mg	0.8 ± 0.2 mg
Flowering time[c]	Feb. to Nov.	Aug. to Nov.

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[a] From Bond and Goldblatt (1984).
[b] Average height at study site is shown in parentheses.
[c] This study.

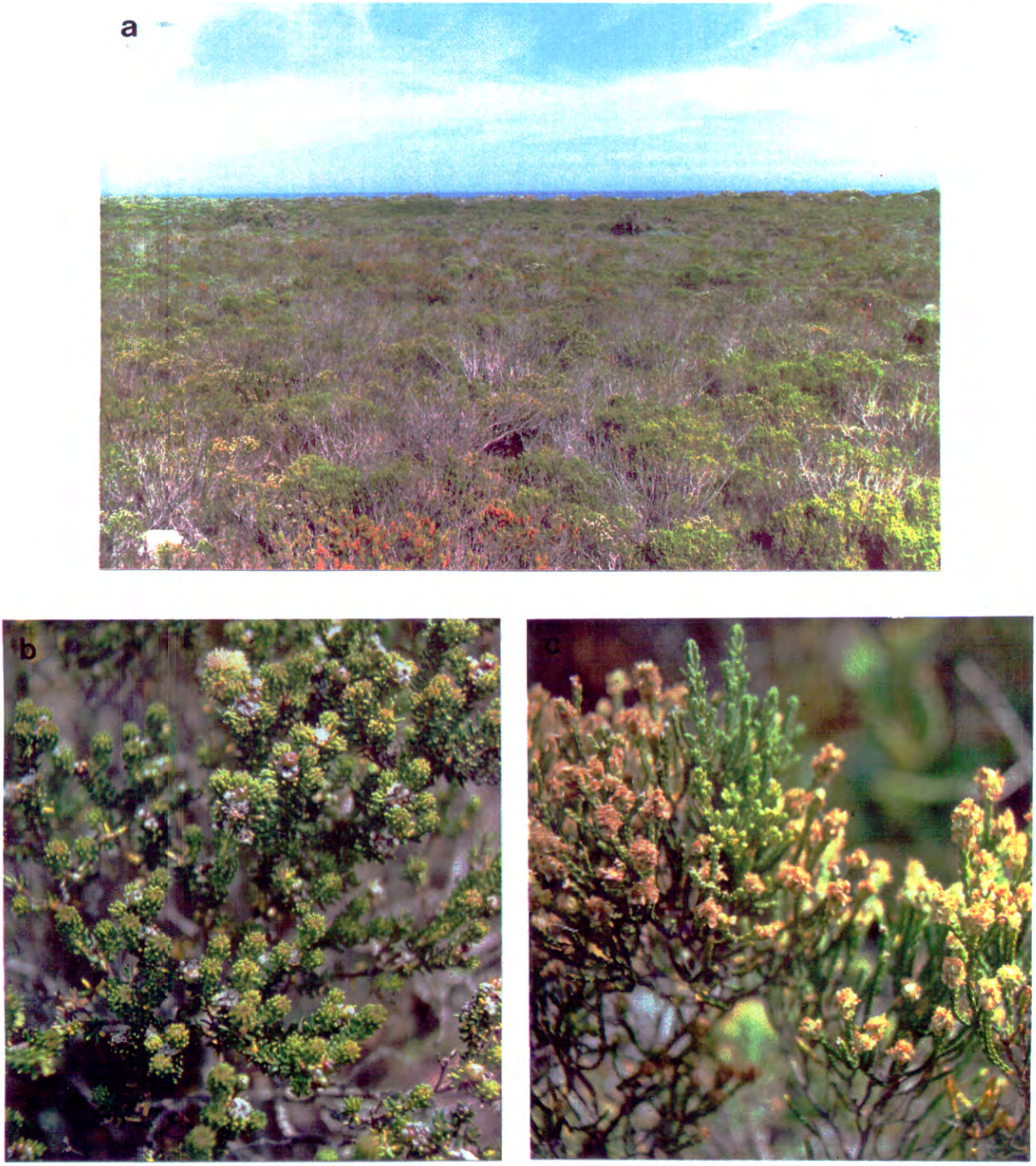

Fig. 1. a) Study site in Dune Asteraceous Fynbos. b) Phylica ericoides. c) Passerina paleacea.

CHAPTER 2: FIRE AND GERMINATION IN TWO ERICOID FYNBOS SHRUB SPECIES

ABSTRACT

Fire-related germination characteristics were investigated in the co-occurring fynbos shrubs *Passerina paleacea* and *Phylica ericoides*. Both species depend on recruitment from soil seed banks for regeneration after fire. A field study indicated that the germination of both species was linked to fire. Laboratory germination studies indicated that the heat effect of fire is a germination cue for hard coated *P. ericoides* seeds. A 70°C treatment for 1 h produced optimal germination as opposed to 100°C or 125°C for 5 minutes, which appeared to cause some seed mortality. The exact nature of the germination cue of *P. paleacea* could not be determined. This species had very strong dormancy which was broken by the artificial treatment of acid scarification, but not by the heat or charred wood treatments used. Germination of *P. paleacea* seeds in an open nursery pointed to a cue related to indirect fire effects associated with the removal of vegetation cover. However, the effects of light, allelopathy, and increased diurnal temperature fluctuation appeared to be excluded. The germination requirements of this species may thus be complex and could include initial seed ageing. The existence of differing fire cues between the two species was proposed as a possible mechanism promoting species coexistence.

Key words: charate, coexistence, dormancy, fire-cue, heat, indirect fire effects, soil-stored seeds.

INTRODUCTION

In the fire-prone fynbos shrublands of the western Cape, South Africa, the survival and expansion of plant populations is dependent on their ability to regenerate after fire. Many fynbos shrub species depend on seedling recruitment from soil seed banks for survival through fires (Kruger 1984). It has been argued that inter-fire conditions do not favour germination (Kruger 1984; Brits 1986a), and indeed it is reasonable to predict that seeds have well developed dormancy broken by fire-related cues. Direct supporting evidence is scarce, however. Also, many species germinate readily without specific fire cues (e.g. coastal sage species in Keeley 1987a; Pierce 1990) and, for many species, establishment between fires may be limited by granivory (Bond and Breytenbach 1985) and herbivory of seedlings (Breytenbach 1984), rather than by dormancy of seeds.

Good evidence for specific mechanisms by which germination is cued to fire are also rare for fynbos species. In other fire-prone mediterranean shrublands, particularly in Californian chaparral, more extensive germination studies have strongly established the fire-related effects of heat and charred wood (Keeley 1987a; 1990; Keeley and Keeley 1987; Parker 1987) as factors promoting germination in many species. Fire may also indirectly influence the germination of seeds stored in the soil, in that it removes vegetation covering the soil. Vegetation removal has been associated with a number of factors which have been linked to the breaking of dormancy in seeds. These include increased light reaching the soil (Christensen and Muller 1975; Keeley 1987a; Keeley and Keeley 1987), higher diurnal fluctuations in soil temperature due to removal of insulation (Thompson and Grime 1983; Brits 1986a; 1987; Murdoch *et al* 1989; Pierce 1990), and the removal of allelopathic substances produced by adult plants (McPherson and Muller 1969; Christensen and Muller 1975).

In fynbos most germination studies have concentrated on the large seeded members of the Proteaceae, especially those with canopy-stored seeds (reviewed by Van Staden and Brown 1977; Deall and Brown 1981; Brits 1986a, b; Brits and Van Niekerk 1986). There has been less emphasis on the small seeded, small-leaved (ericoid) species which comprise most of the 8500 fynbos species (Bond and Goldblatt 1984). Studies in this group with ecological interpretation have been especially rare, and include those on three *Erica* species (Small and Garner 1980; Small *et al* 1982; Van der Venter and Esterhuizen 1988) and on six eastern Cape dune fynbos species (Pierce 1990).

This study sought to determine, in the field, the extent to which germination is linked to fire in two non-sprouting, ericoid, dune fynbos shrub species. Both species have soil seed banks (Chapter 3). Further, in laboratory experiments, the germination characteristics of these species were investigated, with an emphasis on characterizing possible fire-related germination cues. The adult plants of these species appear ecologically similar and are possibly competitively equivalent. They are also co-dominant species at the study site. It was thus hypothesized that they would differ in aspects of their fire-related germination responses, as a possible factor promoting their coexistence (Grubb 1977; Cowling 1987).

MATERIALS AND METHODS

Study species and study site

The ericoid shrubs *Passerina paleacea* (Thymelaeaceae) and *Phylica ericoides* (Rhamnaceae) were selected for study.

Nomenclature is according to Bond and Goldblatt (1984), and the species will hereafter be referred to by their generic names. They are the dominant shrubs at the study site in Dune Asteraceous Fynbos (Cowling *et al* 1988) on the farm Groot Hagelkraal (34°40'S, 19°30'E), 45 km west of Cape Agulhas. The climate is mediterranean, with 65% of approximately 450 mm falling in the winter months from May to October. As is typical of mediterranean shrublands, this site is subject to recurrent fires (Kruger 1984, Keeley 1986). It was last burnt 25 to 30 years previously. The populations of both species appear to be even aged, which is consistent with the limitation of recruitment to the immediate post-fire environment (Kruger 1984). Both species disperse their seeds in early summer when moisture levels are low, adding to a soil seed bank (Chapter 3). They are obligate seeders depending on these soil-stored reserves for population replacement following fire (Chapter 4). *Passerina* seeds are passively dispersed, while *Phylica* seeds are ballistically dispersed and have elaiosomes for possible ant dispersal.

Field observations of fire-linked germination

The study site was burned in May 1990. In August 1990, following seedling recruitment during the wet winter, five small "islands" of unburnt fynbos were selected. These generally occur where rocks break the path of a fire, resulting in a "shadow" of unburnt vegetation downwind. On each of these "islands" seedlings of both species were counted in a 1 m^2 quadrat near to the edge of the unburnt vegetation, and in a matched quadrat close by in the burnt area, on apparently similar soil substratum. Seedling numbers in the burnt and unburnt areas were compared using t-tests.

Germination of seeds in soil cores

Germination of *Passerina* and *Phylica* from soil cores collected before fire was compared to germination from cores collected after fire. Soil cores were collected at the study site three weeks before it was burnt in May 1990, and again five days after the fire. On each occasion 120 soil cores (each 5 cm in diameter and 5 cm deep) were collected at intervals on transects traversing a 50 m X 50 m area. The cores were combined in groups of four, and each of the 30 combined samples then spread to a depth of 1 cm on the surface of a tray containing potting soil. The trays were placed in an open nursery at Kirstenbosch Botanical Gardens (130 km west of the study site) where they were exposed to rain and sun, and were kept moist during dry periods. Emerging *Passerina* and *Phylica* seedlings were counted monthly between May and October 1990. Once counted, seedlings were removed. A log-linear model was fitted to total seedling counts from all trays, for each sampling time, for each species, using the Statgraphics computer package (STSC, Inc.).

Laboratory germination experiments

Seed was collected from *Passerina* and *Phylica* in December 1989 by placing bags over mature plants shortly before seed dispersal. Many *Passerina* seeds were empty, and floatation in water was used to separate them from plump seeds (i.e. filled with endosperm). The plump seeds were used in further germination trials. Unless otherwise indicated the seed was 3 to 6 months old at the start of the trials. Various treatments were applied to the seeds before sowing 25 seeds in each of four 9 cm diameter petri dishes for each treatment, unless otherwise indicated. Petri dishes contained 3 layers of S&S 90 mm filter paper saturated with a 0.75 $g.l^{-1}$ antifungal benlate solution (Benomyl fungicide, Du Pont). Elaiosomes were removed from *Phylica* seeds to reduce fungal growth. Petri dishes were placed in plastic bags and incubated under controlled environmental conditions with a light/dark cycle at $20^{o}/10^{o}C$ for 14/10 hours, unless otherwise indicated. The above protocol was found to be suitable by Pierce (1990).

Germination experiments were monitored at weekly intervals, and germination was defined as emergence and elongation of the radicle. Total germination percentages after 90 days were recorded. The germination percentages of seeds of receiving various treatments were compared to that in untreated controls in which seeds were 3 months old. Where treatment differences were not obviously highly significant, t-tests on arc-transformed data were used for comparison (see also Keeley 1987a and Pons 1989a). The following treatments were performed.

i) Acid and mechanical scarification

Acid scarification was used in an attempt to break possible coat imposed dormancy (Bewley and Black 1985) in the hard coated seeds, thus allowing their viability to be assessed. Pre-treatments of soaking seeds in concentrated sulphuric acid for 5, 15 and 30 minutes were applied, followed by washing with distilled water. Mechanical scarification was also attempted. *Phylica* seeds were individually manipulated with tweezers, and the distal end drawn rapidly across P400 sand paper while applying light pressure (as in Auld 1986c). *Passerina* seeds were rubbed in a group between two pieces of P400 sand paper for two minutes.

ii) Heat and charate treatments

To investigate the role of fire in breaking dormancy in *Passerina* and *Phylica*, a number of pre-treatments were applied to simulate field effects associated with fire. Firstly, dry heat treatments of 70°C for 1 hour, 100°C for 5 minutes and 125°C for 5 minutes (after Keeley 1987a) were applied to seeds prior to sowing. Seeds were also treated with charred wood (charate). It has been shown that the type of wood used in such studies is not important (Keeley and

Pizzorno 1986) and thus commercially available doweling was used. This was charred (but not ashed) with a propane torch and ground into small pieces which were passed through a 1 mm screen. 0.2 g of this powder was added to petri dishes along with the seeds during incubation (after Keeley 1987a). Seed used in the charate treatment was 10 months old.

iii) Alternating temperatures

It has been hypothesised that wider diurnal fluctuations in temperature in bare soil in burnt areas, when compared to soil covered by vegetation, may be an indirect fire-related germination cue (Brits 1986a, 1987, Murdoch *et al* 1989, Pierce 1990). The $10^{o}C/20^{o}C$ temperature fluctuation used approximates that measured in the upper 1 cm of soil under the canopy in early winter (Appendix A). For comparison, a treatment was applied in which seeds were incubated at $5^{o}C/25^{o}C$. This resembles temperatures measured in the upper 1 cm of bare soil on clear days in early winter (Appendix A). A further temperature fluctuation of $15^{o}C/30^{o}C$ was also used to test the germination response to a high temperature regime.

iv) Effects of seed ageing and burial

To assess possible effects of ageing of seeds over the period during which experiments were carried out, 10 month-old untreated seeds were incubated under the control conditions. Furthermore, burial effects on seed germination were studied by excavating and incubating seeds which had been buried for 8 months in mesh bags at the study site. Only four replicates of ten seeds were used for *Passerina* and four replicates of six seeds for *Phylica*, due to lack of seeds at the time of burial. As a control for this experiment, seeds stored in the laboratory for 8 months were also incubated with the same replication.

v) Germination of __Phylica__ seeds from soil seed banks

Further experiments used seeds of *Phylica* which had been recovered from the soil seed bank under mature fynbos. Untreated, they were incubated for 90 days before remaining ungerminated seeds received a heat treatment of 70°C for 1 hour and were incubated for a further 60 days. Seeds which still remained ungerminated were acid scarified for 15 minutes and incubated for a further 60 days. In another experiment *Phylica* seeds were recovered from the soil seed bank shortly before and again shortly after fire. These seeds were incubated with a replication of 5X5 seeds, and germination was compared between the two sampling times.

RESULTS

Germination in burnt and unburnt areas

For both *Phylica* and *Passerina*, field observations showed many more seedlings in burnt areas than under unburnt vegetation (Table 1). A few *Phylica* seedlings were found under mature fynbos, but no *Passerina* seedlings were observed. However, in the burnt areas *Passerina* seedlings were on average five times more numerous than *Phylica* seedlings.

Germination of seeds from soil cores

A log-linear model fitted to seedling numbers counted in soil samples (Table 2) included species and fire effects, and a species-time interaction. All possible effects had to be included in the model, because if even the least significant factor (i.e. the species-fire interaction) was excluded, the resulting model would be rejected ($X^2=6.267$; df=1; $p<0.05$). This meant that significantly more *Passerina* seedlings were counted in trays than *Phylica* seedlings. Overall counts were also significantly greater after fire, but not equally so for both species. Examination of actual counts indicated that the fire effect in the model was due to a significant increase for *Phylica* from before to after fire, while the smaller increase for *Passerina* was possibly due to chance. *Phylica* germination thus appeared to be stimulated directly by the fire, while that of *Passerina* was not. Thus, although no *Passerina* seedlings were observed under mature fynbos (Table 1), many seeds germinated when removed in soil samples from below unburnt fynbos to a nursery (Table 2).

Laboratory germination experiments

i) Dormancy and viability

In laboratory germination experiments, untreated *Passerina* seeds failed completely to germinate, and germination of *Phylica* seeds was low (Table 3). Acid scarification was successful in breaking dormancy in both species, with highest germination recorded for a 15 minute treatment when compared to 5 and 30 minutes. Under this treatment the 95 % germination of *Phylica* seeds was significantly higher than the 73 % germination of *Passerina* seeds. If these figures are used as a measure of seed viability, then *Phylica* seeds are significantly more viable than those of *Passerina*. Mechanical scarification was also highly successful in breaking dormancy in *Phylica*, but in *Passerina* the treatment used was less successful.

ii) Heat treatments

Heat treatments on seeds produced highly significant increases in the germination of *Phylica*, but not of *Passerina* (Table 3). A heat treatment of 70°C for 1 hour produced a germination level for *Phylica* comparable to acid scarification. A treatment of 100°C for 5 minutes also increased germination significantly, but less than in the 70°C treatment. Most ungerminated seeds under the 100°C treatment appeared to have overcome a dormancy mechanism involving the prevention of water uptake, but were killed by the heat treatment. This was indicated by the swelling of these seeds from water uptake, although they failed to germinate. In untreated seeds, swelling always preceded germination, while ungerminated seeds almost never became swollen. A treatment of 125°C for 5 minutes gave significantly lower germination than in untreated seeds of *Phylica*. It apparently broke a mechanism inhibiting water uptake, but killed the seeds, once again as indicated by the swelling of most ungerminated seeds.

iii) Charate treatment

Charate treatments failed to break dormancy in *Passerina* and *Phylica* (Table 3). A slight inhibition of *Phylica* germination was observed.

iv) Alternating temperatures

Alternative incubation temperature regimes of 5°C/25°C and 15°C/30°C failed to produce any germination of *Passerina* seeds (Table 3). *Phylica* seeds gave significantly lower germination at 15°C/30°C and significantly higher germination at 5°C/25°C (Table 3), when compared to the 10°C/20°C temperature cycle. *Phylica* germination at 5°C/25°C was almost three times lower than for optimal heat and acid scarification treatments, however.

v) Effects of ageing and burial of seeds

Ten month-old untreated seeds of both species did not have significantly different germination responses to the untreated 3 month-old controls (Table 3). It would thus appear that seed aging effects are insignificant over the period in which these studies occurred. Burial of seeds for 8 months did not affect the strong dormancy in *Passerina*, but did produce enhanced germination of *Phylica* when compared to 8 month-old laboratory-stored seeds (Table 3).

vi) Germination of Phylica seeds from the soil seed bank

Phylica seeds removed from the soil seed bank under mature vegetation germinated untreated at 4±2 % ($\bar{x}$±SE; *n*=4X25 seeds). This is significantly lower than that of untreated seeds collected from plants (Table 3) (t=2.70; p=0.036). This finding is inconsistent with that in the burial experiment of *Phylica* above, in which enhanced germination appeared to result from burial. Further heat treatment at 70°C for 1 hour of remaining ungerminated seeds boosted total germination to 40±6 %. Acid scarification of remaining ungerminated seeds further raised the total germination to 68±3 %. This is a measure of the minimum viability of *Phylica* seeds in the soil seed bank. In further studies 10±5 % ($\bar{x}$±SE; n=5X5 seeds) of *Phylica* seeds which had been removed from the soil seed bank shortly before fire germinated, while 76±8 % of seeds removed from the seed bank soon after fire germinated. This was further evidence of the stimulation of *Phylica* germination by fire.

vii) Germination rates

The rate of germination of acid scarified seeds of *Phylica* and *Passerina* did not differ markedly (Fig 1). *Passerina* seeds needed approximately a week longer than *Phylica* seeds to germinate. This was the only treatment in which most seeds of both species germinated. Germination of *Phylica* under the 70°C heat treatment was slower than its germination under the acid treatment.

Table 1: Seedling numbers per m^2 ($\bar{x}$ ± SE) of *Passerina paleacea* and *Phylica ericoides* in burnt and adjacent unburnt fynbos following a fire in May 1990. Seedlings were counted in August 1990 in 5 matched pairs of 1 m^2 plots. Significant differences are from t-tests; $*=p \leq 0.05$; $***=p \leq 0.001$.

	Unburnt	Burnt	
Phylica ericoides	4 ± 1	16 ± 3	*
Passerina paleacea	0 ± 0	.85 ± 13	***

Table 2: Total numbers of seedling of *Passerina paleacea* and *Phylica ericoides* germinating in 30 trays containing soil samples collected before and after fire. See also Table 3 (Chapter 3).

	Pre-fire	Post-fire
Phylica ericoides	6	23
Passerina paleacea	44	50

Table 3: Percentage germination ($\bar{x}$±SE) of seeds of *Phylica ericoides* and *Passerina paleacea* in response to various treatments. Seeds were incubated at 14h/10h, 20°C/10°C in light/dark and *n*=4X25 seeds, unless otherwise indicated. Significance levels are those from t-tests on arc-transformed data. Each treatment is compared with the untreated control in which seeds were 3 months old ([b] is an exception). *=$p \leq 0.05$; **=$p \leq 0.01$; ***=$p \leq 0.001$; NS=not significant.

Treatment	*P. ericoides*		*P. paleacea*	
Untreated (3 month-old)	14 ± 2		0 ± 0	
Untreated (10 month-old)	9 ± 2	NS	0 ± 0	NS
Mechanical scarification	91 ± 2	***	5 ± 2	*
Acid 15min	95 ± 2	***	73 ± 3	***
Heat 70°C/1h	94 ± 4	***	0 ± 0	NS
Heat 100°C/5min	71 ± 3	***	0 ± 0	NS
Heat 125°C/5min	4 ± 2	*	0 ± 0	NS
Charate	4 ± 1	*	0 ± 0	NS
Incubation at: 5°C/25°C	35 ± 5	**	1 ± 1	NS
15°C/30°C	0 ± 0	***	0 ± 0	NS
Stored 8 months[a]	4 ± 3		0 ± 0	
Buried 8 months[a]	38 ± 8	***[b]	0 ± 0	NS[b]

[a] Replication was n=4X10 seeds for *Passerina* and 4X6 seeds for *Phylica*.

[b] Germination of seeds buried for 8 months is compared with that of seeds stored in the laboratory for 8 months.

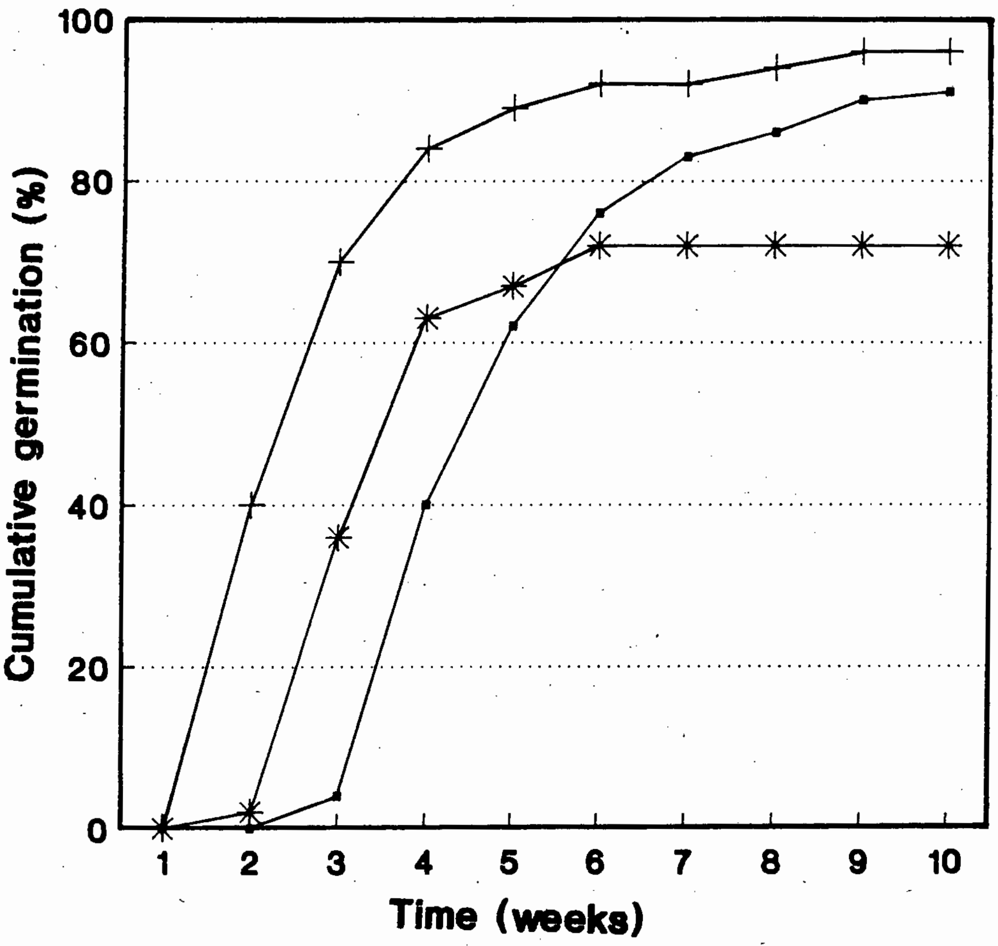

Fig. 1. Cumulative percentage germination of *Phylica ericoides* with pre-treatments of acid scarification for 15 min (—+—) and heat at 70°C for 1 h (—■—), and of *Passerina paleacea* with acid scarification for 15 min (—✳—).

DISCUSSION

The germination of both *Phylica ericoides* and *Passerina paleacea* appeared to be linked to fire. In *Phylica* heat from fire was the specific germination cue. In *Passerina* the exact nature of the germination cue could not be determined, but evidence pointed to a role of indirect fire effects associated with the removal of vegetation cover.

Germination in mature and burnt fynbos

Seeds of both species have a high degree of dormancy, as evidenced by low germination when untreated in laboratory experiments, and the observation of low numbers of seedlings in mature bush. *Passerina* had especially strong dormancy, as no seeds germinated untreated in the laboratory, and no seedlings were observed in unburnt, mature vegetation. The possibility that many seeds germinated in mature fynbos, but seedlings died before monitoring, appeared unlikely as casual observations over two years never detected *Passerina* seedlings in unburnt areas. A few seedlings of other species were always observed. Furthermore, on the boundary between burnt and unburnt vegetation, over a range of a few centimeters, numbers of *Passerina* seedlings varied from about 100 per m^2 in the burnt area, to zero in the unburnt area.

Approximately 10 % of untreated *Phylica* seeds germinated, and low numbers of seedlings were always observed in mature fynbos. Similarly, most fire-cued species in chaparral have some potential for germination between fires (Parker and Kelly 1989). In burnt areas *Phylica* seedling numbers were higher. Seed removed from the soil seed bank after fire also had higher germination than that removed before fire.

Effects of heat on *Phylica* germination

The breaking of dormancy in *Phylica* was due to the effect of heat, mainly from fire, but possibly helped by increased soil temperatures due to the removal of insulating vegetation. Heat has been implicated in the breaking of dormancy in many species in fire-prone environments (e.g. Keeley 1987a; Keeley and Keeley 1987; Parker 1987). Notably, obligate seeding species of the chaparral genus *Ceanothus*, whose seeds and adult plants physically resemble *Phylica* (and which are also in the Rhamnaceae), also have dormancy broken by heat (Keeley 1987a). They have long-lived seeds and recruitment is confined to the immediate post-fire conditions (Keeley 1987a). Heat also stimulated germination in the fynbos species *Erica hebecalyx* (Van de Venter and Esterhuizen 1988), and in two *Agathosma* species (Blommaert 1972). However, in six eastern Cape dune fynbos species, heat treatments of 80°C for 5 minutes and 100°C for 20 minutes did not stimulate germination, which was generally high in untreated seeds (Pierce 1990).

Phylica seeds appear to have physical dormancy (*sensu* Baskin and Baskin 1989), which results from the hard coats of seeds preventing imbibition of water. Evidence for this is that seeds swell before they germinate, but no swelling occurs in seeds that remain dormant. Also, dormancy is broken by acid and mechanical scarification which affect the integrity of the seed coat. In such seeds a pallisade layer of cells impregnated with water repelling substances is responsible for water impermeability (Baskin and Baskin 1989). It is thought that this type of seed remains impermeable until a special anatomical region of the seed coat is affected by a specific process, rather than by general mechanical breakdown in the soil (Baskin and Baskin 1989). Temperature is probably the most important environmental factor regulating this process (Baskin and Baskin 1989), an example of which is the disruption of the strophiolar plug by high temperature in *Acacia kempeana* (Hanna 1984). After the seed coat becomes permeable, such hard coated seeds imbibe water and are capable of germinating over a wide range of temperatures in light and darkness (Baskin and Baskin 1984). However, some seeds have a low temperature stratification requirement (Keeley 1990). Thus the seeds do not have to be at the soil surface to germinate, but only close enough for environmental conditions such as fire to render them permeable. More detailed studies are needed to confirm these characteristics in *Phylica*.

The optimum temperature treatment of 70°C for one hour for *Phylica* was within the range of 60°C-80°C which proved most successful for stimulation of germination in *Acacia suaveolens* (Auld 1986b). Below this temperature range the *Acacia* seeds remained impermeable, and above it seed death was likely. Seed death with treatments of over 120°C for a few minutes have also been reported for heat stimulated chaparral species (Keeley *et al* 1985; Keeley 1987a; Parker 1987).

Possible germination cues for *Passerina*

i) Indirect fire-effects

In *Passerina* no specific treatment such as heat or charate was found to break dormancy. However, circumstantial evidence pointed to germination being cued to some factor associated with the removal of vegetation cover by fire. This was indicated by the ready germination of seeds from soil samples collected from the study site before fire (Table 2). These samples were layered in trays and placed in the open, thus simulating bare soil.

The exact nature of such an indirect fire effect is uncertain. Commonly proposed mechanisms associated with vegetation removal include allelopathy, i.e. the inhibition of germination by compounds leached from adult plants or microbial toxins in the litter (McPherson and Muller 1969).

This is inhibition is released when the plants are destroyed by fire. The importance of this mechanism has been questioned, however (e.g. Hobbs 1984; Keeley 1984; Keeley *et al* 1985; Keeley and Keeley 1989). It further seems unlikely to be the germination cue in *Passerina* as seeds collected from plants were dormant, although they had never been exposed to plant leachates in the soil.

Increased light reaching the soil due to vegetation removal has also been proposed as a dormancy breaking mechanism (Christensen and Muller 1975; Keeley 1987a; Keeley and Keeley 1987). It has, however, generally been applied to species which exploit smaller gaps in the vegetation, rather than those whose germination is specifically cued to fire (Keeley 1987a, 1990). Also, seeds of *Passerina* were still dormant when incubated in the light, and so this mechanism does not appear to function in this species.

Removal of vegetation also increases the diurnal temperature fluctuations in soil, which may be a cue for germination (Thompson *et al* 1977; Vazquez-Yanes and Orozco Sergovia 1982). This mechanism was proposed for six eastern Cape dune fynbos shrubs (Pierce 1990) and for some fynbos Proteaceae (Brits 1986a, 1987). These studies compared germination at constant temperatures to germination at fluctuating temperatures. However, even under the canopy, soil temperatures fluctuate. Thus a fluctuating temperature cycle similar to that under vegetation needs to be compared to a second cycle, similar to that in bare soil. In the laboratory a 5°C-25°C temperature cycle, simulating that in bare soil in early winter (Appendix A, Brits 1987), failed to break dormancy in *Passerina*. It is possible that this test did not mirror environmental conditions closely enough. More likely, however, is that increased fluctuating temperature is not the major fire-related germination cue for *Passerina*. The increase in temperature from canopy covered soil to bare soil is not very great and temperatures in gaps in the canopy resemble those in burnt areas (Appendix A). Thus, it seems unlikely that species whose germination is strongly cued to fire will have their dormancy broken by increased alternating soil temperatures alone. In summer, temperature differences between burnt and unburnt areas may be greater than in early winter when measurements were made, but recruitment of *Passerina* was high following fire in May. Thus the effect of summer temperatures were excluded.

ii) Direct effects of fire

It is possible that germination of *Passerina* seeds in the soil samples collected before fire (Table 2) was not due to indirect fire effects associated with vegetation cover, but to a substance in the potting soil on which samples were layered. The most likely substance is charred or decomposed wood. Negative results in charate tests argue against this, however. Charate also did not stimulate germination in *Phylica* and in six eastern Cape dune fynbos species (Pierce 1990), but is widely reported in chaparral species (e.g. Keeley *et al* 1985; Keeley 1987a; Keeley and Keeley 1987). It is also possible that some inorganic substance such as nitrate (Bewley and Black 1985; Pons 1989b) could break dormancy by being present in higher concentration after fire (Pons 1989b). Such a substance could have been sufficiently concentrated in the potting soil used.

The inability to break the dormancy of *Passerina* seeds in the laboratory, except by highly artificial acid scarification, may mean that this species has complex natural germination requirements. Possibly a number of requirements must be met (Bewley and Black 1985). Changes due to seed aging may be important (Parker and Kelly 1989) and it may be that specific fire cues only break dormancy if seeds have aged sufficiently. For example, *Arctostaphylos canescens* seeds removed from the soil germinated readily on addition of charate, but freshly collected seeds less than one year old required addition of gibberellic acid to the charate to stimulate germination (Parker 1987). Another *Passerina* species, *Passerina vulgaris* showed no response to charate in two year old seeds (Pierce 1990). This species also had very strong dormancy, which was not broken by any of the treatments used (Pierce 1990).

Implications for coexistence

The existence of differing fire-related germination characteristics between *Passerina* and *Phylica* may help to explain their coexistence (as predicted by Grubb 1977; Schat 1983). Differing germination responses by each species to different fires could mean regeneration of different species is favoured in different fires (Keeley 1987a), leading to coexistence in the long term (Cowling 1987). For example, relatively cool burns, usually occurring in winter and early spring or in young vegetation (Van Wilgen 1987), may lead to much reduced germination of heat stimulated *Phylica* seeds. *Passerina* seeds apparently do not depend on the heat effect of fire, and thus would germinate in their usual numbers, giving this species the advantage. Reduced germination of seeds with lower fire temperature has been documented in the field for myrmecochorous fynbos Proteaceae (Bond *et al* 1990), in hard seeded species of the chaparral genus *Ceanothus* (Morgan and Neuenschwander 1987; Parker and Kelly 1989) and in the Australian *Acacia suaveolens* (Auld 1986b). However, reduced germination after wet season burns has also been explained for some species by the increased lethal sensitivity of seeds to heat under moist conditions (Parker 1987). Another possible scenario is one in which fynbos is unburnt for very long periods. Widespread senescence may occur (Kruger and Bigalke 1984), in which event *Phylica* may be more successful than *Passerina* in colonising gaps, as its germination appeared less strictly linked to fire. It may be, however that germination is never limiting on population replacement following fire and that coexistence is maintained predominantly at other levels such as the variation in seedling mortality patterns with different fires (further discussed in Chapter 4). Such fire-controlled mechanisms of coexistence argue against the use of uniform prescribed burns commonly practiced in fynbos management (Van Wilgen and Richardson 1985), a view that has recently been widely supported in fynbos (Pierce 1990), chaparral (Parker 1987; Parker and Kelly 1989; Keeley 1990) and Australian heath (Bell *et al* 1987).

Limitations and suggestions

In this study, the seed used in germination experiments was collected from a single year's seed crop and was under one year old. Pierce (1990) found, however, that the germinability of untreated seed varied by up to 50% from one year to the, next and from seed one year old to two years old. Thus ideally such studies should be done on a number of years seed crops and on seed up to several years in age. It is also recommended that germination studies include seeds removed from the soil seed bank. In these seeds the effects of ageing and burial are integrated as they would be in the field, and results will reflect more closely germination responses in nature. If *Passerina* seeds had been removed from the soil and used in this study, more insight may have been gained into the germination cue of this species.

Furthermore, the study of germination cues would benefit from field experiments, for example applying treatments such as shadecloth and charate to cleared plots in the field. It is possible that some level of germination of *Passerina* may occur in mature vegetation, but that seedlings rapidly die before being monitored. This may also be more closely studied.

CHAPTER 3: SOIL SEED BANKS IN TWO NON-SPROUTING FYNBOS SHRUB SPECIES: PERSISTENCE AND DYNAMICS IN RESPONSE TO FIRE

ABSTRACT

The soil seed banks of two non-sprouting fynbos species, *Passerina paleacea* Wikstrom and *Phylica ericoides* L., were studied using a number of methods. These included direct seed counts and germination of seed from soil samples collected before and after seed dispersal, and before and after fire. Seed burial experiments and a harvesting experiment in the field were also carried out. Using direct seed counts, *P. ericoides* was found to have a seasonally constant seed bank estimated at 278±450 seeds per m^2 ($\bar{x}$±sd), while seed bank estimates for *P. paleacea* varied between 441±620 seeds per m^2 before seed dispersal, and 737±919 seeds per m^2 afterwards. The larger size of the seed bank of *P. paleacea* was attributed to greater seed production compared to *P. ericoides*, rather than to longer survival of seed in the soil. Seed bank estimates from germination were lower than those from direct seed counts. Both species had seasonally persistent seed banks as they were not depleted over the year following seed input. Fire appeared not to kill significant numbers of seeds, and seed banks were mostly, but not completely, depleted during the winter following fire. Fire directly stimulated germination of *P. ericoides* seeds in the soil, although it appeared that the dormancy of many seeds was not broken. Results are discussed in relation to the adaptions of seeds to survive fire risks. Implications of results for burning of fynbos and commercial harvesting of *P. ericoides* are also discussed.

Key words: Direct seed count, dispersal, fire, germination, harvest, seasonal persistence, seed bank.

INTRODUCTION

For non-sprouting shrubs in fire-prone environments the replacement of populations after fire is determined primarily by the availability of either soil-stored or canopy-stored (serotiny) seed. In the fire-prone fynbos shrublands of South Africa, serotiny in the Proteaceae has been relatively well studied (e.g. Bond 1984; 1985; Bond *et al* 1984; Le Maitre 1987b), while soil seed banks have received little attention (Pierce 1990). The only investigations which have attempted to quantify soil seed banks have been on six eastern Cape dune fynbos species (Pierce 1990) and on seed banks across a forest-fynbos boundary (Manders 1990). Soil seed banks have been better studied in other fire-prone shrublands, including Californian chaparral (e.g. Keeley 1977; 1987b; Kelly 1986;

Zammit and Zedler 1988), Australian shrublands (e.g. Auld 1986a) and European *Calluna* heath (e.g. Mallik *et al* 1984; Willems 1988).

The sizes of soil seed banks vary enormously for different species at different sites (Leck *et al* 1989). In fynbos figures of between 5 seeds per m^2 for *Agathosma stenopetala* and 825 seeds per m^2 for *Passerina vulgaris* have been recorded (Pierce 1990). In chaparral reported sizes vary from 87 seeds per m^2 for *Ceanothus lecodermis* (Keeley 1977) to 28177 seeds per m^2 for *Arctostaphylos viscida* (Kelly 1986), while sizes of between 12.4 seeds per m^2 for *Acacia suaveolens* (Auld 1986a) and 3200 for *Eucalyptus populnea* (Hodgkinson *et al* 1980) have been recorded in Australia. In British *Calluna* heath 2000 to 9000 seeds per m^2 were reported for the dominants *Calluna vulgaris* and *Erica cinerea*, and between 0 and 700 seeds per m^2 for other species (Mallik *et al* 1984). Generally, bigger seed banks have been found for smaller seeds, and smaller seed banks for larger seeds (Parker and Kelly 1989).

Seed bank sizes and dynamics are affected by rates of input by parent plants and losses due to decay, predation, death, deep burial and germination (Simpson *et al* 1989). Also affecting seed bank sizes are the site of sample collection and differences in sampling techniques (Parker and Kelly 1989).

A knowledge of the dynamics of seed banks of component species is important for predicting their persistence in a community (Parker *et al* 1989). The longevity of seeds in the soil is the most important dynamic characteristic of seed banks. Differences in the longevity of seeds are related to different environmental selection pressures, with persistence being selected where species depend on seeds to maintain the population through a period of risk (Parker *et al* 1989).

A major risk faced by non-sprouters in fire-prone shrublands is the possibly of parent plant death before or at the time of fire, with future survival depending on seed banks (Keeley 1990). In such environments persistence may be examined on two levels. Firstly, when recruitment is limited to the post-fire period, long-term persistence of seeds may ensure survival of the seeds from the death of the parent until the next fire. This has been observed in chaparral for herbaceous species, whose seed must often survive the full fire cycle of 50-100 years, and in perennials that are short-lived in comparison to the average fire cycle (Keeley and Zedler 1978; Keeley and Keeley 1989; Parker and Kelly 1989). Secondly, seasonal persistence of seeds for at least one year after dispersal, will ensure that sufficient seeds remain for population replacement if a fire occurs in any season. Thus, even for species in which adult plants survive the full fire cycle, seasonal persistence may be expected. Persistence of seed can also act as a buffer in years of low seed production, and can allow seed banks to build up to higher levels than is possible in a single year (Cavers 1983).

Not all species in fire-prone shrublands have persistent seed banks. In chaparral many species have transient seed banks which germinate shortly after dispersal (Keeley 1990). However, these may largely be limited to species capable of surviving fire by resprouting, with new individuals being recruited in the interfire period (Keeley 1990; Parker and Kelly 1989).

Knowledge of seed bank dynamics has implications for fynbos management. Firstly, the use of controlled fires is widespread and the season and frequency of these fires can be largely controlled (Van Wilgen and Richardson 1985). If seed banks of non-sprouters are transient, then the season of fire relative to seed release is important (Le Maitre 1987a; 1988). Fires in different seasons may favour different species, possibly promoting coexistence (Cowling 1987; Pierce 1990), but the most common natural fire season, i.e. summer and autumn (Van Wilgen 1984), would probably result in the best recruitment of most species. This has been shown for Cape Proteaceae with canopy-stored seed (Bond 1984; Bond *et al* 1984; Van Wilgen and Viviers 1985) and soil-stored seed (Le Maitre 1987a; 1988). Also, very long fire intervals may exceed the life-spans of plants, which would then depend on long-lived seed banks for survival until the next fire (Parker and Kelly 1989; Zedler and Zammit 1989). Shorter fire intervals may mean that seed banks do not build up sufficiently for population replacement (Pierce 1987).

A further implication of persistence in seed banks in fynbos is for commercial harvesting of flowers. This is a growing industry and is concentrated in areas of high species endemism and poor conservation status, thus threatening many species (Greyling and Davis 1989). One effect of flower harvesting is to remove seed before it is added to the seed bank. If seed banks of harvested species are not seasonally persistent, then heavy harvesting in one year would deplete the seed banks. This could result in poor recruitment of seedlings if fire occurs during the following year (or in subsequent years if plants do not rapidly recover).

In fynbos, seeds must not only be present in the seed bank at the time of fire, but must survive the fire. In addition, the effects of fire may directly or indirectly stimulate germination (Chapter 2). Subsequent to the fire, seed banks are expected to be depleted to various extents by mass germination of seeds (Pierce 1990). Such effects of fire on seed banks have been poorly studied in soil-stored seeds (except for the stimulation of germination by fire - see Chapter 2). Pierce (1990) found marked reduction, but not complete depletion of seed banks of six fynbos species in 18 month-old vegetation when compared to mature vegetation. Extensive depletion would leave few seeds from which recruitment might occur if a second fire occurred before plants reached reproductive maturity (Zedler *et al* 1983; Fox and Fox 1986; Parker and Kelly 1989).

This study aimed to determine the sizes of soil seed banks of two ericoid (i.e. small leaved) fynbos shrub species. The dynamics of their seed banks over one year were investigated, with an emphasis on determining whether seed banks were seasonally persistent. A number of approaches were used, including direct counts of seeds in soil samples, germination of seeds from soil samples, and seed burial in mesh bags. A field experiment was also carried out. The current years seed crop was removed before fire by harvesting, and the effect of this treatment on seedling recruitment after fire was examined. This is one of very few experimental field studies on seed bank dynamics (Leck *et al* 1989). The effects of fire on seed banks were also studied by counts and germination of seeds in soil samples collected before and after fire. Results are discussed with reference to these species adaptions to face the risks of fire. Implications for flower harvesting and burning of fynbos are also discussed.

MATERIALS AND METHODS

Study species and study site

The ericoid shrubs *Phylica ericoides* and *Passerina paleacea* were selected for study. Nomenclature is according to Bond and Goldblatt (1984), and the species will hereafter be referred to by their generic names. They co-occur in vegetated coastal dunes at the study site on the farm Groot Hagelkraal (34°40'S, 19°30'E), 45 km west of Cape Agulhas. Soils are relatively shallow (0.25 m - 0.5 m), well drained, calcareous dune sands overlying Pleistocene calcrete (Die Dam land system) (Thwaites and Cowling 1988). The vegetation is Dune Asteraceous Fynbos (Cowling *et al* 1988), and comprises a fine leaved shrubland with a field layer of evergreen hemicryptophytes. The study species are equal co-dominant shrubs at the site. *Passerina* cover is approximately 20 % and *Phylica* cover 15 % (Chapter 4). Their distribution is also remarkably uniform across the local landscape (Chapter 4)), as is the vegetation height (50-70 cm). The climate is mediterranean, with 65% of approximately 450 mm of annual rainfall occurring in the winter months from May to October. As is typical of mediterranean shrublands, the site is subject to recurrent fires (Kruger 1984; Keeley 1986), usually in the dry summer and autumn months (Van Wilgen 1984). It was last burnt 25 to 30 years previously. Both species disperse their seeds in November and early December, when moisture levels are low, contributing to a soil seed bank. They are obligate seeders, depending on these soil-stored reserves for population replacement following fire. Seedling recruitment between fires is low (Chapter 2, Chapter 4). Seed dispersal by *Passerina* is passive, while *Phylica* seeds are dispersed ballistically and have elaiosomes for possible ant dispersal. *Phylica* is commercially harvested for the wildflower industry.

Counting seeds in soil samples

The dynamics of the soil seed banks of *Phylica* and *Passerina* were studied by sorting and counting seeds from soil samples collected before and after seed dispersal, and before and after fire. Samples were collected in late September 1989, shortly before seed dispersal by both species, and in mid-December 1989, shortly afterwards. Further samples were collected in mid-April 1990, three weeks before the study site was burnt in a controlled fire, and again 5 days after the fire in mid-May. Sampling was repeated in October 1990 to assess the depletion of the seed bank following the winter after fire. Both in September and December 1989, 50 samples were taken at each of three sites. These sites were 30 m X 30 m blocks, somewhat haphazardously selected in apparently homogeneous vegetation within the 2 ha general study area. The study was divided in this way to assess the site-to-site local variability in seed bank sizes and avoid results reflecting possible localized effects only. In April, May and October 1990, 100 cores were taken in a single 50 m X 50 m area overlapping the original three sites. Soil cores were collected at intervals on transects traversing the sampling areas. All soil cores were 5 cm in diameter and 5 cm deep and included the litter layer. The approach of collecting more smaller samples rather than fewer larger samples was used (Roberts 1981; Thompson 1986; Bigwood and Inouye 1988). The total areas sampled were 3 X 981 cm^2 on the first two occasions and 1 X 1963 cm^2 on the last three occasions. This is within the range commonly used in seed bank studies (Leck *et al* 1989), but is still not sufficient for very accurate determination of seed bank sizes. This is a common problem with seed bank studies as methods used are very time consuming (Bigwood and Inouye 1988). The 5 cm sampling depth was thought adequate as a pilot study showed most *Passerina* seeds to be within this range. It has also been widely observed that seed density declines markedly below this depth, and this is the most commonly used sampling depth in seed bank studies (Roberts 1981, Leck *et al* 1989). Furthermore, seedlings of six eastern Cape dune fynbos species did not emerge from seeds planted below a depth of 5 cm (Pierce 1990). Thus seeds below this depth may not reflect potential recruitment.

Soil cores were dried for two to four weeks at room temperature and seeds were sorted by sieving and scanning under a stereomicroscope. Most *Passerina* seeds were empty (i.e. lacked endosperm) and the most efficient method of distinguishing them from plump seeds (filled with endosperm), was to crush the seeds. Almost all *Phylica* seeds were plump. As they were less numerous, it was feasible to distinguish plump seeds from the few empty ones by sinking them in water, thus retaining the seeds for germination experiments (see Chapter 2). The numbers of plump seeds per sample were recorded and were converted to estimate the number of seeds per m^2 in the seed bank (given that 509.3 samples represent 1 m^2 of surface area at the study site).

Germination of seeds in soil samples

The seed bank dynamics of *Phylica* and *Passerina* were also studied by the germination of seeds in soil samples. As before, samples were collected in September and December 1989, before and after seed dispersal. Further sampling was done in April 1990, 3 weeks before a fire, and in May 1990, 5 days after the fire. Soil cores were collected as before, except that 120 cores were collected at each sample time in an area 50 m X 50 m. This gave a total sampling area of 2356 cm^2. Samples were stored in a dry, cool place until they were set up for germination. Samples were combined in groups of four, and each of the 30 groups were spread to a depth of 1 cm on the surface of a tray containing potting soil. The trays were placed in an open nursery at Kirstenbosch Botanical Gardens (130 km west of the study site). They were exposed to sun and rain from May to October 1990, and kept moist during dry periods. Emerging *Phylica* and *Passerina* seedlings were counted monthly and seedlings were removed once counted. The numbers of emerging seedlings in each sample were converted to an estimate of germinable seeds per m^2 in the seed bank (given that 127.4 samples represented 1 m^2 of surface area at the study site).

Harvesting experiment

The seasonal persistence of the seed banks of *Phylica* and *Passerina* was also studied in an experiment which compared numbers of seedlings emerging after fire in harvested and non-harvested plots. Three sites, each 30 m X 30 m, were chosen in apparently homogeneous vegetation at the study site. These corresponded to the sites in the seed counting study. Replication was to avoid results reflecting a localized effect. Within each site, 1 m^2 plots were permanently marked in a block design and various treatments were randomly applied to them. In each site, 7 plots were left as controls, 7 were harvested for *Passerina*, and 7 were harvested for *Phylica*. Harvested plots had all flowers of the respective species removed in the plot, and for approximately 1.5 m around it. This occurred prior to seed development in 1989, and harvesting was done in such a way as to minimize the loss of biomass. The study site was burnt in May 1990. *Phylica* and *Passerina* seedlings were counted in the 1 m^2 plots in October 1990, following winter and spring recruitment after the fire. If significant numbers of seeds did not disperse into the 1 m^2 plots from beyond the harvesting boundaries, then the 1989 seed crop of the harvested species was effectively removed from the soil seed bank of the plot. Recruitment of the harvested species in harvested plots would thus have to occur from seeds remaining in the seed bank from at least 1.5 years previously.

It is not expected that many seeds would have entered the harvested plots from beyond the harvested boundaries. *Passerina* is passively dispersed, and the ballistic dispersal of *Phylica* does not exceed the distance from plot to harvested boundary (personal observation). Ant dispersal of elaiosome-bearing *Phylica* seeds could in theory distribute seeds over greater distances, but these distances are generally limited (Culver and Beattie 1978; Berg 1981; Bond and Slingsby 1983; Auld 1986a). The efficiency of ant dispersal has also been questioned, especially for small seeds (Bond and Slingsby 1983; Auld 1986a; Pierce 1990), including for two other *Phylica* species (Musil and De Witt 1990). Also, seed dispersal in fynbos generally appears to be limited (Moll and Gubb 1981), and even species with specific dispersal mechanisms, most seed is still dispersed below the parent plant (Fenner 1985; Howe 1986).

Furthermore, seedling recruitment of *Phylica* and *Passerina* after fire were correlated to pre-fire cover in the same plots, with no additional variation explained by pre-fire cover in the areas immediately surrounding plots (Chapter 4).

Seed storage and burial

Seeds were freshly collected from *Passerina* and *Phylica* in November 1989. Plump seeds filled with endosperm were sorted from empty seeds by floatation. For each species, eight mesh bags containing plump seeds were buried 2 cm below the soil surface at the study site. Bags contained 15 *Phylica* seeds or 25 *Passerina* seeds each. Four bags for each species were excavated after four months, and the remaining bags after eight months. Plump seeds remaining in the excavated bags were counted and tested for viability by germination following a 15 minute treatment with concentrated sulphuric acid. This proved effective in breaking dormancy in both species (Chapter 2). The method of incubation was as in Chapter 2.

In addition to burial, seeds were also stored in a cool, dark place in the laboratory and the number of remaining plump and viable seeds similarly determined after four and eight months.

Statistical analyses

Log-linear models were fitted to explain differences in seed or seedling counts. These models are used to predict which factors are important in explaining observed variation in count data, while eliminating unimportant factors. The theory of generalised linear models (McCullagh and Nedler 1989) and the statistical package GLIM (Baker and Nedler 1978), were used to fit log-linear models to explain the variation in seed counts made in September and December 1989. The effects of species, time of sampling and site, as well as the interactions between these factors were noted. Total seed numbers counted in all 50 samples at each site at each time for each species were used as the variables. This made the patterns of variation easier to interpret. The model was fitted using an overdispersion parameter to allow for greater variation than in the Poisson distribution, thus accounting for factors such as clumping of seeds. This parameter was estimated by dividing the Pearson chi-square by its degrees of freedom after fitting an initial log-linear model, which included site by time and species by time interactions.

GLIM was also used to model the effects of harvesting and site on seedling numbers for each species in the harvesting experiment. Plot replication was taken into account by adding it as an extra factor level. An overdispersion parameter (or scale factor) was used to allow for extra variation in the data due to seedling clumping. This parameter was estimated by dividing the Pearson chi-square by its degrees of freedom after fitting an initial model which included only a replication effect.

Log-linear models were fitted to remaining seed bank data sets using the Statgraphics computer package (STSC, Inc.). This could not allow for overdispersion, but it was adequate for dealing with the simple two-way comparisons. In this way seed counts were compared between April and May 1990 and between April and October 1990. Seedlings numbers germinating from samples collected in September and December 1989 were similarly compared, as were those from samples collected in April and May 1990. Total seed or seedling counts in all samples for each species at each time were used as the variables.

One-way ANOVA on arc-transformed data was used to compare the germination of seeds in burial and laboratory storage experiments.

RESULTS

Seed bank dynamics: direct seed counts

In a pilot study, 32 *Passerina* seeds were counted in 36 soil samples, each 5 cm in diameter and 15 cm deep. 27 seeds

(84%) were at 0-5 cm (including the litter layer), 4 seeds (13%) were at 5-10 cm, and only 1 seed was at 10-15 cm in depth. All further samples were 5 cm in depth.

Only 6% of *Passerina* seeds were plump (i.e. contained endosperm) (*n*=3366), while *Phylica* seeds were 96% plump (*n*=288). Only plump seed numbers are further reported.

The seed bank of *Passerina* was larger than that of *Phylica* (Table 1). The average seed bank size in the combined three sites before dispersal (September 1989) was estimated to be 441 ± 620 seeds per m^2 ($\bar{x}$ ± sd; *n*=150) for *Passerina* and 278 ± 478 seeds per m^2 for *Phylica*. After dispersal (December 1989) the seed bank size averages were 737 ± 919 seeds per m^2 for *Passerina* and 279 ± 424 seeds per m^2 for *Phylica*. This indicated an average increase of 1.6 times for *Passerina* and no change for *Phylica*. A log-linear model attributed the variation in seed counts of *Passerina* and *Phylica*, at three sites, before and after dispersal, to the effects of species, time of sampling, and the interaction between species and time (Scaled deviance for model = 5.978; df=8; scale factor = 3.299). This meant that the difference in seed counts between the species was significant, as was the difference between the times. The inclusion of a species-time interaction in the model indicated that the two species reacted differently to time. This is consistent with the explanation that the seed bank of *Passerina* increased significantly from before to after dispersal, but that of *Phylica* remained constant. There was no site effect in the model, which indicated that differences between the sites were insignificant. Thus, samples on further occasions were collected from a single site only.

There was very little difference between the seed bank sizes estimated for both *Passerina* and *Phylica* shortly before fire (April) when compared to shortly after fire (May), but *Passerina* had approximately twice the seed bank size of *Phylica* (Table 2). A log-linear model fitted to total seed counts of each species on each of these occasions included species effects only (Pearson's chi-squared for model = 0.335; df=2; p=0.846). This indicated that the difference in seed counts between the two species was significant, and that the effects of fire on seed bank counts were not significant for both species.

Seed bank estimates after the first winter following fire (October) showed an approximately five-fold reduction for *Passerina*, and an approximately two-fold reduction for *Phylica*, when compared to pre-fire seed bank estimates (Table 2). A log-linear model fitted to seed counts in April and October included species and time effects, and a species-time interaction. The full model was needed as a model excluding the least important effect (i.e. the species -time interaction) was rejected (Pearson's chi-square for rejected model = 4.99; df=1; $p<0.05$). No meaningful statistics can be obtained from a full model fit itself. Thus the seed bank of *Passerina* was significantly larger than that of *Phylica*, and the seed banks of both species were significantly reduced by losses over the winter following fire. This reduction was different for the two species.

The variance to mean ratio of all seed counts (n=500) was 619 for *Phylica* and 331 for *Passerina*. As these values were very much greater than 1, this suggests clumping of seeds in the seed bank (Whittaker 1975).

Seed bank dynamics: Germination of seeds in soil samples

The seed bank sizes estimated from seedlings emerging in soil samples showed similar values before and after dispersal for both species (Table 3). A log-linear model fitted to seedling counts from soil samples collected before and after seed dispersal included a species effect only (Pearson's chi-squared for the model = 1.201; df=2; p=0.549). Thus counts of *Passerina* seedlings were significantly higher than for *Phylica*, but no significant differences were found between counts from soil samples collected before dispersal, when compared to those collected after dispersal.

Estimates of seed bank sizes by germination were higher in soil samples collected immediately after fire than in those collected before fire for both species, especially for *Phylica* (four-fold increase) (Table 3). A model fitted to seedling counts before and after fire, included species and fire effects, and a species-fire effect interaction. (The full model was accepted because a model excluding the interaction was rejected; Pearson's chi-square = 6.267; df=1; p<0.05). Thus, significantly more *Passerina* seedlings were counted than those of *Phylica*; overall counts were significantly greater after fire than before fire; and this effect was different for the two species. Examination of the actual counts suggested that there was no fire effect on *Passerina* and that the fire effect in the model was due to the increase in germination of *Phylica* from samples collected after fire.

Seed bank estimates (seeds per m^2), for both species and at all sampling times, were substantially lower when using the germination method, than when using the counting method (Tables 1, 2, 3). For *Passerina* estimates from counts were between 4.3 times (post-dispersal) and 1.2 times (pre-dispersal) higher; the range for *Phylica* was 16 times (post-dispersal) and 2.8 times (post-fire) higher. *Phylica* gave especially low estimates from samples collected before fire. The number of seeds germinating from soil samples after fire were used as an estimate of the minimum viable number of seeds in the soil. They were compared to the number of plump seeds counted in the same volume of soil collected at the same time. This gave the viability of plump seeds to be 50% for *Passerina* and 35% for *Phylica*.

Harvest experiment and seedling recruitment

The fire resulted in a very clean burn, with only the burnt stumps of adult plants remaining in all plots. There was no constant trend for *Passerina* to have lower seedling densities in harvested than unharvested plots (Table 4). There were approximately 40 % fewer *Phylica* seedlings in two of the harvested plots, but the same number as non-harvested in the third plot. A log-linear model fitted to seedling counts for plots showed that for both species the effects of harvesting and site were insignificant (Table 5). Thus the removal by harvesting of all seed from the last seed crop before fire in and around each plot, had no significant effect on post-fire recruitment of both species. The variation in seedling counts was explained by variability between the plot replicates due to the clumping of seedlings. This variation was accounted for in the model by including a scale parameter (overdispersion factor). The greater scale parameter calculated for *Passerina* indicated that its seedlings were far more clumped than those of *Phylica*.

The density of seedlings counted in unharvested plots in the field was far lower for both species than the density of seedlings emerging from soil samples collected after fire. For *Passerina* an average of 93 seedlings per m^2 was counted, whereas an estimated average of 212 seedlings per m^2 (Table 3) germinated from soil samples (i.e. 2.3 times as many). Corresponding values for *Phylica* were 20 and 98 seedlings per m^2 respectively (i.e 4.9 times more). The seedling counts in the field were also far lower than the number of seeds counted as lost from the seed bank from just after the fire in May 1990 to October 1990 (418 seeds per m^2 for *Passerina* and 163 seeds per m^2 for *Phylica*) (Table 2). Thus, most of these seeds did not germinate and survive as seedlings.

Seed storage and burial

There was no loss of plumpness of *Passerina* or *Phylica* seeds after 8 months of laboratory storage, but about 20 % loss for both species after 8 months of burial (Table 6). There was no significant differences in the viability of remaining plump seeds over both treatments and time intervals for each species (*Passerina*: F=1.057, p=0.403; *Phylica*: F=0.846, p=0.495). The viability of *Phylica* (approximately 90%) was higher than that of *Passerina* (approximately 50%). Thus, most seed appeared to survive up to eight months, with no reduction in viability, although up to 20% of potentially viable seed was lost.

Table 1. Estimates of plump seeds per m^2 ($\bar{x} \pm sd$) in the soil seed banks of *Passerina paleacea* and *Phylica ericoides* at three sites before and after seed dispersal by both species (n=50). The total numbers of plump seeds counted in each group of 50 samples are also given.

Sampling time	Site	*Passerina paleacea*		*Phylica ericoides*	
		Seeds/m^2	Total seeds	Seeds/m^2	Total seeds
Pre-dispersal (Sep. 1989)	1	315±524	31	367±609	36
	2	570±760	56	224±359	22
	3	438±535	43	244±427	24
Post-dispersal (Dec. 1989)	1	907±1109	89	306±424	30
	2	695±808	68	214±343	21
	3	611±797	60	316±492	31

Table 2. Estimates of plump seeds per m^2 ($\bar{x}\pm$sd) in the soil seed banks of *Passerina paleacea* and *Phylica ericoides* from seed counts before fire, 5 days after fire, and at the end of the winter germination period after fire (n=100). Total numbers of plump seeds counted in each group of 100 samples are also given.

Sampling time	*Passerina paleacea*		*Phylica ericoides*	
	Seeds/m^2	Total seeds	Seeds/m^2	Total seeds
Pre-fire (April 1990)	565±738	111	290±356	57
Post-fire (May 1990)	525±665	103	280±371	55
Post-winter (October 1990)	107±243	21	117±249	23

Table 3. Estimates of germinable seeds per m^2 ($\bar{x}$±sd) in the soil seed banks of *Passerina paleacea* and *Phylica ericoides*. Estimates were made from counts of seedlings germinating from 30 soil samples collected on each of four occassions. Total numbers of seedlings counted in each group of 30 samples are also given.

Sampling time	*Passerina paleacea*		*Phylica ericoides*	
	Seeds/m^2	Total seedlings	Seeds/m^2	Total seedlings
Pre-dispersal (Sep. 1989)	259±227	61	21±59	5
Post-dispersal (Dec. 1989)	212±207	50	17±44	4
Pre-fire (Apr. 1990)	187±166	44	25±51	6
Post-fire (May 1990)	212±174	50	98±114	23

Table 4. Seedlings per m^2 ($\bar{x}\pm sd$) of *Passerina paleacea* and *Phylica ericoides* counted in harvested and unharvested plots following fire and subsequent winter germination. Harvested plots had the last seed crop of the respective species removed in and around the plot during the year before fire. There were 7 replicate 1 m^2 plots for each treatment in each of 3 sites.

Species	Site	Number seedlings / m^2	
		Unharvested	Harvested
Passerina paleacea	1	87±56	49±16
	2	80±58	106±69
	3	114±74	119±53
Phylica ericoides	1	23±21	15±5
	2	25±21	14±13
	3	21±11	21±11

Table 5. Marginal effects of harvesting and site on the number of seedlings of *Passerina paleacea* and *Phylica ericoides* recruited after fire. Results are from generalized linear models applied to each species to explain the variation in seedling counts in seven harvested and seven unharvested plots in each of three sites. NS=not significant.

Species	Model	Scaled deviance	Df[a]	Change in dev	Df[a]	
Passerina	mean	36.74	41			
	mean+harvest effect	36.73	40	0.01	1	NS
	mean+site effect	32.06	39	4.68	2	NS
	mean+harvest X site	29.50	36	7.24	5	NS
Phylica	mean	38.17	41			
	mean+harvest effect	36.35	40	1.82	1	NS
	mean+site effect	38.10	39	0.07	2	NS
	mean+harvest X site	35.21	36	2.96	5	NS

Scale parameter for *Passerina* = 38.72
Scale parameter for *Phylica* = 10.18

[a] Degrees of freedom.

Table 6. Percentage remaining plump seeds ($\bar{x}$±sd) of *Passerina paleacea* and *Phylica ericoides* and their percentage viability ($\bar{x}$±SE) after laboratory storage or burial for 4 and 8 months. Seed numbers used in the tests are shown in parentheses in the column headings.

Treatment	Time (months)	*Passerina paleacea*		*Phylica ericoides*	
		Plump (4X25)	Viable (4X10)	Plump (4X15)	Viable (4X6)
Laboratory storage	4	100±0	50±5	100±0	96±4
	8	100±0	48±4	100±0	87±4
Burial	4	91±2	48±8	98±4	87±4
	8	80±12	63±8	80±10	92±5

DISCUSSION

Seed bank dynamics

a) Seasonal response to seed inputs and losses

The seed bank size of *Passerina* was larger than that of *Phylica* by all methods of seed bank estimation. *Passerina* seeds are also smaller than those of *Phylica*, thus fitting the general rule of smaller seed, bigger seed bank (Parker and Kelly 1989). The bigger *Passerina* seed bank is likely to be due to the input of more seed, rather than to longer seed survival. Approximate seed production per meter square of area at the study site in 1989 was 2600 seeds for *Passerina* and only 70 seeds for *Phylica* (Chapter 4). Thus, *Passerina* produced many more seeds than *Phylica*, most of which were lost before incorporation into the seed bank (further discussed in Chapter 4). Also, once in the seed bank, there appeared to be a greater loss of seeds from the seed bank of *Passerina* than from that of *Phylica*. This was indicated by the seasonal fluctuation detected in the *Passerina* seed bank size. This difference was only detected by direct seed counts, however, and not by the other methods used. It is possible that this is due to a difference in sensitivity of the methods. Seedling counts in the harvest experiment and germination from soil samples are indirect methods of measuring seeds in the soil. Therefore, relatively small changes in the numbers of seeds may not be detected. They may be masked by variable factors affecting seed germination and seedling mortality prior to monitoring. Direct seed counts are not affected by such factors, and may have been able to detect a fluctuation in the *Passerina* seed bank. Seed burial experiments may be expected to be more sensitive still, but they detected no difference between the seed longevity of these species. Perhaps the small number of replicates and relatively short burial time prevented a distinction being made.

The stability of the *Phylica* seed bank, despite new seed input, is not surprising when considering the small amounts of seed produced relative to seed bank size. Unless *Phylica* seed production is much higher in other years (which seems unlikely - see Chapter 4), then persistence of seeds is clearly important in enabling this species to build up its seed bank to the level observed (i.e. 4 times bigger than the years seed production). An increase in seed bank size with vegetation age has also been reported for the chaparral species *Ceanothus cordulatus* (Keeley 1990). Such building up of the seed bank of *Phylica* lends weight to the argument that it has longer-lived seeds than *Passerina*.

b) Immediate response to fire

Fire appeared not to kill significant numbers of seeds in the seed bank. It is possible that many of the plump seeds counted after fire had been killed, but would still take some time to decay. However, germination of seeds in soil samples also showed no reduction, in what were obviously viable seeds, from before to after fire. Manders (1990) also found no significant reduction of seed from before to after fire in fynbos on a forest margin. Mallik *et al* (1984) found increased germination from soil samples collected shortly after fire in British heath when compared to those collected before fire. Such increased germination, apparently due to stimulation by fire, was also apparent for *Phylica* seeds in soil samples, but there was no strong evidence for stimulation of *Passerina*. *Passerina* germination is, however, apparently cued to fire (Chapter 2), and thus the difference observed between the species may be due to differing mechanisms of the fire related cues (discussed in Chapter 2).

c) Losses during the first winter after fire

Most seeds were lost from the seed banks of both species during the first winter after fire. Their fate is largely a mystery. Only a fraction of the seeds established as seedlings following winter recruitment. The remaining seeds may have decayed, perhaps after being damaged by fire. However, many seeds must have been viable (as indicated by the germination of numerous seeds in soil cores collected after fire) and must have germinated, but either seedlings did not emerge, or emerged, but died before monitoring.

The observation that seed banks were not totally depleted during the winter following fire suggests that dormancy was not broken in all seeds. Remaining seeds could potentially allow vegetation recovery if the next fire occurred before plants reached reproductive maturity. This is provided that many of the seeds were still viable, were not lost from the seed bank in the following few years, and were not irreversibly buried too deeply. Losses to germination in the few years after the first winter are likely to be limited as Pierce (1990) found insignificant germination in the second and third year after fire for six dune fynbos shrub species. Zedler *et al* (1983) found very poor recruitment of obligate seeders with soil seed banks in chaparral following two fires in rapid succession in chaparral.

Persistence of seed banks

a) Seasonal persistence

The soil seed banks of both *Phylica* and *Passerina* were seasonally persistent and thus were not depleted over the year following seed input. This was indicated by the large seed banks still existing shortly before new seed input. This seed had survived in the soil for almost a year. Even for *Passerina*, for which a difference could be detected from before to after dispersal, the majority of seeds appear to have survived intact for one season. Further evidence for persistent seed banks was provided by the survival of 80% of seed in mesh bags for the 8 month period of burial, with no loss of dormancy. The presence of persistent seed banks was confirmed in the harvest experiment, in which removal of the current years seed crop resulted in no significant reduction in seedling recruitment after fire.

b) Long-term persistence

While seasonal persistence of *Phylica* and *Passerina* seed banks appeared certain, long-term persistence (for 10, 20 or 50 years) is uncertain. If the adult life spans are shorter than the fire cycle (unknown) and new recruits are limited to the post-fire period (Chapter 4), then the ability of seed banks to persist through to the next fire is uncertain. From seed burial experiments, the half-lives of seed may be calculated at 2.1 years for both species (given 20% of seed is lost every 8 months), i.e. 3.5% of seed remains after 10 years. These values are not accurate, however. Burial of more replicate seeds for longer periods with more frequent excavations would be needed for realistic estimates. The seed initially lost may represent the elimination of less hardy seed, with remaining seed being more resistant to decay (Holmes 1989). The fact that seed banks do not attain very large sizes, despite decades of new seed input, does seem to suggest that most seed survives only a few years. If so, it seems that persistence has evolved to protect against relatively short-term fire risks, rather than long-term survival if the adult populations senesce. These include protection against fire in all seasons and against low seed production in some years. Seed banks could also build up over a few years, but stabilize when seed input equals seed loss.

c) Persistence in other studies in fire-prone shrublands

Pierce (1990) observed relatively stable seed banks in six fynbos shrubs from sampling once a year over three years, despite very variable seed production. These species also appeared to have seasonally persistent seed banks, with between 49% and 88% of seeds surviving intact after 14 months of burial. These seed banks were not thought to be persistent over very long terms, however, as no seed of fynbos shrub species were found under grassland and thicket in eastern Cape dune fynbos. These vegetation types were proposed as successional consequences of high and low disturbance frequencies respectively.

Persistence has similarly been observed in many dominant non-sprouting chaparral shrubs (Parker and Kelly 1989). For some of these species fairly long-term persistence, for 20 years and more, is also suspected (Quick and Quick 1961; Keeley 1990). Chaparral species with persistent seed banks have also been observed to be dormant, and also responded to environmental disturbance cues (Parker and Kelly 1989; Keeley 1990). Species of the chaparral genus *Ceanothus*, which physically resemble *Phylica* and are also in the Rhamnaceae, have long lived seeds with dormancy broken by the heat effects of fire (Keeley 1987). Seeds of the Australian species *Acacia suaveolens* have a half-life of 10.7 years (Auld 1986a) and also respond to heat (Auld 1986b).

d) Consequences for fire in fynbos

The presence of persistent seed banks suggests that the season in which fire occurs is not critical for the regeneration of these two species. However, fire season may affect seed germination and seedling survival (Le Maitre 1988), and at these levels may affect population replacement after fire. Le Maitre (1988) found reduced recruitment of two fynbos Proteacea species with soil-stored seeds after fire in spring (before seed dispersal) when compared to fire in late summer and autumn (after dispersal). The dynamics of the seed banks of these species were not studied, however, and thus this pattern could not specifically be pinpointed to a seasonal fluctuation in seed bank levels. Reduced recruitment of Proteaceae with canopy-stored seed after winter and spring burns has also been noted (Bond *et al* 1984). Possible explanations have included seasonal fluctuations in pre-burn seed reserves, seasonally-related depletion of post-burn reserves, or seasonal differences in the probability of seedling survival (Bond *et al* 1984). The detection of a seasonal fluctuation in the seed bank of *Passerina*, but not of *Phylica*, may indicate that the season of fire could affect the species composition at this level.

Such an effect would probably not be great, however, as large numbers of *Passerina* seeds were present even when seed bank levels were at their lowest. Other factors such as seedling mortality patterns are likely to mask any fluctuations in the seed bank (Chapter 4). The question of how recruitment varies with fires in different seasons may only be adequately addressed by actually burning in different seasons.

A further consequence of persistent seed banks is that sufficient time should be allowed between fires for seed banks to accumulate (Pierce 1987). The minimum time is uncertain, but is likely to be at least for several years after the plants reach reproductive maturity. The Australian species *Acacia suaveolens* needed 2-5 years to reach reproductive maturity and a further 6 years to maximize seed bank levels (Auld 1987).

e) Consequences for flower harvesting

The stable, persistent seed bank of *Phylica* also indicated that intense commercial harvesting of this species in one year would not deplete the seed bank. An intense harvest could be risked in the year preceding a planned burn, even if this killed the harvested plants. Recruitment could then occur from buried seed stores. However, repeated annual harvesting would be expected to deplete the seed bank. Also, sufficient time should be allowed after fire for seed banks to accumulate before harvesting. Harvesting also damages the harvested plant itself and any harvesting method must also take plant recovery into account. Experiments in Appendix B investigated the recovery of harvested plants and indicated that harvesting should not exceed 50% of the flowers in the canopy at any time. If harvested at this level, then a recovery period of a few years should be allowed.

Seed bank clumping

At the scale of the three 50 m X 50 m sites within the general study area, both seed banks and seedling recruitment were relatively homogeneous. This is probably due to a homogeneous distribution of parent plants, as observed in Chapter 4. At a small scale, however, both seeds and seedlings were highly clumped. Such clumping has been widely observed for both seeds (e.g. Thompson 1986, Fowler 1988, Pierce 1990) and seedlings (e.g. Keeley and Keeley 1981, Bond 1984, Pierce 1990). This is expected as seeds would be dispersed in clumps around parent plants and may collect in depressions in the soil (Parker *et al* 1989). Also, certain "safe sites" (*sensu* Harper 1977) may favour seed germination and seedling survival, and seed and seedling predation patterns may be variable (Janzen 1971; Fenner 1985; Louda 1989). It was somewhat surprising that *Passerina* seedlings were more clumped than *Phylica* seedlings. *Phylica* seeds have elaiosomes and as such would be expected to be highly clumped in ant nests. Perhaps ant burial of these smaller elaiosome bearing seeds does not occur very efficiently (Bond and Slingsby 1983; Auld 1986a; Pierce 1990) and seeds in ant nests may be buried too deeply for fire stimulation of germination (Auld 1986a). It certainly seemed that the combined ballistic and ant dispersal mechanisms of *Phylica* resulted in effectively more even dispersal than the completely passive dispersal of *Passerina*. Similar effects were also observed by Musil and De Witt (1990) when comparing myrmecochorous and passively dispersed species.

Comparison of methods

The estimation of smaller seed bank sizes by germination than by direct counting was expected as many counted seeds may not be viable. Many viable seeds may also not germinate, and seeds may germinate but die before seedlings are counted. This was especially apparent for *Phylica* in samples collected before fire, where it seemed most seeds remained dormant as they had not received the correct fire-cue. Using a combination of both methods is thus more precise and has been recommended (Conn *et al* 1984). Most seed bank studies, however, use only germination, with fewer using seed counts and very few both (Leck *et al* 1989).

Viability estimates of seeds in the soil were made by comparing numbers of seedlings germinated from soil samples to numbers of plump seeds counted. This assumes that fire completely broke dormancy in viable seeds and that all germinating seeds were counted as seedlings. However, germination of acid scarified *Phylica* seeds which had been removed from the soil was 68% (and 95% for fresh seeds) (Chapter 2). This was higher than the 35% viability estimate by the above method. Thus it seems that not all viable seeds were counted as seedlings when soil samples were incubated. Perhaps the heat effect of fire, which stimulates germination of *Phylica* (Chapter 2), was not sufficient to break dormancy in all seeds. The 50% viability estimate for *Passerina* is likely to be closer reality, however, as the viability of seeds collected from plants was measured by germination to be 50% in this chapter and 70% in Chapter 2.

Limitations and remaining questions

Questions unanswered include the long term persistence of seeds in the soil. Seed burial experiments need to continue for a number of years, with more frequent excavation of seeds. Also the fate of most seeds lost from the seed bank during the first winter after fire is unknown. This question could be more closely addressed by field experiments using known amounts of seed with frequent monitoring and tagging of seedlings. General seed bank studies should also ideally be continued for more than one year, as seed production, seed predation and other factors may vary from year to year, and may affect seed bank sizes and dynamics, although not necessarily (Keeley 1987b; Pierce 1990). Most approaches to seed bank studies are not very sensitive and thus the simultaneous use of a number of methods was valuable. The field experiment in particular was important in validating conclusions made from other observations.

CHAPTER 4: COMPARATIVE LIFE HISTORIES OF TWO CO-OCCURRING ERICOID FYNBOS SHRUB SPECIES

ABSTRACT

The life cycle dynamics of two co-occurring, non-sprouting fynbos species, *Passerina paleacea* and *Phylica ericoides*, were studied. These species are both dependent on soil-stored seeds for population persistence in fire-prone fynbos, and both have small hard-coated seeds with germination linked to fire. A seed budget was constructed to further investigate similarities and differences between these species. *P. paleacea* produced many (2600±2198/m^2) ($\bar{x}$±sd), smaller (0.8 mg) seeds, and maintained a larger soil-stored seed bank (441±619-737±916 seeds/m^2) ($\bar{x}$±sd), despite high losses (>80%) after dispersal. Large numbers (93±60/ m^2) ($\bar{x}$±sd) of smaller *Passerina* seedlings germinated and established during the first winter after fire, but suffered high mortality (46%) during their first summer, apparently as a result of drought. Seedling mortality appeared to be the main factor limiting the number of *P. paleacea* individuals recruited after fire. *P. ericoides*, in contrast, produced fewer (69±187/m^2), larger (2.5 mg) seeds. The soil seed bank was larger (278±476 seeds/m^2) than seed input in one year, which indicated that it accumulated over a number of years, and possibly that post-dispersal seed losses were low. Far fewer (23±18/m^2) *P. ericoides* seedlings established during the first winter after fire and this appeared to be limiting on population recruitment. Germination failure in many seeds may have been important. *P. ericoides* seedling losses were low (17%) during their first summer. The recruitment of both species was severely restricted in mature vegetation, although *P. ericoides* appeared to have more potential for recruitment than *P. paleacea* in the interfire environment. Results were used to suggest possible means of non-equilibrium coexistence.

Key words: Coexistence, fire, germination, life history, limits to recruitment, soil seed bank, seedling mortality.

INTRODUCTION

Properties of ecosystems cannot be explained mechanistically without a clear understanding of population-level phenomena. Thus, understanding the role of fire in ecosystems requires knowledge of the life histories of component species (Keeley 1981). The life history of a plant consists of all stages through which it passes from fertilization to death. These components constitute a life history strategy, implying a set of adaptive responses accumulated over evolutionary time (Wilbur *et al* 1974). It is the means by which the number of surviving offspring is maximized under particular ecological conditions (Silvertown 1982).

In Cape fynbos, as with other mediterranean shrublands, fire is the most important disturbance factor (Kruger 1984; Keeley 1986), and is one of the most important selective agents in the evolution of life history traits (Naveh 1975; Gill 1981; Cowling 1987). All fynbos species must have life histories enabling them to persist through fire and selection has resulted in many successful "designs".

Small-leaved (ericoid) fynbos shrubs comprise most of the 8500 fynbos species (Bond and Goldblatt 1984), but have been particularly poorly studied (Pierce 1990). Most of these shrubs are non-sprouters and apparently rely on soil-stored seed banks for recruitment (Kruger 1984). This recruitment appears to be limited to the immediate post-fire environment (Kruger and Bigalke 1984; Manders and Cunliffe 1987). For many of these species adult plants appear similar and their adaptions for regeneration may have many similarities. However, they are likely to differ in the finer aspects of their reproductive phases. Such differences are probably largely due to differing constraints imposed by pre-evolved genetic resources, and may often have little ecological significance. In certain instances, however, differences may be important, notably where they affect recruitment levels after fire, and where they affect the relative composition of different species in communities.

Limitations to population recruitment after fire could occur at any of the seed or seedling stages, where probabilities of mortality are generally high (Harper 1977; Werner 1979; Fenner 1987; Louda 1989). These stages can be divided into the following processes: a) seed production, b) seed dispersal, c) seed storage, d) germination, e) seedling establishment, and f) passage of seedling to adult. Mortality patterns or failure at any stage may decide the fate of a population (Cavers 1983). However, high mortality at a certain stage will not necessarily affect population recruitment (Harper 1977; Louda 1982a, b; Andersen 1989). For instance, limited seed production or high seed losses to pre- or post dispersal seed predation will only affect population recruitment if it prevents the accumulation of a seed bank large enough to exploit available "safe sites" (*sensu* Harper 1977) for seed germination, seedling establishment and passage of seedling to adult (Andersen 1989). Even if all safe sites are not exploited, but recruits are numerous enough to undergo density-dependent mortality, then the population will not be affected (Fenner 1985; Andersen 1989). Competition between species for safe sites is in fact likely to produce a substantial oversupply of seeds as far as the population is concerned (Andersen 1989). To interpret the impact of seed losses at any stages of the life cycle on population recruitment, the overall seed dynamics through the life cycle need to be considered.

Differences between the reproductive adaptions of different species may allow their coexistence. They may have different abilities to exploit different "regeneration niches" (Grubb 1977). The traditional equilibrium view of communities has explained coexistence of species in terms of competition, resource use and niche overlap (Caswell 1982). Non-equilibrium viewpoints have, however, received increasing attention in recent years (e.g. Picket 1980; Chesson and Warner 1981; Shmida and Ellner 1984; Denslow 1985; Williams and Hobbs 1989). These predict coexistence from disturbance, dispersal and environmental heterogeneity (Caswell 1982). In the non-equilibrium state continued coexistence may be due to the fact that competitive interactions are not fully resolved. This is because the variability in disturbance and environmental fluctuations associated with disturbance cause the balance of advantage to favour each species in turn (Grubb 1977; Fenner 1985). The non-equilibrium view has been applied to fire-prone fynbos (Cowling 1987), in which "fire-induced transient niches" may differ spatially and temporally for a given fire and may differ between different fires. This may lead to differential establishment of different species (Cowling 1987). The variable environment determines whether or not there is, at a particular time and place, suitable conditions for flower formation, pollination, good seed set, germination, establishment of juvenile plants, or passage to adult (Grubb 1977). Differences between species at any of these stages may promote their coexistence by enabling them to exploit different transient regeneration niches or transient "patches" (Denslow 1985). However, any difference in regeneration characteristics observed between two species will not necessarily have the potential to affect relative species abundance. If differences are at levels which may be limiting on population recruitment, and if these differences may be influenced by variable disturbance or environmental factors, then this is good evidence for possible means of coexistence.

In this study the life cycle dynamics of two co-occurring ericoid fynbos shrubs species, *Phylica ericoides* and *Passerina paleacea*, were investigated. The adults of both species are physionomically similar. Both are finely branched shrubs with small, ericoid leaves, similar heights and no obvious differences in root structure. They may be regarded as trophically equivalent (Shmida and Ellner 1984) and, hence, competitively similar. These species also have many similarities with respect to their reproductive strategies. Both are obligate seeders depending on seasonally persistent seed banks (Chapter 3) for regeneration after fire. Regeneration occurs almost exclusively after fire and both species have hard coated seeds with germination cued to fire (Chapter 2). Both species disperse seed in November and December. However, a number of differences between the species are readily apparent (Table 1), and previous studies have shown that these species have different fire-related germination cues (Chapter 2) and different seed bank sizes (Chapter 3). To further study the similarities and differences between the two species a "seed budget" (Mallik *et al* 1984) was constructed. The relative abilities of the species to recruit in the interfire environment was also investigated. Results were used to assess the significance for each species of limitations and losses at different life history stages and as a basis for suggesting possible means of non-equilibrium coexistence. The importance of population studies covering various stages of the life cycle, as opposed to isolated components only, has often been emphasized (e.g. Auld 1987; Price and Jenkins 1987; Parker *et al* 1989).

MATERIALS AND METHODS

Study site and study species

The study site is in Dune Asteraceous Fynbos (Cowling *et al* 1988) on the farm Groot Hagelkraal ($34^{o}40'$S, $19^{o}30'$E), 45 km west of Cape Agulhas. It comprises a fine-leaved shrubland with a field layer of evergreen hemi-cryptophytes. *Passerina* *paleacea* and *Phylica ericoides* (hereafter referred to by their generic names) are the dominant shrub species, and comprise approximately 20% and 15% of the total cover respectively. Nomenclature is according to Bond and Goldblatt (1984). The study site is subject to recurrent fires and was last burned 25 to 30 years previously. Populations of the two shrub species appeared even aged. The climate is mediterranean, with 65% of approximately 450 mm of rain falling in the winter months from May to October. More details of the study site are given in Chapter 3.

Seedling recruitment and survival in mature vegetation

Twenty randomly located 1 m^2 plots were permanently marked in mature fynbos. In spring (September) 1989 these were searched for seedlings of *Passerina* and *Phylica* recruited during the previous winter (identified by the presence of cotyledons), as well as for non-reproductive plants less than 15 cm high. The count was repeated the following autumn (April 1990) in the same plots to assess survival of seedlings and young plants through the summer drought. Counts in autumn and spring were compared using *t*-tests on the matched pairs of data. Thirty *Phylica* seedlings were also individually marked in spring and the survival of each was checked the following autumn.

Cover and numbers of adult plants

Adult *Passerina* and *Phylica* plants were counted in 49 X 1 m^2 plots arranged in a grid pattern in each of three 30 m X 30 m sites. These were subjectively chosen in apparently homogeneous vegetation within the general study area. Chi-squared analysis on total counts at each site was used to compare plant numbers between the sites. The percentage cover values of each species were also estimated in the same plots, and the three sites were compared using one-way ANOVA on arc-transformed percentages.

Seed production

Seed production in *Passerina* and *Phylica* was determined by placing net bags over plants shortly before seed release. Eighty *Phylica* and 40 *Passerina* shrubs were bagged, but only 25 *Passerina* bags were not destroyed, apparently by small mammal seed predators. Plants selected for bagging included a range of sizes and were randomly chosen. However, plants were excluded when their structure made it difficult to attach the bags. Seeds were hand sorted and the number of intact seeds produced by each plant was counted. The long and short diameters of all bagged plants were also measured and the approximate surface area of each bush was calculated. Thus, seed production per m^2 of shrub canopy was determined. This was done as it appeared that seed production would be related to shrub cover rather than to shrub volume, as flowers in both species tended to be concentrated on the surface of the canopies. An estimate of seed production per m^2 of area at the study site was also made using percentage cover values determined for each species. After counting, seeds from the different bushes were combined for each species. The percentage of plump seeds (i.e. containing endosperm) was then determined by sinking 10 X 100 seeds of each species in water (plump seeds sink). Fifty seeds of each species were also weighed.

Post-fire seedling establishment and survival

Following a controlled fire in May 1990 and seedling recruitment during the subsequent winter, seedlings were counted in October 1990. Counts were made in 7 X 1 m^2 plots randomly located in each of three 30 m X 30 m sites at the study site. The plots corresponded to the unharvested plots in Chapter 3. The sites corresponded to those in which adult plants were counted, and the general study site was divided in this way to prevent results reflecting a localized effect only. A two-way ANOVA was used to assess differences in seedling counts between the species and the sites. Seedling counts were log-transformed. Root lengths of 20 randomly selected seedlings of each species were also measured.

Prior to the fire, estimates of percentage cover were made and numbers of parent plants were counted in the 1 m^2 plots. The percentage cover was also estimated in 3 m X 3 m areas with the 1 m^2 plots at their centers (i.e. in each plot plus surrounding area). Each of the above factors were correlated to the number of seedlings counted within the 1 m^2 plots using stepwise regression (Statgraphics computer package). Seedling counts were log-transformed, adult numbers were square root-transformed and percentage cover values were arc-transformed, sufficiently normalising the data.

Seedlings were counted again in the same plots in March 1991 to assess seedling mortality during the preceding dry period. A two-way ANOVA on arc-transformed percentage mortality values was used to assess differences between species and sites.

Seed budget

A budget was constructed for comparison of estimates of numbers of plants or propagules per m^2 at the study site for *Passerina* and *Phylica* at different stages of their life cycles. This included results from this chapter, as well as seed bank sizes from Chapter 3.

RESULTS

Seedling recruitment and survival in mature vegetation

No *Passerina* seedlings were counted in mature vegetation and only one small, non-reproductive individual was found (Table 2). Very few *Phylica* seedlings recruited in the current year were counted. These suffered significant losses over their first summer, although most of them survived (Table 2). Furthermore, of 30 marked *Phylica* seedlings, 23 (77%) survived the first summer in mature vegetation, although many appeared unhealthy at the end of this period. Small, non-reproductive *Phylica* plants were also found which were approximately as numerous as the seedlings recruited in one year (Table 2). Very few *Phylica* plants were seen that were possible intermediates between the small plants counted and mature plants.

Adult plant numbers and cover

Passerina had a greater number of adult plants and a higher percentage cover than *Phylica* in all three sites at the study area (Table 3). Both species had no significant differences in cover between the sites, and *Phylica* had no significant difference in plant numbers between the sites (Table 3). However, significantly higher numbers of *Passerina* individuals were found in site 2, but this difference was not very great (Table 3). Thus, data were combined for the three sites to give an overall percentage cover ($\bar{x}\pm$sd; n=147) of 20±16% for *Passerina* and 15±10% for *Phylica*. Adult plant numbers per m^2 ($\bar{x}\pm$sd; n=147) of 10±7 for *Passerina* and 6±4 for *Phylica* were similarly obtained. Adult *Passerina* plants were more clumped than *Phylica* plants. This was indicated as the variance to mean ratio for plant density (n=147) was 12.8 for *Passerina*, and 6.7 for

Phylica (Whittaker 1975). Also, over ten *Passerina* plants were counted in 44% of the plots, with a maximum of 35 plants in one plot. Over ten *Phylica* plants were found in only 17% of the plots, with a maximum of 22 plants in one plot.

Seed production

Passerina produced 36 times more seeds than *Phylica* when calculated for the total study site (Table 4). *Passerina* seed was 78±3% plump ($\bar{x}$±sd; n=10 X 100 seeds), while *Phylica* seed was 97±1% plump. Many seeds of both species were also shrunken and not properly formed and were not counted. *Phylica* seeds with elaiosomes removed had a mass approximately three times that of *Passerina* seeds (Table 1). When comparing plump seed production per m^2 of canopy area, *Passerina* produced about 30 times as much seed as *Phylica*. When the difference in seed mass between the species is taken into account, *Passerina* still produced 10 times more seed mass than *Phylica*. All bagged *Passerina* plants produced seed, while only 40% of *Phylica* plants produced any seed. If all non-producing plants are excluded, then the remaining *Phylica* plants produced 1136 ± 1737 seeds per m^2 of canopy cover ($\bar{x}$ ± sd), which was still far lower than that of *Passerina* (Table 4).

Seedling recruitment and survival after fire

Approximately four times more *Passerina* seedlings than *Phylica* seedlings were counted following the first winter after fire (Table 5). Thus, there were significant differences between the species (F=45.1; p<0.001), but there were no significant differences between the sites (F=0.4; p=0.715). Counts in all sites were combined to give seedling numbers per m^2 ($\bar{x} \pm sd$; n=21) of 93±60 for *Passerina* and 23±18 for *Phylica*. Seedling numbers were best correlated to the pre-fire percentage cover of parent plants in the 1 m^2 plots, with the best correlation being obtained for *Passerina* (Table 6). Plant numbers and percentage cover in the 3 m X 3 m areas including and surrounding the plots explained no further variation in the seedling counts (Table 6). *Passerina* seedlings (variance to mean ratio = 119.4; n=21) were observed to be far more clumped than those of *Phylica* (variance to mean ratio = 44.7; n=21). Up to 50 *Passerina* seedlings could be observed in some areas less than 10 cm X 10 cm. Seedling root lengths of *Phylica* were 37 ± 7 mm ($\bar{x}$ ± sd; n=30), while *Passerina* root lengths were shorter at 28 ± 8 mm. The roots of *Phylica* seedlings were also distinctly thicker.

Seedling mortality during the first five months of the dry summer was approximately twice as high for *Passerina* than for *Phylica* (Table 5). This species difference was significant (F=18.8; p<0.001), as was the difference in mortality between the sites (F= 3.4; p=0.042). Examination of the data indicated that the site difference was due mainly to both species suffering far lower mortality in site 2 than the other sites (Table 5).

Seed budget

Passerina had greater numbers of plants or propagules than *Phylica* at all life cycle stages examined (Table 7). Plant numbers and seed bank sizes of the two species differed by a factor of approximately two (Table 7). However, *Passerina* produced about 40 times more seed than *Phylica*, and four times more seedlings were counted after fire (Table 7). The life cycle stage at which *Passerina* lost most seed was between seed dispersal and incorporation of seed into the soil seed bank. The production of over 2000 seeds per m^2 on average was only observed to boost seed bank levels by approximately 300 seeds per m^2. *Phylica*, however, produced far fewer plump seed than were counted in the seed bank. The seed banks of both species were largely, but not completely, depleted during the winter following fire. *Passerina* appeared to lose a greater proportion seeds during this period. A greater proportion of *Passerina* seeds were also observed as seedlings after the winter following fire, but they suffered greater mortality during the first summer when compared to *Phylica* seedlings.

Table 1. Characteristics of *Passerina paleacea* and *Phylica ericoides*.

Characteristic	*Phylica ericoides*	*Passerina paleacea*
Family	Rhamnaceae	Thymelaeaceae
No. spp. in genus in Cape flora[a]	150	18
Distribution[a]	Cape Pennininsula to Port Elizabeth	Cape Penninsula to Bredasdorp
Habitat[a]	Dunes to lower slopes	Sandy flats to lower slopes
Shrub height[ab]	0.15-0.9m (0.45m)	0.3-1.0m (0.5m)
Pollination	Insect	Wind
Dispersal	Ballistic and ant	Unspecialised
Seed mass[c] ($\bar{x}$±sd)	2.5 ± 0.4 mg	0.8 ± 0.2 mg
Flowering time[c]	Feb. to Nov.	Aug. to Nov.

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[a] From Bond and Goldblatt (1984).
[b] Average height at study site is shown in parentheses.
[c] This study.

Table 2. Numbers of seedlings and small, non-reproductive plants (NR) per m^2 ($\bar{X}\pm sd$) of *Passerina paleacea* and *Phylica ericoides* counted in mature vegetation in spring (September) 1989 and the following autumn (April). Counts were made in the same 20 X 1 m^2 plots on both occasions. Significant differences are from *t*-tests on matched pairs. **=p<0.01; NS=not significant.

Species	Type	Number / m^2		Sig.
		Spring	Autumn	
Passerina paleacea	Seedlings	0 ± 0	0 ± 0	NS
	NR	0.1±0.2	0.1±0.2	NS
Phylica ericoides	Seedlings	3.7±2.3	2.9±1.8	**
	NR	3.4±2.1	3.3±2.2	NS

Table 3. Numbers of adult plants per m^2 ($\bar{x}\pm sd$) and percent cover ($\bar{x}\pm sd$) of *Passerina paleacea* and *Phylica ericoides* in mature vegetation at three sites. Counts and cover estimates were made in 49 X 1 m^2 plots at each site. Significant differences between numbers in the sites are from Chi-squared analysis on total counts. Significant differences between cover at the sites are from one-way ANOVA on arc-transformed percentages. NS=not significant; ***=p<0.001.

Species	Site	Number per m^2		Percent cover	
Passerina paleacea	1	9 ± 5		17 ± 13	
	2	12 ± 8	***	22 ± 16	NS
	3	8 ± 7		20 ± 17	
Phylica ericoides	1	6 ± 3		15 ± 9	
	2	6 ± 5	NS	15 ± 12	NS
	3	6 ± 4		16 ± 9	

Table 4. Seed production by *Passerina paleacea* and *Phylica ericoides* ($\bar{x}\pm$sd). Seed was collected from 80 *P. ericoides* plants and 25 *P. paleacea* plants.

	P. paleacea	*P. ericoides*
Intact seeds/m^2 of canopy	16991 ± 14305	468 ± 1270
Plump seeds/m^2 of canopy[a]	13253 ± 11158	454 ± 1232
Viable seeds/m^2 of canopy[b]	9674 ± 8145	432 ± 1170
Plump seeds/m^2 of area at the study site[c]	2611 ± 2198	69 ± 187

[a] Assumes a constant plumpness of 78% for *P. paleacea* and 97% for *P. ericoides* as determined after mixing seeds from different plants.

[b] Assumes a constant viability of 73% for *P. paleacea* and 95% for *P. ericoides* (see Chapter 2).

[c] Assumes constant seed production over the study site and uses the average % cover values determined for *P. paleacea* (19.7%) and *P. ericoides* (15.2%).

Table 5. Seedling numbers per m^2 ($\bar{x}\pm SE$) of *Passerina paleacea* and *Phylica ericoides* counted in October 1990 (following germination during the first winter after fire), and in March 1991 (after a further five summer months), together with percentage mortality ($x\pm SE$). Seedlings were counted in 7 X 1 m^2 plots at each of 3 sites.

Species	Site	Number seedlings per m^2		Mortality
		October 1990	February 1991	(%)
P. paleacea	1	87 ± 21	38 ± 11	53 ± 8
	2	80 ± 22	49 ± 10	32 ± 9
	3	114 ± 28	58 ± 22	52 ± 6
P. ericoides	1	23 ± 8	19 ± 8	26 ± 7
	2	25 ± 8	23 ± 8	10 ± 4
	3	21 ± 4	16 ± 8	19 ± 4

Table 6. Stepwise regression analysis with log seedling numbers counted after fire in 21 X 1 m^2 plots as the dependent variable. Independent variables were canopy cover (arc-transformed) and plant numbers (square root transformed) pre-fire in the 1 m^2 plots, and canopy cover in 9 m^2 areas surrounding and including the plots (arc-transformed). F to enter the model = 4.0.

Passerina paleacea

Variable in model	Coeff.	F-remove	Variables not in model	P. Corr.	F-enter
Cover/m^2	2.449	22.15	Numbers/m^2	0.037	0.025
			Cover/9 m^2	0.052	0.049

R^2: 0.538 Adjusted: 0.514 MSE: 0.220 d.f.: 19

$$\log \text{seedlings} = 3.310 + 2.449\ (\arcsin \sqrt{\text{cover}/m^2}\ )$$

Phylica ericoides

Variable in model	Coeff.	F-remove	Variables not in model	P. Corr.	F-enter
Cover/m^2	2.644	11.65	Numbers/m^2	0.333	2.239
			Cover/9 m^2	0.183	0.622

R^2: 0.380 Adjusted: 0.348 MSE: 0.299 d.f.:19

$$\log \text{seedlings} = 1.869 + 2.644\ (\arcsin \sqrt{\text{cover}/m^2}\ )$$

Table 7. Estimates of numbers of plants or propagules per m^2 of area at the study site ($\bar{x}\pm$sd) for *Passerina paleacea* and *Phylica ericoides* at various stages of their life cycles[a].

Life cycle stage	*Passerina paleacea*	*Phylica ericoides*
Adult plants	10 ± 7	6 ± 4
Plump seed produced in 1989	2611 ± 2198	69 ± 187
Seed bank sizes:		
i) by counting	441 ± 619- 737 ± 916[b]	278 ± 476
ii) by germination	218 ± 170	100 ± 110[c]
Seed bank size (by counts) after depletion during first winter after fire	107 ± 243	117 ± 249
Seedlings counted after the first winter after fire (October 1990)	93 ± 60	23 ± 18
Seedlings surviving five months later (February 1991)	49 ± 40	19 ± 17

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[a] All estimates are summerised from results presented in this chapter, except for seed bank sizes, which are from Chapter 2.

[b] A seasonal fluctuation in seed bank size was observed.

[c] Germination from samples collected after fire.

DISCUSSION

Passerina and *Phylica* have many overall similarities in their adaptions to their fire-prone environment. These include obligate reseeding from small, hard coated, soil-stored seeds with germination linked to fire (Chapter 2; Chapter 3). However, closer examination has revealed many differences in their regeneration processes. Relative to *Phylica*, *Passerina* produced many, smaller seeds, each with less chance of eventually being recruited as a seedling and surviving to become a mature individual. *Phylica* produced far fewer, relatively large seeds, and had specific adaptions for dispersal and the protection of seeds. Each *Phylica* seed appeared to have a better chance of eventual survival to produce a new adult individual.

Seed production

The inverse relationship observed between seed size and number for *Passerina* and *Phylica* is generally found in species of comparable size (Harper 1977). It is thought that if a plant has a certain amount of resources to allocate to seed production it may either produce smaller amounts of larger seeds, or larger amounts of smaller seeds (Harper 1977). However, this does not fully explain the differences observed between the numbers of seeds produced by *Passerina* and *Phylica*. When seed mass was taken into account, *Passerina* produced approximately ten times greater mass of seeds per canopy area than *Phylica*. Thus, if seed mass was taken as a measure of reproductive effort (Harper *et al* 1970), then the reproductive effort of *Passerina* was approximately ten times greater than that of *Phylica*. However, reproductive effort is better measured by including the cost of all reproductive structures as well as seed (Gadgil and Solbrig 1972). *Phylica* has a number of additional reproductive features which must to some extent account for the difference in seed mass produced. These include elaiosomes for ant dispersal and capsules for ballistic dispersal and possibly seed protection before dispersal. *Passerina* seeds have no special features for dispersal or seed protection prior to dispersal. *Phylica* also has larger (although fewer) insect pollinated flowers with a much longer flowering time, while *Passerina* has smaller wind pollinated flowers. Seed production by *Phylica* may also be much higher in other years or in younger vegetation. Pierce (1990) and Keeley (1987b) found seed production in several perennial shrub species to be extremely variable from year to year in fynbos and Californian chaparral respectively. However, it is possible that seed production by *Phylica* would never be very much higher than that observed. Casual observations of numbers of developing seed capsules indicated that seed production by *Phylica* would be low in 1990 as well as 1989. Results also corresponded to those of Pierce (1990) in which low seed production was also recorded for three myrmecochorous fynbos species, with much higher seed production by another *Passerina* species, *P. vulgaris*.

Post-dispersal seed losses

Much more seed was produced by *Passerina* than was found in the seed bank. Thus, post-dispersal losses for this species appeared to be high. This has similarly been observed for some chaparral shrub species which may produce up to 99 % more seed than is found in the soil seed bank (Keeley 1977; 1987b). Most of this seed loss is likely to have been due to predation (Keeley and Hay~~e~~s 1976; Harper 1977; Janzen 1977; Crawley 1983; Bond and Breytenbach 1985; Kelly 1986; Louda 1989). Also, Pierce (1990) recorded similarly high seed losses for *Passerina vulgaris* in eastern Cape dune fynbos, and showed insect and rodent predators to be active in removing seeds. Species producing dense seed crops are often highly predated (Louda 1989), and some species disproportionately attract consumers (Crawley 1988). *Passerina* seeds are obviously attractive as collection bags were frequently ripped open by rodent seed predators. Species producing large numbers of smaller seeds often have no specific mechanism to counter predation, and depend on at least a few seeds escaping (Thompson 1987). Large numbers of seeds have also been associated with predator saturation, and with attempts to saturate the environment to occupy all microsites (Cavers 1983). Certain environmental conditions may also favour species which produce many seeds, especially if seed predation and density-dependent mortality are reduced (Louda 1989).

Phylica produced much less seed in one year than was found in the seed bank. This implied that seed banks build up from seed inputs over a number of years, and also may imply low seed loss to factors such as predation after dispersal. Predators usually prefer larger seeds, but not necessarily, especially if seeds are not very abundant (Janzen 1975; Thompson 1987). The seed dispersal mechanisms of *Phylica* may further lower local seed density, further reducing predator interest. Ant burial may also help seeds escape predation (Berg 1981; Bond and Slingsby 1983). Ants burial may also place seeds in more fertile environments (Culver and Beatie 1983), but it may not be very efficient and seeds may be buried too deeply (Auld 1986a). *Phylica* may also expend more energy on resistant seed coats (McKey 1979) and even possibly on chemical defences (Janzen 1969), as part of its approach of producing fewer propagules of higher quality.

Seed banks, germination and seedling establishment after fire

Once seeds are buried, predation is thought to be negligible (Thompson 1987), although pathogen activity can cause major losses (Cook 1980). *Passerina* and *Phylica* both appeared to suffer low losses, especially *Phylica*, which was found to have exceptionally stable seed bank through the year

(Chapter 3). The seed bank of *Passerina* was bigger than that of *Phylica* by a factor of approximately two. This appeared to be due to greater seed production by *Passerina*.

During the first winter following fire the seed bank of *Passerina* was mostly depleted. Seedlings counted at the end of the first winter numbered ten times more than individuals in the pre-fire population. Thus it appeared that population recruitment for *Passerina* was not limited by the number of seedlings establishing during the first winter after fire, or at any previous stage. Thus, the high losses to predation did not seem to affect the population. The average seedling density of 93 seedlings per m^2 for *Passerina* was similar to the 95 seedlings per m^2 counted for another *Passerina* species, *P. vulgaris*, in eastern Cape dune fynbos (Pierce 1990).

For *Phylica*, approximately four times fewer seedlings were counted at the end of the first winter when compared to *Passerina*. This was despite the observation that the seed bank of *Phylica* was approximately half as big as that of *Passerina* and that *Phylica* had a higher proportion of viable seeds in the soil seed bank than *Passerina* (Chapter 3). The low numbers of *Phylica* seedlings counted indicated that *Phylica* recruitment appeared to be limited by the poor establishment of seedlings during the first winter after fire. Seedlings were, however, approximately four times more numerous than the parent plants before fire, but may be expected to undergo a certain amount of mortality from environmental factors (Specht 1981; Midgely 1988; Pierce 1990). This limitation could have been largely due to germination failure of many *Phylica* seeds. This is indicated by the observation that the seed bank of *Phylica* appeared to have been less depleted than that of *Passerina* during the winter. *Phylica* seeds are stimulated to germinate by the heat effects of fire (Chapter 2), and thus the temperature of the fire could have been too low to stimulate the germination of many seeds, especially those buried more deeply. However, most *Phylica* seeds still appeared to have been lost from the seed bank over the winter following fire. This indicated that most seeds either germinated or were killed by fire. Seeds may have germinated and died before seedlings were counted, although this is perhaps unlikely in view of the good survival of *Phylica* seedlings over the more stressful summer period. Many seeds could also have been killed by the heat effects of fire, although this was not indicated for *Phylica* in Chapter 3. Perhaps a fine balance exists between seed death and germination stimulation by various fire intensities at various soil depths. It is also possible that the estimates of seed lost over the winter period were higher than in reality as the seed bank sampling methods were not very sensitive (Chapter 3).

Seedling mortality

Both *Passerina* and *Phylica* seedlings suffered mortality during their first summer. Mortality was probably due to drought stress (Cook 1979; Wellington and Noble 1985; Auld 1987; Enright and Lamont 1989) and herbivory may cause some loss (Breytenbach 1984; but see also Bond 1984; Midgely 1988). *Passerina* seedlings suffered far higher mortality than those of *Phylica*. This difference was probably due to the larger seedlings of *Phylica*, with longer roots, having better access to moisture in the dry summer. Larger seedling size has commonly been associated with increased seedling survival (Primack 1987; Keeley 1990; Musil and De Wit 1990) and may also give increased competitive ability (Black 1958). These correlations do not always exist, however, and may not persist (Fenner 1985; Thompson 1987).

Phylica seedlings appeared likely to undergo almost exclusively density-indepentent mortality as they were not very numerous and were relatively evenly dispersed. *Passerina* seedlings also appeared likely to undergo mostly density-independent mortality as most seedlings seemed sufficiently scattered relative to their size, that competition between them was likely to be weak. Furthermore, for both species, density-dependent mortality did not seem to occur readily as up to 35 *Passerina* adults and up to 26 *Phylica* adults were counted in 1 m^2 plots in the pre-fire vegetation. However, in some instances up to 50 *Passerina* seedlings were found in an area of about 10 cm X 10 cm, in which event some density-dependent mortality is certain to result. Such a mixture of density-dependent mortality in seedling clumps and density-independent mortality in more scattered seedlings has been observed in fire-prone Australian shrublands (Wellington and Noble 1985; Enright and Lamont 1989). The highest mortality from both density-dependent and density-independent effects is expected to occur during summer drought (Wellington and Noble 1985).

The high mortality of *Passerina* seedlings during their first summer appeared to limit the numbers of this species recruited after fire. The large numbers of seedlings recruited were substantially thinned out and mortality in subsequent years is likely to further reduce their numbers. The final number of *Passerina* seedlings surviving to adulthood may be a function of the number of available "safe" microsites (Andersen 1989), with the severity of environmental conditions in the years following fire determining which sites are "safe enough". After their first summer, the relative proportions of *Passerina* and *Phylica* seedlings were not very different to from the relative proportions of adults in the pre-fire vegetation. Thus, if the initial advantage of *Phylica* seedlings in the first year does not persist, and subsequent mortality for both species is similar, their relative abundance will be similar to that before fire. If the seedlings of the two species suffer substantially different mortality in subsequent years, then their relative abundance will change. Seedling numbers of both species can still be reduced by approximately four times before they resemble pre-fire adult numbers.

Recruitment in mature vegetation

Recruitment of *Phylica* and *Passerina* in mature vegetation was severely restricted. No *Passerina* seedlings were observed in mature vegetation. This is probably mostly due to the very strong dormancy observed for *Passerina*, which is broken by fire related cues (Chapter 2). Also, if some seeds do germinate, then the small seedlings of *Passerina* with small, thin cotyledons may be very susceptible to mortality in mature vegetation. However, several *Phylica* seedlings were always observed in mature vegetation and some persisted as small, non-reproductive plants. The dormancy of *Phylica* seeds is weaker than in *Passerina* (Chapter 2), and the larger *Phylica* seed size may facilitate seedling survival under the canopy (Thompson 1987; Keeley 1990). The majority of *Phylica* seedlings were observed to survive their first summer in mature vegetation, but most were expected to die within the following year as the numbers of small, non-reproductive plants were low (similar to seedling numbers recruited in one year). Also, in other fynbos sites and in chaparral, few seedlings are found in mature vegetation and most appear to die (Wicht 1948; Montygierd-Loyba and Keeley 1987; Parker and Kelly 1989; Pierce 1990). This has been attributed to competition from adults, especially due to their effects of lowering soil moisture in the upper soil layers when compared to bare soil after fire (Schlesinger *et al* 1982; Hastings *et al* 1989). Higher herbivory in vegetated areas may also be important (Breytenbach 1984).

Under normal circumstances in mature vegetation, the ability of the surviving small *Phylica* plants to develop into adults is doubted. No intermediates between these small plants and adults were noticed in casual observations. Thus it appears that recruitment of reproductively mature *Phylica* plants in the interfire period is rare. However, it is possible that the small *Phylica* plants may act as a type of "seedling bank" (Vlahos and Bell 1986), from which colonization of gaps may occur during senescence in older stands of fynbos (Keeley 1986). In chaparral some species may establish seedling banks and some seedlings may even mature (Christensen and Muller 1975). This has largely been observed for species whose germination is not specifically cued to fire, however (Keeley 1990). No increase in *Phylica* recruitment under senescent shrubs was noticed, but older stands with bigger gaps, and thus much reduced adult competition, may be needed (Keeley 1986). The dispersal mechanisms of *Phylica* may also facilitate seed dispersal into gaps.

Coexistence of *Passerina* and *Phylica*

Several suggestions can be made for possible non-equilibrium means of coexistence of *Passerina* and *Phylica* based on observed differences. The most important differences are likely to be at the life cycle stages which are limiting on recruitment. *Phylica* appears to be limited by establishment of seedlings in the winter following fire. This may be affected by germination and seed mortality during fire, which both depend on fire intensity. Different fires can have different intensities (Van Wilgen 1987) and fire intensities can vary locally within a fire and even between different microsites (Davis *et al* 1989). This may lead to *Phylica* recruitment being differentially favoured after different fires and in different sites within a fire. Early mortality of *Phylica* seedlings could also perhaps have played a role in limiting seedling establishment during the first winter. Such mortality is likely to be effected by environmental conditions during the winter, which could also vary for different fires and between sites within a fire, resulting in differential recruitment patterns. *Passerina*, however, is not limited by seedling establishment and its recruitment would not be affected by the above factors.

Passerina recruitment appeared to be limited by seedling mortality during summer drought in the years following fire. The environmental conditions affecting seedling survival through summer may vary with different fires and thus affect the relative abundance of *Passerina* from one fire to the next. For example, in other systems, seedling survival has been shown to depend on the length of the first rainy season. This is as seedlings may reach greater sizes and be better equipped to cope with summer drought (Specht 1981; Williams and Hobbs 1989). Differences in the effects of drought could also exist between different localities and different microsites within one fire. Patterns of water run-off and patchiness of soil characteristics may result in more and less favorable sites for seedling survival. This may explain the significant difference in survival of *Passerina* between the three subsites at the general study site.

The above mechanisms explain how differential recruitment of *Phylica* and *Passerina* could occur in response to different, variable environmental factors. This may explain coexistence in these species (Grubb 1977). These mechanisms provide both species with different abilities to exploit different "fire induced transient niches" (Cowling 1987), which may allow the balance of advantage to favour each species in turn (Grubb 1977).

Phylica and *Passerina* are always intermixed at the study area, with both species present in almost any random 1 m^2 area. It would thus seem that there must always be at least some local patches and microsites within the landscape where

Passerina seedling survival may occur, and where germination and establishment of *Phylica* seeds may occur. These sites of survival for both species appear to be determined by fundamentally different processes and would therefore be independent and would often not correspond. This would always allow some space for both species on both a large and small scale.

Less common scenarios can also be envisaged which could affect coexistence and relative species abundance, for example fire frequency. Very long interfire periods may lead to the senescence of the original *Phylica* and *Passerina* populations. This may give a relative advantage to *Phylica*, if it does indeed have better potential for interfire recruitment. Very short fire intervals could favour *Phylica* if fire occurs before reproductive maturity. This is if the larger numbers of longer-lived seeds ungerminated after the first winters recruitment were still available for recruitment (Chapter 3). However, *Passerina* may gain the advantage shortly after reproductive maturity due to larger seed production, especially if predation is reduced in young vegetation. *Phylica*, in contrast appears to build up a seed bank over several years.

There is increasing evidence that such fire induced non-equilibrium means of coexistence are important in fire-prone environments, which argues against the uniform use of prescribed burns (e.g. Keeley 1987a; Parker and Kelly 1989; Pierce 1990). This also supports Christensen's (1985) contention that the "optimal fire regime" is a meaningless concept.

Limitations and suggestions

The main shortcomings of this study were that it was conducted over one year only and involved only one fire. Also, it was conducted at one site only in relatively old vegetation. Thus, the variation in seed production, seed predation and seed banks from year to year and in different aged variation were not assessed. Variation in seedling establishment and mortality after different fires was also not assessed. Comparisons made in the seed budget must especially be viewed with caution, for the above reasons, and due to the high variation in the data collected. Also, errors may be compounded by the scale effects of determining values per m^2 for the study site from limited sampling. However, general trends were clear and it is felt that conclusions made were relatively well founded.

Remaining questions include closer investigation of the sources of seed and seedling mortality. Also, monitoring of seedling mortality needs to be continued for several years and the effects of interspecific and intraspecific competition need to be examined. There was also no information on pollination, pre-dispersal seed predation and microsite effects.

CHAPTER 5: GENERAL CONCLUSIONS

The approach of using a number of methods to study a range of characteristics of *Passerina paleacea* and *Phylica ericoides* proved effective. Much information was collected revealing many interesting patterns in the adaptions of these species to their fire-prone environment. It was particularly useful to have two relatively similar species for comparison, as this highlighted the distinctive features of each, and enabled the formulation of coexistence hypotheses.

MAJOR FINDINGS

Germination

Seeds of both *Passerina* and *Phylica* had a high degree of dormancy which appeared to be broken by fire-related cues. The germination of *Phylica* was stimulated by the heat effects of fire. A 70°C treatment for 1 h produced optimal germination when compared to 100°C and 125°C for five minutes, which appeared to cause some mortality.

Passerina had especially strong dormancy, but the precise germination cue could not be established. Dormancy could only be broken by the highly artificial treatment of acid scarification, and not by the heat and charred wood treatments used. Circumstantial evidence pointed to a role of indirect fire-effects associated with the removal of vegetation. However, the effects of light, allelopathy and increased diurnal temperature fluctuations appeared to be excluded. The germination requirements of *Passerina* may thus be complex and may include an initial seed ageing requirement.

Seed banks

The seed banks of both species were seasonally persistent and were not extensively depleted over the year following seed input. Seed bank estimates from direct seed counts for *Passerina* varied from 441 ± 620 ($\bar{x} \pm$ sd) seeds per m^2 before seed dispersal to 737 ± 919 seeds per m^2 after dispersal. The seed bank of *Phylica* was stable at 278 ± 450 seeds per m^2. Seed bank estimates from germination were lower for both species. Fire appeared not to kill significant numbers of seeds, but seed banks were much reduced during the first winter after fire. Most seeds lost from the seed banks were not observed as seedlings following the first winter, and their fate is uncertain. This was the first study in fynbos which assessed soil seed bank dynamics through the year and in response to fire.

Life cycle dynamics

Relative to *Phylica*, *Passerina* produced many more, smaller seeds. When the difference in seed mass was taken into account *Passerina* produced a far greater total mass of seed per area of canopy than *Phylica*. To some extent this difference is likely to be accounted for by specific energy requiring features in *Phylica*, for example adaptions for insect pollination and dispersal.

Most *Passerina* seeds appeared to be lost to predation before being incorporated into the soil seed bank. However, these high losses were not limiting on *Passerina* recruitment. *Phylica* produced far fewer seeds in one year than the number of seeds in the seed bank. This indicated that seed losses before incorporation into the soil seed bank may be low and that most seeds survive at least a few years in the soil, thus accumulating a larger seed bank. The seed bank of *Passerina* was bigger than that of *Phylica* due to higher seed input.

Many more *Passerina* seedlings established during the winter after fire than those of *Phylica*. Post-fire recruitment of *Phylica* in fact appeared to be limited by the low numbers of seedlings establishing. It is possible that this limit was largely due to germination failure of many *Phylica* seeds, which is probably affected by fire intensity.

Phylica seedlings suffered low mortality during their first summer drought. *Passerina* seedlings suffered high losses, however, which appeared to be the factor limiting post-fire population recruitment in this species. It is likely that the smaller *Passerina* seedlings with shorter roots had less access to moisture during this period. Final numbers of *Passerina* seedling surviving to maturity may be a function of the number of "safe" microsites, with the intensity of drought in the years following fire determining which sites are "safe enough".

Recruitment of both species was severely limited in mature vegetation. This is likely to be due to a lack of fire-linked germination cues and increased seedling mortality in mature vegetation. No *Passerina* seedlings were ever seen in mature vegetation and it appeared that most of the few *Phylica* seedlings that were observed, died within a few years. A few *Phylica* seedlings did, however, persist as small, non-reproductive individuals, which could possibly take advantage of gaps formed in older, senescent vegetation.

Coexistence

The above results indicated that *Phylica* recruitment could vary with fire intensity and that *Passerina* recruitment could vary with different environmental conditions associated with summer drought after fire. Both of these factors may vary from fire to fire and from patch to patch within a fire, leading to differential recruitment. This could facilitate coexistence (Grubb 1977; Cowling 1987). It would appear that there are always some microsites where *Phylica* seedlings could establish and some where *Passerina* seedlings could survive. These sites would not necessarily correspond and could often be sufficiently isolated from each other that competitive interactions are insignificant. Thus, on both smaller and larger scales, *Passerina* and *Phylica* could always be intermixed.

Practical implications

The existence of persistent seed banks in *Phylica* and *Passerina* does not give any indication that a specific season of burn should be favoured. However, the season of burn may affect the intensity of the burn and subsequent seedling survival (Le Maitre 1987a; 1988). The recruitment of the species may be affected by these processes and thus at these levels the season of fire may still affect recruitment. The full effects of fire in different seasons can only be assessed by actually burning in different seasons. The fire in this study occurred in mid May and resulted in reasonable recruitment levels. A fire in mid summer would probably be hotter and may alter the recruitment of *Phylica*. The coexistence mechanism proposed argues against the uniform application of prescribed burns if species diversity is to be maintained (Keeley 1987a; Parker and Kelly 1989; Pierce 1990).

The existence of persistent *Phylica* seed banks indicates that intense harvesting of this species in one year will not deplete the seed bank. Thus, reduced recruitment would not result if a fire occurred in the year following an intense harvest. However, poor recovery of the harvested plants does place limits on harvesting intensity (Appendix B). Also, harvesting of *Phylica* in young vegetation is not recommended as seed banks should be allowed to accumulate. Harvesting year after year is also likely to deplete seed banks.

LIMITATIONS AND SUGGESTIONS

The major weakness of this study was that it was conducted over a period of one year only and included one fire only. Also, it was conducted at one site comprised of relatively old vegetation. Thus the generality of the results is uncertain. Seed production especially may vary from year to year (Keeley 1987b; Pierce 1990) and in vegetation of different ages (Auld 1987). However, seed banks of several perennial shrub species have been found to be relatively stable over three years in fynbos (Pierce 1990) and over ten years in chaparral (Keeley 1987b). Nevertheless, this study should ideally have been repeated over a number of years.

Germination studies should also ideally have used seed up to several years old as this may affect germination.

The large variation in data also limits its value. Especially for seed bank studies, sufficient sampling to reduce variance was prohibitive. The simultaneous use of a number of methods in this instance was useful, with the field experiment in particular giving confidence to the conclusions reached.

Results from the "seed budget" must be viewed with some caution for the above reasons. Also, errors may be compounded when determining numbers of individual seeds or seedlings per m^2 for the study site from limited sampling. Generally, however, it is felt that trends were obvious and that the conclusions reached were relatively well founded.

Many questions still remain concerning the reproductive ecology of *Passerina* and *Phylica*. The exact germination cue of *Passerina* is still not known. Experiments using older seed or seed removed from seed banks may give some clue, as may field experiments. The long term persistence of the seed banks of the species studied is also uncertain, and seed burial experiments should continue for ten or more years. An especially interesting question concerns the sources of losses of seeds before incorporation into the soil seed bank. Predation experiments with constant observation would be required and need especially to consider the role of myrmecochory in *Phylica*. Also uncertain is the fate of seeds lost over the first winter after fire, but not establishing as seedlings. This could be studied in field experiments using known amounts of seeds collected from the soil seed bank, and frequently monitoring the fate of seed and seedlings. Generally little is known about seedling mortality and tagged seedlings could be specifically monitored. Exclosures could be used to determine the effects of herbivory in mature vegetation and after fire. Seedling mortality could also be monitored for several more years, perhaps even until reproductive maturity. The role of density-dependent effects in seedlings and adults of *Passerina* and *Phylica* are also uncertain and competition experiments in the field or nursery would be informative. Pollination biology and pre-dispersal seed predation were also not studied. Other interesting questions include the effects of vegetation age on seed production, seed banks and senescence, and the effects of different fire intensities on seeds at different soil depths.

Germination and seed banks have generally been poorly studied in fynbos and still need further attention. Other species could have different germination cues and different seed bank characteristics. More species need to be studied before any generalizations can be made. The "seed budget" approach was also useful and could be applied to other species.

APPENDIX A: FLUCTUATION OF SOIL TEMPERATURES UNDER THE FYNBOS CANOPY AND IN BARE SOIL AFTER FIRE

Introduction

Diurnal temperature fluctuations were measured in soil under a mature fynbos canopy, and in bare soil after fire. Increased temperature fluctuation in bare soil after fire has been proposed as a method of breaking dormancy of seeds in fire-prone environments. It was thus intended that such an increase be measured for use in germination trials of seeds of *Phylica ericoides* and *Passerina paleacea* (Chapter 2).

Methods

Soil temperatures were measured in adjacent burnt and unburnt areas at the study site (described in Chapters 2, 3 and 4) in dune fynbos. Measurements were made shortly before dawn and at midday on four days in early and mid-winter 1990. Measurements were made at this time of year as it preceded germination of *P. paleacea* and *P. ericoides* following a fire in May 1990. A hand held thermometer was used to read temperatures at 0-1 cm depth and at 3-4 cm depth, and 5 repeats of each measurement were made. In the unburnt site midday readings were made both under the canopy and in open patches between shrubs. All four days on which measurements were made were clear sunny days, thus giving maximum temperature differences between bare and covered soil.

Results

Diurnal temperature fluctuations were higher in the burnt area than under the canopy (Table A). However, open patches in the vegetated area had temperature fluctuations closer to those in the burnt area than those under the canopy (Table A). The fluctuations were larger at 0-1 cm in depth than at 3-4 cm in depth in all cases.

Table A. Average ($\bar{x}\pm sd$) as well as minimum and maximum soil temperatures in mature dune fynbos and in an adjacent unburnt area, pre-dawn and at midday. Five repeat measurements were made at each time and place and at 0-1 cm and 3-4 cm depth on each of four clear days June 1990.

Soil cover	Depth (cm)	Temperature (°C)			
		Pre-dawn average	Midday average	Pre-dawn minimum	Midday maximum
Vegetation (under canopy)	0-1	8±2	15±3	8	20
	3-4	10±2	15±2	9	17
Vegetation (open patch)	0-1		22±6		27
	3-4		18±5		23
Burnt area	0-1	6±3	24±7	5	30
	3-4	9±2	20±7	8	24

APPENDIX B: RECOVERY OF ADULT *PHYLICA ERICOIDES* PLANTS AFTER HARVESTING AT DIFFERENT INTENSITIES

Introduction

The commercial harvesting of wild flowers has become an increasingly important disturbance in fynbos. Much of this industry is concentrated in areas of high species endemism and poor conservation status: thus, many species are threatened (Hall and Veldhuis 1985; Greyling and Davis 1989). However, the industry has grown to involve millions of rands and has become a valuable source of income in what are agriculturally marginal areas (Greyling and Davis 1989). It has been proposed that conservation-minded flower harvesting can in fact be a method of conserving large areas of fynbos (Greyling and Davis 1989). This is because the exclusion of grazing animals and removal of alien vegetation are in the flower pickers interest, as is the long-term interest of conserving valuable harvested species. The problems that threaten this ideal are often of a sociological or political nature, but a lack of understanding of the ecological effects of flower harvesting is also a major problem.

Harvesting damages plants directly and also reduces seed input into seed banks. This seed is then no longer available for regeneration, especially after recurrent fynbos fires. Clearly a proportion of flowers must be left unharvested if populations of harvested plants are not to be severely depleted. Many differences in opinion exist, however, as to the intensity and frequency at which conservation-minded harvesting of different species should occur. While flower pickers each seem to have their own ideas, little concrete evidence exists, especially in the literature. Some research undertaken to address other problems has, however, been useful for providing guidelines. This is mostly limited to the Proteaceae. Harvesting of the small, ericoid "greens" is particularly poorly understood (Greyling and Davis 1989).

Phylica ericoides (hereafter referred to by its generic name) is a small-leaved (ericoid) shrub species which is commonly harvested. It is 0.15 m to 0.9 m high and has small (approximately 10 cm diameter) compound white flowers. It occurs in dunes and lower slopes from the Cape Penninsula to Port Elizabeth (Bond and Goldblatt 1984). Different flower pickers harvest *Phylica* at a variety of intensities. To resolve conflicts in opinion, the effects of harvesting this species were studied.

Aspects of the seed biology of *Phylica* were also studied (Chapter 3), and thus an understanding was also gained of the consequences of a reduction of seed input from harvesting. In these studies *Phylica* was found to have seasonally persistent seed banks. Thus, population replacement was not expected to be threatened by a fire in the year following very intensive harvesting, even if harvested plants produced no seed in that year. In such circumstances, recruitment of new individuals of this non-sprouting species after fire could occur from seeds stored in the soil. However, high intensity harvesting could damage plants to the extent that they do not recover sufficiently to maintain seed bank levels in subsequent years, should a fire occur at a later date. Thus the recovery of mature *Phylica* plants from harvesting at different intensities was investigated.

Methods

In April 1989, 25 mature *Phylica* plants were selected and different harvesting treatments were randomly assigned to them. Five plants were left unharvested, while five were harvested at each of the following intensities: 25%, 50%, 75% and 100%. The plants selected were of a size commonly harvested commercially and harvesting was at the usual time of year. Branch sizes cut were also similar to those used in commercial picking (40-50 cm). The *Phylica* plants were in 25-30 year old Dune Asteraceous Fynbos (Cowling *et al* 1988) on the farm Groot Hagelkraal (34°40'S, 19°30'E), 45 km west of Cape Agulhas. Flower numbers were counted before and after harvesting. The harvesting intensities refer to the percentage reduction in the numbers of flowers. One year later (in April 1990) the flower numbers were again counted, and increases and decreases relative to pre- and post-harvest numbers were noted. General observations of the recovery of plants from harvesting were also made.

Results

For all harvesting intensities flower numbers increased from the numbers remaining after harvesting, to those counted the following year (Table B1). The factor of increase was higher for higher harvesting intensities (Table B1). This indicated that harvested plants had additional resources available for flower production on remaining unharvested branches. No regrowth occurred from any of the cut branches. Thus, the one exception was that plants harvested at 100% did not recover at all. Casual observations indicated that plants harvested at 50% and 75% had more multiple arrangements of flower heads on branches than unharvested plants, which usually had only one or two flower heads per branch.

When comparing flower numbers originally present before harvesting to those counted the following year (Table B2), varied results were obtained. Unharvested plants showed a total increase, while those harvested at 25% and 50% appeared to have recovered to approximately the same number of flowers as those counted before harvesting. Harvesting at 75% led to a large overall decrease in flower numbers, while 100% harvesting appeared to kill the plants.

Discussion

Harvesting of plants appeared to leave additional resources for flower production on remaining branches, thus facilitating plant recovery. However, harvesting at more than 50% appeared to cause damage from which plants could not reasonably recover in one year. It also seemed that harvesting at even moderate intensity (e.g. 25%) for a few years in succession would rapidly reduce the number of larger branches, severely restricting the canopy. This was because no regrowth occurred from harvested branches and the length of harvested branches was several times longer than the yearly growth of new shoots (apparent from node to node measurements). Harvesting at 100% appeared to kill plants, with no regrowth observed. Younger plants may have more potential for resprouting from cut branches after harvesting or the harvested plants may resprout in subsequent years, but this is probably unlikely. General observations of

Phylica plants harvested commercially in previous years also showed no regrowth from cut branches.

The low numbers of replicates, the relatively crude estimates of flower numbers, and the lack of statistical analyses are recognized as weaknesses in this study. The suitability of flower numbers as a measure of plant recovery may also be questioned. It is thought, however, that these weaknesses are offset by the rapid easy nature of this experiment. Such studies could easily be carried out for various species by users of the land. General trends were readily observed and may readily be applied to harvesting practice. Ultimately only the vigilance of the flower pickers themselves may avert the destruction of many plant populations.

Recommendations

Given the above results, general observations in the field, and some intuition, the following recommendations can be made for conservation-minded harvesting of *Phylica ericoides*.

The harvesting intensity should never exceed 50%. If harvesting is at this level, then it should be followed by a number of years of non-harvesting so that plants may recover. The length of this period can only be judged by year to year field observations, but is likely to be at least five years. If harvesting occurs more often, then it seems that the intensity should be kept as low as 25%. Harvesting of the same plants in consecutive years is not recommended.

It is also recommended that harvesting should not occur for a number of years after fire, until plants have been reproductively mature for several years. This is to allow seed banks to accumulate as they were found to be persistent and larger than seed input in one year (Chapter 3, Chapter 4).

Table B1. Flower numbers ($\bar{x}\pm sd$) immediately after harvesting at different intensities, and again one year later. The factor by which flower numbers increased is also given ($\bar{x}\pm sd$). *n*=5.

Harvest intensity (%)	Number of flowers		B/A
	Immediately after harvest (A)	One year after harvest (B)	
0	700±310	850±335	1.25±0.15
25	960±251	1340±250	1.42±0.14
50	590±303	1060±546	1.91±0.44
75	330±91	660±114	2.08±0.45
100	0	0	-

Table B2. Flower numbers ($\bar{x}$±sd) before harvesting at different intensities, and again one year later. The factor by which flower numbers increased is given ($\bar{x}$±sd). *n*=5.

Harvest intensity (%)	Number of flowers		B/A
	Before harvest (A)	One year after harvest (B)	
0	700±310	850±335	1.25±0.15
25	1280±335	1340±250	1.07±0.11
50	1180±605	1060±546	0.95±0.22
75	1320±363	660±114	0.52±0.11
100	1080±322	0	-

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