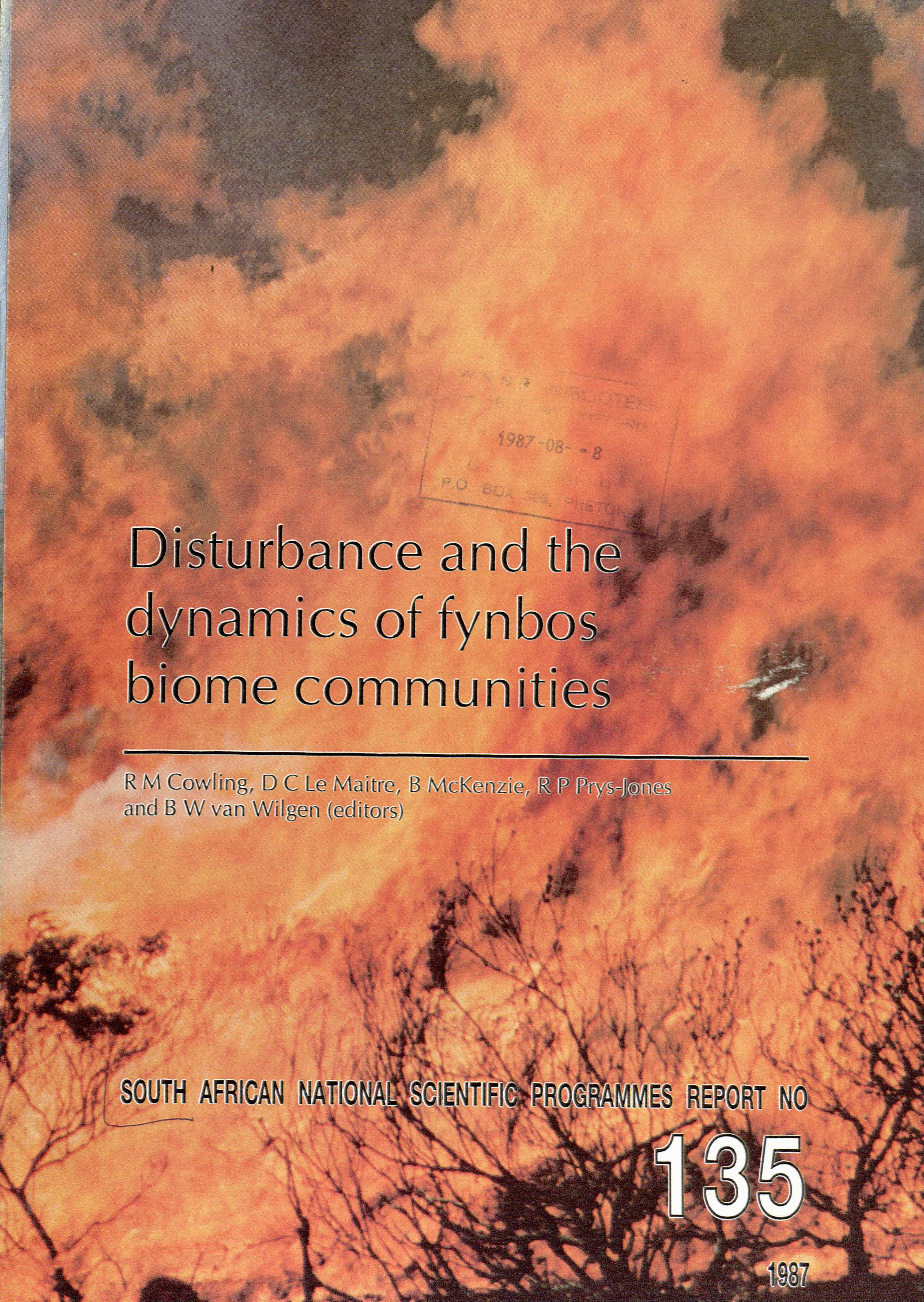

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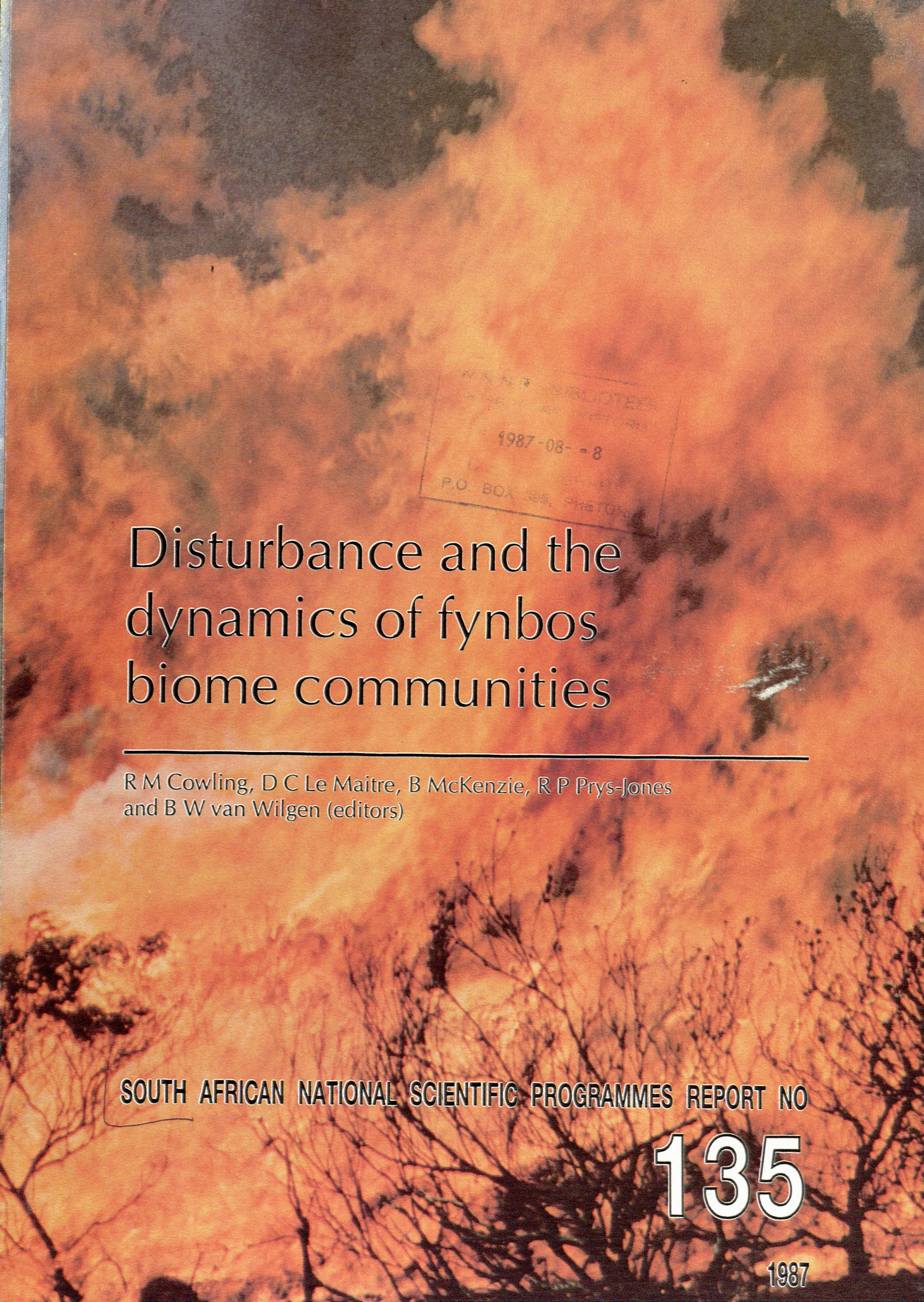

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PREFACE

The Fynbos Biome Project is a cooperative research programme administered and coordinated within the CSIR's National Programme for Ecosystem Research. Since the initiation of the Fynbos Biome Project in 1977, there has been a substantial growth in knowledge on the structure and functioning of fynbos biome communities.

An important component of the National Programme is the communication of research results through meetings, reviews and syntheses. This volume comprises papers selected from the eighth annual research meeting of the Fynbos Biome Project, held at the University of Cape Town in June 1986. It forms part of a continuing process of rapid and effective dissemination of information on Fynbos Biome Project activities to students and researchers.

ACKNOWLEDGEMENTS

The production of this volume would not have been possible without the enthusiastic support of the fynbos biome research community. We thank especially those who participated in the review workshop held after the eighth annual research meeting of the Fynbos Biome Project. Tisha Greyling in Cape Town and Lynette van Niekerk in Pretoria are thanked for efficient liaison and back-up support.

ABSTRACT

This volume comprises invited review and research papers dealing with the effects of disturbance on the dynamics of fynbos biome communities. Since fire is the most important disturbance factor in the biome, most contributions concentrate exclusively on fire regime effects. The chapters include contributions on fire regimes, life history strategies, canopy- and soil-stored seed bank dynamics, small mammal community dynamics and ecosystem nutrient dynamics. Most chapters address the effect of fire on population level processes and discuss the implications of these for community patterns.

SAMEVATTING

Hierdie volume bevat navorsingsreferate wat op uitnodiging aangebied is en wat handel oor die uitwerking van versteuring op die dinamika van gemeenskappe in die fynbosbioom. Aangesien vuur die belangrikste versteuringsfaktor in die bioom is, fokus meeste bydraes uitsluitlik op die uitwerking van vuur. Die hoofstukke sluit in bydraes oor vuurregimes, strategie van lewensgeskiedenis, saadbankdinamika, gemeenskapsdinamika van klein soogdiere en voedingstofdinamika. Meeste hoofstukke kyk na die uitwerking van vuur op bevolkingsvlakprosesse en bespreek die implikasies hiervan vir gemeenskapspatrone.

1. INTRODUCTION

R M Cowling, University of Cape Town

Disturbance is generally viewed as an event which causes abrupt changes in the structure of a community, displacing it from equilibrial conditions (White 1979; Bazzas 1983; Sousa 1984; Pickett and White 1985). However, it is now widely accepted that in many cases stable equilibrial models of communities are inappropriate (Chesson and Chase 1986). In this context, disturbance is best viewed as an event, extrinsic or intrinsic, which results in the removal of biomass or individuals that directly or indirectly create opportunities for the establishment of new individuals (Sousa 1984). Thus the disturbance regime and community structure and dynamics are inextricably linked. Indeed, the disturbance regime is often a major selective force determining the population structure of communities (Bazzaz 1983; Denslow 1985).

In the fynbos biome, over the last few years, there has been a shift from descriptive studies to research programmes which seek to interpret and predict the responses of communities to disturbances, particularly fire. Much of this research has involved the study of population level processes aimed at explaining and predicting community level patterns. Some of these studies (eg Bond 1984; Bond and Slingsby 1984) have made a large impact on mediterranean ecosystem ecologists and provided a new paradigm for studying dynamics of Southern Hemisphere mediterranean heathlands (Lamont 1985). It was therefore timely to consolidate ten years of research since the inception of the Fynbos Biome Project, into a symposium entitled "Disturbance and the dynamics of fynbos biome communities". The symposium, which formed the eighth annual research meeting of the Fynbos Biome Project, was held on 26 and 27 June 1986 at the University of Cape Town. This volume comprises a selection of papers presented at the symposium and is aimed at providing undergraduate and early postgraduate ecology students with a summary of research results and questions which may stimulate them to explore further. Two of the papers sitable for inclusion will be published elsewhere (Cowling 1987; Brits in press). The contributions are uneven in that some are reviews (Chapters 2, 3, 4 and 7) while others report on mostly unpublished data (Chapter 5 and 6). Even the review articles expose many large gaps in our knowledge and make no claim at being comprehensive.

With the exception of Chile, fire is the major disturbance factor in all mediterranean ecosystems (Keeley 1986) and is one of the most important selective agents in the evolution of life history traits (Naveh 1975; Gill 1981; Mooney and Hobbs 1986; Cowling 1987). Studies on fire regime effects go beyond the academic since fire regime is readily manipulated to achieve management objectives (Mooney and Conrad 1977; Ford 1985; Grubb and Hopkins 1986). Indeed, one of the major challenges facing ecologists in mediterranean regions, as highlighted at the Fourth International Conference on Mediterranean Ecosystems held in Perth during August 1984 (Dell 1984; Dell et al 1986), is to determine the resilience of populations to varying components of the fire regime. Studies of this sort are urgently required in the species-rich communities of mediterranean south-western Australia and the Cape (Kruger 1983; Lamont 1985; Grubb and Hopkins 1986). It is therefore not surprising that all of the contributors to this volume have concentrated on fire as the major disturbance factor in fynbos biome communities.

In reviewing fire regimes in the fynbos biome, van Wilgen (Chapter 2) provides the setting for subsequent chapters. He discusses data from the Groot Swartberg which indicate that although summer and autumn fires are most common, fires can occur at any time of the year. This certainly has profound consequences for species vulnerable to local extinction as a result of "out of season" spring and winter fires (Bond et al 1984). In Chapter 3, Manders and Cunliffe provide a brief overview of fynbos plant life histories and population processes in relation to fire. Many fynbos species, particularly nonsprouters with canopy-stored seed, show dramatic fluctuations in population size under different fire regimes (Le Maitre Chapter 4). This fire-induced population instability could result in clouds of species abundance moving across the landscape and directly affecting species coexistence (Grubb 1986) and lineage turnover (Cowling 1987). Variable post-fire recruitment is probably also common in the Australian kwongan (eg Cowling and Lamont in press) but less so in the sprouter dominated shrublands of the other mediterranean regions (Keeley 1986). Pierce (Chapter 5) presents preliminary data on the dynamics of soil-stored seed banks of fynbos nonsprouters in relation to fire and bushcutting. Plants with these characteristics are overall the most important in terms of species numbers and biomass in the fynbos biome, and also comparable to the nonsprouting chaparral species studied by Keeley (1986). An understanding of the extent to which these species are dependent on seed banks for post-fire recruitment and the extent of annual fluctuations in seed bank size, will provide some predictive insights into post-fire recruitment patterns. Moving to vertebrates, Breytenbach (Chapter 6) presents fascinating data on the post-fire dynamics of small mammal populations and communities. As granivores, many rodent species play an important role in determining fynbos community structure (Bond 1984; Breytenbach 1984). Finally, Mitchell (Chapter 7) provides a brief overview of fynbos ecosystem nutrient dynamics in relation to fire. Along with fire, low levels of all major nutrients are an important determinant of fynbos structure and functioning (Kruger et al 1983). It is therefore important to determine the impact on nutrient cycling of fire and other disturbances such as flower and fruit harvesting, agricultural fertilizers and other pollutants which may increase or deplete nutrient pools. Studies addressing some of these problems are currently in progress.

There are many issues which this volume does not address. Major flaws are that disturbances other than fire (eg bushcutting, cultivation, flower harvesting, grazing, quarrying, road building) are hardly considered and that almost all chapters focus exclusively on fynbos vegetation. Since the early studies of Levyns (1929, 1935) there has been almost no research on disturbance and dynamics of renosterveld. An understanding of community responses to fire and grazing regimes could be important in improving the quality of renosterveld range and thus provide some material argument against its wholesale replacement by cultivation (Cowling et al 1986). On a more academic note it would be interesting to contrast fire resilience strategies of renosterveld shrubs with fynbos ones. Whereas most fynbos shrubs are poorly dispersed and therefore show 'in situ' resilience, many renosterveld shrubs are well dispersed and are resilient 'by migration' (sensu Grubb and Hopkins 1986).

In even greater contrast to fynbos shrubs are the large-leaved sclerophyllous shrubs of the subtropical thickets confined to fire-protected and nutrient-rich patches throughout the biome. In many respects thicket species such as *Cassine maritima*, *Euclea racemosa*, *Olea exasperata* and *Sideroxylen inerme* are similar to the obligate sprouters (eg *Cerocarpus betuloides*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Rhamnus* species) described by Keeley (1986). Both groups of species are non-sprouters; produce bird-dispersed fleshy fruits (or other structure suitable for long-distance dispersal); have no seed banks; lack fire-stimulated recruitment; increase in dominance in the absence of fire; and occupy locally moist sites within their ranges. In the fynbos biome these species will, in the absence of fire, coalesce to form thickets or low forests which are not fire-prone. In these communities disturbance and dynamic processes are more akin to tropical rainforests than mediterranean shrublands (Cowling 1984). Only recently have some aspects of the biology of these species been studied in any detail (Siegfried and Knight 1986).

There is generally little attempt by fynbos biome community ecologists to test and refine models of community structure. A potentially rewarding area, both in terms of theory and opportunities for experimental research is the study of the factors promoting coexistence in species-rich fynbos communities. To what extent does variable post-fire recruitment in response to a stochastically variable fire regime (and/or variable reproductive output) minimize interference competition between trophically equivalent species (Schmida and Ellner 1984) and thus facilitate their coexistence (Denslow 1985; Chesson 1986). As suggested by Grubb (1986) experimental studies are needed to test for interference effects between and among sparse and common species, from the immediate post-fire period until population senescence.

Finally the interactions between disturbance regime and speciation needs to be addressed. Cowling (1987) presents a simple model which attempts to place fire-induced local extinction of fynbos species in the context of allopatric speciation. To unravel the complex web of interactions involving fire, life histories, breeding systems, population dynamics, population genetics and speciation, is an awesome but exciting challenge for fynbos biome biologists.

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2. FIRE REGIMES IN THE FYNBOS BIOME

B W van Wilgen, Jonkershoek Forestry Research Centre

INTRODUCTION

Fire is the most important disturbance factor in fynbos ecosystems. The term fire regime traditionally refers to the combination of the elements of fire frequency, fire season and fire intensity prevalent at any given site (Gill 1974). It is necessary to quantify the current regime to provide the background necessary to discuss the effects of this regime on the ecology of the area. Few areas in the fynbos biome have good fire records. and it is almost impossible to construct the historic (or pre-historic) fire regime in the biome. However, a number of factors will point to the most likely fire regime in an area. The occurrence of fires can be deduced from features of the climate and fuels, and from a knowledge of sources of ignition. Furthermore, a study of the responses of plants and animals to elements of the fire regime will help to clarify the fire regime under which they evolved. Natural fires are caused by lightning and rolling rocks. Over and above this, man has occupied the fynbos biome, and has been using fire, for the past 125 000 years (Deacon et al 1983). The last interglacial period has lasted for 10 000 years. Any major changes to the fire regime over the past 10 000 years would have resulted from the activities of increasing human populations, particularly increases in the sources of ignition.

CLIMATE

The climate over large areas of the western fynbos biome is mediterranean, with dry, warm summers and cold, wet winters. In the east, rainfall is more evenly distributed throughout the year. The eastern inland regions have high evapotranspiration in summer, and this effectively induces a winter rainfall regime (van Wilgen 1984). Fires in western and inland eastern areas will therefore tend to be concentrated in summer. The south-eastern coastal areas experience relatively even average climate in terms of fire danger, and fires will occur during relatively rare suitable conditions, which can occur in summer or winter.

VARIATION IN VEGETATION (FUEL) IN THE FYNBOS BIOME

The vegetation of the fynbos biome is heterogenous, and the variation in vegetation structure is extreme. However, a number of broad categories of vegetation may be recognized (Moll et al 1984).

Forest

This occurs in local, usually small but sometimes extensive, patches. Not usually a fire-prone vegetation type but may burn under extreme weather conditions.

Dry or mesic mountain fynbos

This is the vegetation type for which most fuel-related data are available. Available fuel amounts to some 50 to 100% of the aboveground biomass (van Wilgen et al 1985). Stands with post-fire ages of less than four years do not normally have enough fuel to support a fire, while large amounts of litter accumulate in old stands, and fires are usually possible under even mild climatic conditions in older vegetation (van Wilgen 1982).

Wet mountain fynbos

This vegetation type is characteristic of southern coastal mountain ranges. It has a relatively high biomass and apparently less litter than the previous type (personal observation). Fires do not burn as easily as in the drier fynbos types under moderate climatic conditions, but fire intensities can be high under suitable weather conditions.

Coastal fynbos

Some litter and biomass data are available only for the Pella research site (Mitchell et al 1987). This vegetation type is apparently structurally similar to dry or mesic mountain fynbos.

Renosterveld

No data on the fuel properties of this vegetation type are available. Renosterveld contributes only a very small proportion of the remaining natural vegetation in the fynbos biome, and is therefore not currently important in landscape-level fire patterns, although it would have been in historic times.

Strandveld

This vegetation type is likely to carry fires less often than fynbos because of lower fuel loads, sparse canopy and relatively many succulents (Kruger and Bigalke 1984).

BIOMASS ACCUMULATION AND FUEL DYNAMICS

Available data for dry and mesic mountain fynbos show that, while biomass accumulates steadily with post fire age, the variations in final biomass attained can be quite great. For example, biomass in mature 12 to 20 year old fynbos can vary from 500 to 5 000 gm^{-2} (Kruger 1977; van Wilgen 1982; van Wilgen and Kruger 1985). Decomposition studies have shown that litter decomposes slowly in fynbos (Mitchell et al 1987). Given a constant input of litter, litter mass would accumulate with post-fire age and a steady state between input and decomposition would probably never be reached. Another important factor in litter dynamics that has not been quantified is the effect of termites. Termites are common in many mountain fynbos areas (personal observation), and probably have a considerable impact on litter loads.

If senescence occurs at about 30 years post-fire age, litter input from shrubs ceases although litter mass increases as a result of the contribution of dead plants (van Wilgen 1982). As litter accumulates with increasing stand age, the probability of fire increases (Kruger and Bigalke 1984). Very few fynbos stands survive for periods of longer than 40 years without fire. Due to low decomposition rates, nutrients tied up in litter are released during fires, and plants can be expected to have features which will allow maximum use of post-fire increases in nutrients rather than to be dependent on constant nutrient release by decomposition between fires. Such features, should they be found, would support the hypothesis that component species in fynbos vegetation have evolved with periodic fire as a disturbance.

FIRE FREQUENCY

Fynbos communities will seldom burn, until about four years after the last fire (Kruger 1977). At the other end of the scale, most fires probably occur before 40 years. The interval between fires is relatively long when compared to, for example, grassland, where annual fires are possible. The explanation for the relatively long interval must be sought in differences in the fuel dynamics, climate and sources of ignition between these biomes. Fire frequency depends on (a) fuel being available, (b) sources of ignition, and (c) the weather conditions that coincide with both of these. Each of these are considered below:

(a) Fynbos fuels are relatively course when compared to other fuel types (eg grasslands) (Kruger and Bigalke 1984), and this probably makes them proportionally more difficult to ignite under similar weather conditions. Fuel (particularly dead material) increases with vegetation age, thereby increasing the probability that a source of ignition will cause a fire. Rates of spread can be similar in both young and old fynbos, so that post-fire age does not affect fire size (personal observation).

(b) Data on the frequency of occurrence of sources of ignition in the fynbos biome are scant. Lightning flash densities are lower than in other parts of southern Africa (Edwards 1984). A low incidence of sources of ignition would further explain the relatively long average period between fires in fynbos.

(c) Sources of ignition must occur together with sufficient fuel and suitable weather conditions to result in a spreading fire. Once a fire has started, it can spread at average daily rates of around 0,01 to 0,07 ms^{-1} over large areas (van Wilgen 1985). The longer a fire burns, the higher the chances of the weather changing and thus extinguishing the fire. Long (greater than one week) spells of extreme fire weather occur about once every four years on average (van Wilgen 1985). Fires which occur together with such long periods of high fire danger rarely exceed 35 000 ha in extent.

Studies on the life histories of plants support the hypothesis that fynbos is adapted to fire intervals of between 10 and 30 years. Juvenile periods in fynbos plants do not usually exceed eight years, and where they do, they usually occur in plant species that can escape fires in some way or another (Kruger and Bigalke 1984). Studies on various fynbos species (eg *Staavia dodii*, *Orothamnus zeyheri* and various *Protea* species) have indicated that fire frequencies of about 15 years will ensure survival of these species without undue attrition of populations (Bond 1980; Boucher 1981; Moll and Gubb 1981). Where fire is excluded for more than 30 years, senescence occurs in some *Protea* species, and seed stores become depleted. Poor regeneration may follow such long intervals between fires (Bond 1980), and *Protea* populations can be expected to become seriously depeleted should the interval between fires exceed about 40 years.

FIRE SEASON

Fire season is determined largely by climatic factors and by seasonal variations in fuel properties. For example, seasonal curing of grassland vegetation means that fires can occur readily in winter when grasses are cured but not in summer when they are green. Seasonal curing is not a feature of fynbos vegetation and fire season therefore depends largely on climatic factors.

Several breakdowns of the seasonal occurrence of fires in the fynbos biome show similar trends (Horne 1981; van Wilgen 1981; Kruger and Bigalke 1984). Fires occur mainly in the summer months, but nonetheless do occur in all months of the year (Figure 2.1).

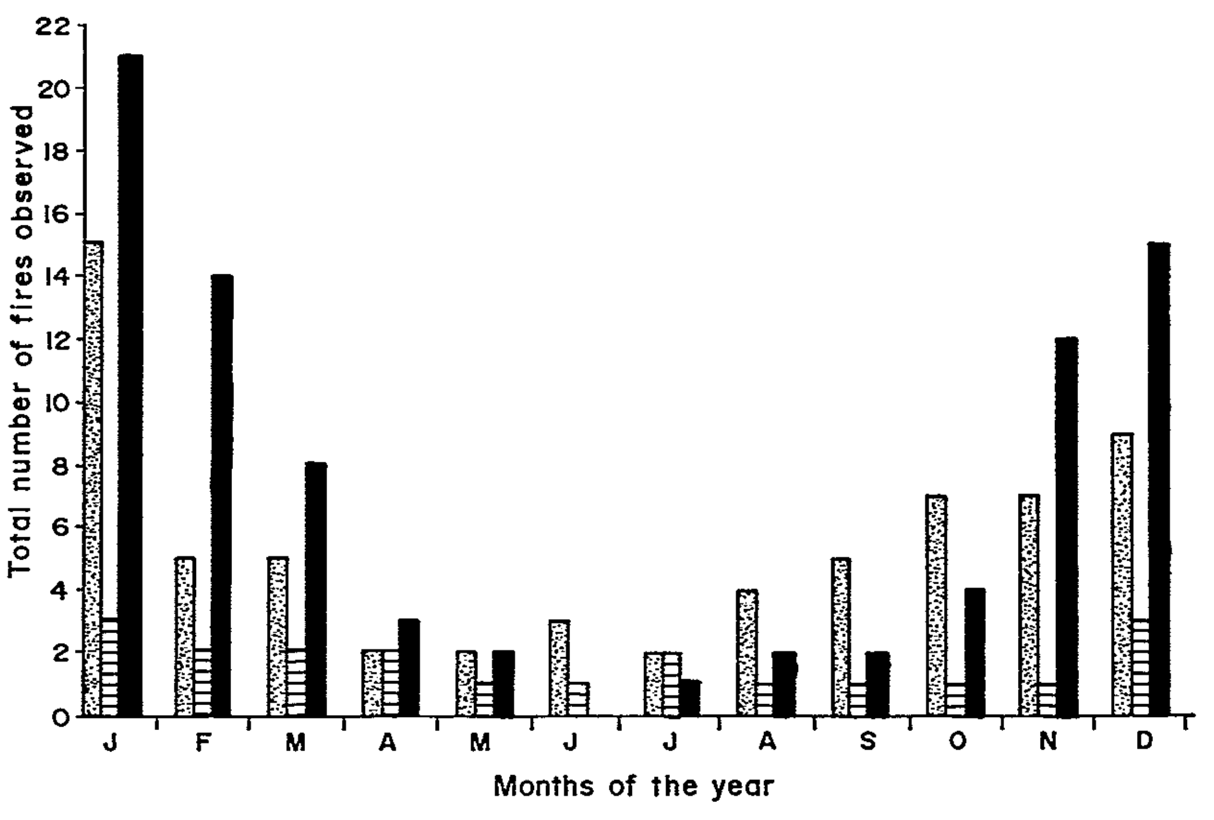

FIGURE 2.1 A typical example of the seasonal distribution of fires in the fynbos biome. This example, from Horne (1981), shows data for fires from the Groot Swartberg from 1951 to 1977. The bars represent fires of different origin (natural = solid bars, unknown = stippled, human = striped).

Van Wilgen (1984) divided the fynbos biome into inland and coastal zones with regard to the seasonality of conditions that will lead to fires. This analysis was done using a fire danger rating system together with climate records from 40 stations in the fynbos biome. There is a clear cycle of high fire danger in summer and low fire danger in winter in the inland regions, which explains why most fires occur in the summer months. In coastal regions fluctuations in the mean fire danger from month to month are not marked. Van Wilgen (1985) argued that mean monthly fire danger levels above a certain magnitude could be used to delimit the duration of the fire season. On the basis of the analysis of fire climate at 40 stations mentioned above, the mean duration of the fire season at 14 coastal stations was 2,5 months, while at 26 inland stations the mean duration of the fire season was 5,4 months (van Wilgen 1985). The length of the fire season increases from south to north and from coastal to inland regions. Changes in fire season will probably have more effect on the biota where the fire season is short and clearly defined than in areas where long or unclearly defined fire seasons are prevalent.

Several biological indicators also point to the summer as the dominant fire season. The Proteaceae show maximum seedling recruitment after late summer and early autumn fires (Bond et al 1984; van Wilgen and Viviers 1985), as does *Widdringtonia cedarbergensis* (Manders 1985). General patterns of phenology, flowering and seed set indicate that maximum flowering activity occurs in late winter and spring (Kruger 1981). This implies that the maximum seed loads will be available in late summer and early autumn. Examples from the fauna include the geometric tortoise (*Psammobates geometricus*), a fynbos endemic reptile. The eggs, which are laid in spring, have a peak hatching period in April-May. Fires after the hatching period would destroy both adults and young, but fires in February or March would facilitate survival of the population (Greig 1982). Spring burning would also affect fynbos birds. Winterbottom (1968) found that the main breeding period in the Hottentots-Holland mountains was in four months from July to October, with 68% of all nests recorded during that period. For the four-month period December to March only four per cent of nests were recorded. Although the timing of bird breeding is probably a response to seasonality in food availability rather than to season of infrequent fires, spring burns will nonetheless cause a setback to breeding bird populations.

FIRE INTENSITY

Although fire intensity is an element of the fire regime, it is difficult to quantify and to interpret (Alexander 1982), and is consequently poorly understood. There are very few data on the intensity of fynbos fires. Available data indicate that fynbos fires can vary in intensity from 200 to 20 000 kW m^{-1} (Bands 1977; van Wilgen et al 1985). Natural or uncontrolled fires, which burn the largest areas under warm and dry conditions, will tend to be high intensity fires. Prescribed fires are burnt under less extreme conditions, and are therefore less intense. With more prescribed burns, the average intensity of fires will drop.

Le Maitre (1986) has shown that fire intensity affects the survival of fynbos sprouting plants. A shift in fire intensity over a number of fire cycles may influence the balance between seeding and sprouting plants.

Changes in fire intensity will change the heat pulse into the soil. For example, soil temperatures during fires in fynbos were much lower than those recorded in higher intensity fires in areas invaded by *Acacia cyclops* (van Wilgen and Holmes 1986). This may have an effect on soil-stored seed banks.

FIRE SIZE

The size of fires will have an influence on the patch dynamics of fynbos landscapes. Very little is known about this aspect of fire ecology. An analysis of the fire history of the Cederberg between 1900 and 1984 (Department of Environment Affairs, Forestry Branch unpublished data) shows that there were a great number of small fires and a few large ones. Fifty-seven per cent of the fires were less than 100 ha in extent, while 82% were less than 1 000 ha. However, fires of greater than 1 000 ha accounted for 90% of the area burnt. It is possible that in precolonial times, large fires would have been more common. Large fires still occur, but the average size of fires may be getting smaller with prescribed burning. The impacts of this are not known.

CONCLUSIONS

Pickett and White (1985) define several descriptors of disturbance regimes. Values for these descriptors for fire in fynbos are presented in Table 2.1.

TABLE 2.1 Definitions of disturbance regime descriptors (after Pickett and White 1985) and their possible values for fire as a disturbance in fynbos ecosystems. The values given are for a hypothetical study area of 50 000 ha of mountain fynbos

Descriptor and definition	Value in fynbos
Distribution (spatial distribution, including relationship to geographic, environmental and community gradients).	No data
Frequency (mean number of events per time period).	1/6 - 1/40 yr
Return interval (the inverse of frequency).	6 - 40 yr
Rotation period (mean time needed to disturb an area equal to the study area).	15 yr
Predictability (a scaled inverse function of variance in the return interval).	No data
Area or size (area per event).	1 - 50 000 ha mean = 1 000 ha?
Magnitude	
(i) Intensity (physical force of the event per area per time).	200 - 20 000 $kW\ m^{-1}$
(ii) Severity (impact on the organism, community or ecosystem).	20 - 90% of biomass consumed
Synergism (effects on the occurrence of other disturbances).	No data

TABLE 2.2 A hypothetical fire regime in the fynbos biome 2 000 yr BP compared to the current situation

Component	2 000 yr ago	Present
Fire frequency	6 - 40 years at random Mean = 20 yr?	6 - 30 years at random Mean = 15 yr?
Fire season	Predominantly late summer	Predominantly autumn, some spring and late summer
Fire intensity	Mainly high	Some high, some moderate
Fire size	Many small fires Some large fires	Many medium sized fires Fewer large fires

The fire regime at any given site is never fixed and fires occur at varying intervals, in varying seasons and at different intensities. Each fire is therefore unique and its effects will depend on both its own parameters and the nature of fires that preceeded it. Nonetheless, there has probably been a shift in the mean fire regime. It may be useful to compare the current mean fire regime with a hypothetical mean fire regime in fynbos 2 000 years ago (Table 2.2). The mean fire frequency has probably increased from once in 20 to once in 15 years due to increasing human sources of ignition. The fire season may have shifted from predominantly late summer to predominantly autumn, with some spring and summer burns, again mainly due to the activities of man. Fire intensity would have decreased on average due to both the more moderate weather conditions under which fires are conducted, and lower fuel loads due to more frequent burning. There are probably also fewer very large fires.

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3. FYNBOS PLANT LIFE HISTORIES, POPULATION DYNAMICS AND SPECIES INTERACTIONS IN RELATION TO FIRE: AN OVERVIEW

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INTRODUCTION

Fynbos is noted for its diversity, some 8 500 species occurring within the Cape Floral Region (Bond and Goldblatt 1984). The reasons put forward for this diversity include environmental diversity and diverse disturbance regimes (Kruger 1979). Fire is the predominant disturbance in fynbos communities (Kruger 1979), and the major selective agent (Cowling 1987). Features of the fire regime, which are usually proposed as important with respect to plant responses, and which may vary between fires, are frequency, season and intensity. In communities with long fire-free intervals such as forest and thicket communities, there is selection for high resource allocation to structural growth and maintenance. In communities experiencing shorter intervals between fires, selection favours reduced juvenile periods, high resource allocation to reproduction and early senescence (Cowling 1987). A fourth parameter of the fire regime, the size of the burn, is important in population studies. Aspects affected by fire size include the "edge effect" of rodent seed predators and the rates of recovery through immigration of populations of groups such as pollinators and herbivores, and also of plant populations which have become locally extinct after the fire.

The variability of the fire regime contributes to the species richness of the fynbos by creating numerous transient niches. A model has been proposed by Cowling (1987) wherein the high numbers of species in fynbos and Australian kwongan is ascribed to population fragmentation as a result of fire, promoting vicariant speciation. Other forms of disturbance, such as those formed by biotic interactions, may also be important in determining community composition.

LIFE HISTORY

A plant's life history consists of all the stages through which it passes between fertilization and death. These components of the life cycle constitute a life history strategy, implying a set of adaptive responses accumulated over evolutionary time (Wilbur et al 1974). As a whole, the life history of a plant is the means whereby reproductive output and the successful establishment of progeny is directly or indirectly maximized. Post-fire succession in fynbos is more a gradual elimination of individuals present at the outset than a replacement of initial species by new colonizing species (Gill and Groves 1981). It follows that all species must have life histories enabling persistence through fire in some form.

Fertilization

Fertilization is the most dynamic of all life history phases. Mortality of gametes may be several orders of magnitude greater than mortality in other phases, and there may be extensive variations in the success of fertilization.

The genetic composition of a population is affected by the mating pattern of its individuals. Some plants are self compatible and self fertilization (autogamy) may occur. In most cases this increases seed set (Lloyd 1980). With cross fertilization seed set may be lower, but the progeny are qualitatively superior in a genetic sense. This is not necessarily due to increased genetic variation, but rather to heterosis - where two different alleles produce favourable effects not duplicated by the two identical alleles in each of the homozygotes (Lloyd 1980).

Fertilization is not generally related to the disturbance regime, but mating systems can affect comparisons based on other strategies. Lamont (1985) for example, found *Leucospermum cuneiforme*, a widespread, "successful" species, to be self compatible.

Seed production

The phenology of seed production is important where the seasonal occurrence of fire is predictable (Pierce 1984). Seed production may be dependent on the occurrence of fire. Certain geophytes, notably the so-called fire lilies (eg *Cyrtanthus angustifolius)* produce seed only in the first few weeks after fire (Levyns 1966).

Other species, such as *Watsonia pyramidata* exhibit mass flowering after a fire, particularly after summer and autumn burns. Seedling recruitment appears to occur only after high levels of flowering in this season (Le Maitre 1984).

Seed size and number

The number of seeds produced varies considerably. In general, there is a trade-off, related to the physical environment, between either small numbers of large seeds or large numbers of small seed. There is also an increased probability of successful germination and seedling survival with larger seeds (Solbrig 1980). Fynbos communities contain a wide range of seed sizes and also of numbers of seeds. There are few studies on this trade-off, both in the fynbos and elsewhere.

Seed production in general is considered to be limited by resources. If this holds true, then low seed set is likely to be the result of abortion to adjust the clutch size resource levels, a tactic particularly useful if the resource level is unpredictable (Willson 1983). Pollination success, therefore, may not explain all the variability seen in seed set.

A knowledge of the size of viable seed banks of a population is essential for predicting post-disturbance recruitment.

Seed dispersal

Seed dispersal has both spatial and temporal components. The temporal aspects for some fynbos species have been covered by Le Maitre (this volume) and Pierce (this volume). Janzen (1970) developed the concept of the population recruitment curve to explain why individuals of the same species are evenly spaced in tropical rainforests. This curve is the function of dispersal distance, seed density and the probability of survival. Combined with the concept of a safe site (sensu Harper et al 1961), several models have been proposed linking population recruitment to dispersal and safe site availability (Hubbell 1980; Green 1983; Geritz et al 1984; Becker et al 1985). None of these models appear to be relevant in the fynbos, where recruitment is confined to post-fire conditions without competition from parent plants.

Dispersal distances in fynbos species are short (Bond 1980; Moll and Gubb 1980; Brits in press; Manders 1986). This limitation has been considered to restrict the seeds to the burnt area where germination and survival are optimal (Midgley 1983), or to keep the seeds in a uniform patch of soil nutrients (Brits 1982). With the dispersal distances reported to date, these areas would have to be, on average, less than a few hundred square meters for this restriction to have an adaptive value.

A more plausible explanation seems to be that there is no need for complex or efficient dispersal systems for seed which will germinate in a post-fire environment lacking competition from parent plants.

Germination and establishment

The reproductive effort of fynbos plants is usually geared for regeneration in the post-fire environment, resulting in even-aged stands. The formation of seed banks, either in the canopy (Le Maitre this volume), or in the soil (Pierce this volume) should be viewed at least partially from the point of the adaptive value of concentrating the reproductive output in the favourable post-fire environment, where potential returns are greatest, and not only as a means of surviving fire.

Fire intensity determines the survival of plants, plant parts and seeds, and the stimulation of seed germination. A reasonably intense fire is necessary to remove the vegetation and litter and create a satisfactory seed bed (Kruger and Bigalke 1984). Litter may prevent germination by forming a physical barrier damping temperature fluctuations, preventing the seeds from imbibing (Brits 1986), or preventing the burial of the seeds and exposing them to granivory (S A Botha personal communication). This is supported by observations on *Mimetes hottentoticus* where a mineral seed bed is required for establishment (Kruger and Lamb 1978). A certain degree of intensity may also be required to volatilize organic compounds which may cause water repellency, or allelopathic germination inhibitors (Kruger and Bigalke 1984). Some hard seeded species, such as the Restionaceae, appear to require intense fires (Kruger and Bigalke 1984), possibly to break some form of mechanical dormancy.

Observations on the regeneration of *Erica* species have revealed that establishment is delayed for at least 12 months after the fire (Adamson 1935; Martin 1966; P T Manders personal observation), by which time the environment has been considerably modified. This has lead to speculation that seeds of this group are short lived, or do not survive the fire, and that seed has to be dispersed into the burnt area from adjacent unburnt vegetation. If so, this is an example where the size of the burnt area could influence the population response quite considerably. An alternate proposal is that special requirements for the initiation of germination may exist, such as the development of mycorrhizal associates (Martin 1966).

Delays in germination until the second autumn after a fire were noted for *Protea repens* at Pella and *P odorata* at Malmesbury (R J Cunliffe personal observation). An understanding of the mechanisms behind these delays could provide considerable predictive insight into recruitment patterns.

Limited regeneration does occur within mature stands, for example in *Protea laurifolia* (P T Manders personal observation), and there is also some regeneration in senescent stands of serotinous species (Bond 1980). If this regeneration is sufficient to achieve replacement levels of a particular species, the population should not be termed senescent.

Germination and establishment are generally observed together. A greater understanding of this phase of the life cycle could be reached by detailed study of germination and the fate of newly-germinated seedlings, rather than by simply counting established plants as done by Bond et al (1984) and Van Wilgen and Viviers (1985).

Growth and maturity

The period of growth and maturity is the least dynamic within the life cycle of a plant. The age of first reproduction is important in population dynamics. When generations overlap, the length of the prereproductive phase will affect the rate at which parental genes enter the gene pool. In most environments there is an advantage in reducing the age of first reproduction, or compensating for a delay in the time of reproductive maturation by an increase in survival and age-related fecundity (Willson 1983). In the fynbos there is little advantage in producing seed soon after a fire if regeneration is not likely to occur until the next fire. This is particularly pertinent in species where seed viability decreases with time, as has been demonstrated in the Proteaceae (Van Staden 1978; Coetzee 1984).

Senescence

Senescence in fynbos is largely confined to those species which are killed by fire, and is probably a consequence of evolution in an environment with a short fire interval (six to 40 years) (Van Wilgen this volume), where prolonged survival will not have an adaptive value.

Reduced post-fire regeneration in both Proteaceae and other dicotyledonous nonsprouting species has been demonstrated in vegetation over 40 years old (Bond 1980). What happens to the community after the reduction in population size or local extinction of these species poses an important question. The present assemblage of species may be a product of an imposed short-interval fire regime, causing the community to appear to senesce with prolonged absence of fire.

LIFE HISTORY STRATEGIES

Plants may either die after fire or resprout from protected buds. Comparisons between sprouting and nonsprouting have received considerable attention and are presented here as an example of fire effects on life history strategies.

Sprouting enables an individual to survive fire, and involves no reproductive or genetic process at all. Nonsprouting species, on the other hand, undergo a reproductive process, providing genotypic variation on which natural selection can act. In contrast, sprouting results in the persistence of an individual's genes within a population. Survival through the fire and the initiation of growth from an established root system affords the individual a competitive advantage over seedlings.

Species which are obligate nonsprouters have a complete turnover in generations with each fire. Wells (1969) points out that nonsprouters are therefore subjected to greater frequency of natural selection, as well as greater selection intensity resulting from competition from sprouters in the seedling phase. Wells supports this argument by demonstrating greater speciation within nonsprouting chaparral species. In South African Proteaceae there is also a predominance of nonsprouters: *Leucadendron* 93%, *Leucospermum* 75%, *Mimetes* 85%, *Protea* 60%, *Sorocephalus* 90%, *Spatalla* 100% and *Vexatorella* 100% (Lamont et al 1985). Seed production in itself has several properties conducive to rapid natural selection (Grime 1979). Seeds are numerous, allowing rapid multiplication, they are independent, providing dispersal potential, and stress tolerant, permitting dormancy as an adaptive trait in some species.

The balance between nonsprouters and sprouters will vary in relation to fire frequency (Kruger 1983). Keeley (1977) proposed a model describing the reasons for changes in the relative abundance of these strategies resulting from short and long intervals between fires. With short intervals, there are fewer dead shrubs and lower fuel loads. Frequent low-intensity fires result in low sprouter mortality thus creating few openings for seedlings. These conditions do not favour nonsprouters. With long fire intervals more fuel accumulates and fires are intense, resulting in greater mortality of sprouters, and therefore more openings for seedlings. These conditions favour nonsprouters. This model was supported by data showing more nonsprouters in those parts of California with lower intensities of lightning fires (Keeley 1977).

In the fynbos biome riverine forests and scree thickets burn least often but almost all species are sprouters, contradicting the above model. Reproductive output in many fynbos nonsprouters declines in populations older than 20 to 40 years. Dwindling seed banks in senescent populations results in low post-fire recruitment (Bond 1980). In the juvenile period before this, insufficient seed is available for population replacement (Kruger and Lamb 1978). After fire in either the juvenile or the senescent phases, increased dominance of sprouters is concomitant with the reduced size of nonsprouter populations.

Sprouters do not necessarily react positively to short intervals between fire, they merely tend to suffer fewer adverse effects than obligate nonsprouters. Zedler et al (1983) studied the effects of a very short (one year) interval burn in a chaparral community. As expected, the nonsprouter *Ceanothus oliganthus*, was most adversely affected. However, there was also a high mortality of sprouters even amongst species with well developed lignotubers.

CONCLUSIONS

While the effects of disturbance are usually detected at community level, studies at the population level are required to gain a predictive understanding of the mechanisms of community dynamics.

Although fire is the major form of disturbance in the fynbos biome, and an obvious management tool, there are other disturbances which require a life history and population approach in order to understand and predict their effects on community structure. Flower harvesting, for example, affects populations directly by causing mortality, and by reducing the size of seed populations. A knowledge of life histories can be used to predict the effects of flower harvesting, and also to determine sustainable yields. Consideration of the impacts of grazing should include those relevant to population dynamics, such as suppression of flowering and depletion of seed banks.

Lamont (1985) warns of the dangers of seeking "all-embracing paradigms" in plant population ecology. It would seem that a knowledge of the complete life history of the species in question, together with an understanding of the processes involved, is needed to develop a predictive ability in management of the species. Studies involving processes should be within a life history framework and conversely, studies of specific attributes should also be considered within the context of the complete life history.

A consistent theme in this discussion has been the importance of the immediate post-fire environment for the occurrence of the most dynamic phases of the plants. Population studies require concentrated efforts to study the processes involved at this stage.

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4. DYNAMICS OF CANOPY-STORED SEED IN RELATION TO FIRE

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INTRODUCTION

Over the last decade there has been increasing recognition that evolution and ecology are inseparable. As Real (1983) states: "Evolutionary processes do not occur outside an environmental context and ecological interactions are not devoid of history". Harper (1977) also emphasizes the fundamental importance of this approach: "Ecology is looking at evolution in action... The study of population biology ought to display those forces that are important at the level of the individual and what sort of variation is important in determining survivorship and reproduction... Biotic forces are more powerful than environmental forces in generating diversity, the environment tends to act on a geographic scale and the biotic factors on a local scale." These quotes set out the framework around which this review is built.

BACKGROUND

Plants with canopy-stored seed (CSS) are defined here as those which have delayed seed release and no persistent seed reserves in the soil (Bond 1980), although successive annual seed crops may not accumulate on the plant. The term serotiny is only used when there is an overlap between successive crops of mature seed on the plant itself so that a seed bank accumulates (Le Maitre 1985a).

Canopy-stored seed in the fynbos biome

Canopy-stored seed is found in many vegetation types around the world and is particularly associated with infertile, shallow, rocky and drought prone soils (Naveh 1974; Bond 1984). CSS and serotiny are common in woody formations where fire is a major disturbance factor (Gill 1981a). In the Northern Hemisphere CSS seems to be restricted to the Coniferae but it is found in many genera in different families in both the Coniferae and Dicotyledonae in Australia (Gill and Groves 1981) and in the fynbos (Table 4.1). In the Dicotyledonae CSS is restricted to taxa with condensed inflorescences or follicles so that seed retention does not involve major morphological modifications. This suggests that phylogenetic and morphological factors are major determinants of the taxonomic distribution of the CSS syndrome.

In the fynbos most CSS taxa are in the Proteaceae (Table 4.1) and this is the only group which has been studied in detail (Lamont et al 1985). This review is largely confined to that family but also refers to data from Australian Proteaceae growing in shrublands analogous to the fynbos.

CSS is particularly common in the Proteaceae in Australian heath and Cape fynbos (Lamont et al 1985). The syndrome appears to be better developed in the Australian Proteaceae where for some species, seed release is fire-dependent (Gill 1976; Wardrop 1983; Lamont and Cowling 1984; Cowling and Lamont 1985a). Seed release in the Cape Proteaceae occurs as soon as the tissues of the persistent, woody inflorescences (cones) dry out (Brits 1982; Bond 1985). The serotinous fynbos Proteaceae rarely retain their cones in a closed condition for longer than three to six years (Williams 1972; Bond 1985), whereas viable seed are retained for longer than 15 years in the cones of south-western Australian *Banksia* species (Cowling et al in press).

TABLE 4.1 Taxa with canopy-stored seed found in the fynbos biome and probable modes of dispersal. Data from Baker and Oliver (1967), Williams (1972), Rourke (1980), Bond and Goldblatt (1984) and herbarium specimens

Taxon	No species	Seed type and mode of dispersal
Proteaceae		
Protea	68	Hairy, wind
Aulax	3	Hairy, wind
Leucadendron	9	Hairy, wind
Leucadendron	37	Winged, wind
Bruniaceae		
Brunia	7	Persistent perianth, wind
Nebelia	6	Persistent perianth, wind
Berzelia	12	Persistent perianth, wind
Asteraceae		
Phaenocoma	1	Sparse pappus, wind
Helipterum	17	Sparse pappus, wind
Cupressaceae		
Widdringtonia	3	Smooth, poor
Ericaceae		
Erica	1	Fine, wind
Mesembryanthemaceae[1]		
eg Ruschia	c.130	Fine, water
Erepsia	c. 40	Fine, water

[1] CSS in this group is probably widespread but little documented other than an account of seed release mechanisms of karroid taxa (Ihlendfeldt 1971).

Fire and the evolution of serotiny in the African Proteaceae

Fire regime has undoubtedly played a major role in the evolution of fynbos plant life cycles (Gill 1975; Cowling 1987). The fire regime in turn is determined directly by the climate and indirectly by the edaphic and climatic controls on the vegetation and the fuel it produces (Walker 1981). Palaeoecological data suggest that the dominant vegetation of the lowlands changed from forest during the Miocene (Coetzee et al 1983; Scholtz 1985) to grassy vegetation with gallery forest during the early Pliocene (Hendey 1983). Only during the late Pleistocene and Holocene did shrublands become dominant (Hendey 1983). The extent to which forest covered the montane areas is not known, but the higher areas would probably have supported shrublands allied to the fynbos montane flora. The onset of a "summer-dry" climate (c 3 my BP) (Deacon 1983a) would have had a significant effect on the plant communities because of the associated changes in fire regime. It is possible that these changes resulted in less frequent, more intense fires than under the warmer summer rainfall Pliocene climate. Promethean man, both as hunter-gatherer and herder, has had a major impact on the current vegetation (Singh et al 1981; Deacon 1983b) particularly through an increase in fire frequency and a change in spatial patterns (Hallam 1985; van Wilgen this volume).

The Proteaceae of the Miocene forests were probably similar to the savanna and (rarely) closed forest genus *Faurea*, not only in floral morphology (Rourke 1973) but also in their ecology, tree-like form and unspecialized, insect-pollinated flowers (Johnson and Briggs 1981). Like *Faurea* they would have occurred in open woodland on the lowlands and probably also in the montane areas (Beard 1958; Rourke 1972). I suggest that they had already diversified into the major generic lineages and seed biology syndromes (Tables 4.2 and 4.3). The lowlands probably experienced a savanna-type fire regime in the grassy woodland vegetation during the Pliocene and Pleistocene (Hendey 1983). The Proteaceae of these woodlands could have resembled modern species such as *Protea nitida* (Haynes 1976) and certain *Banksia* species (Abbott 1985), with CSS but no serotiny, rapid development of a lignotuber and epicormic sprouting. The development of the serotinous inflorescence, and the loss of the ability to sprout, are probably a consequence of changes in fire regime and general selective pressures during the late Pleistocene and Holocene as outlined above.

TABLE 4.2 The generic lineages possibly present in the Proteaceae at the beginning of the Cenozoic era, partly based on Rourke (1984). The initial development of seed biology syndromes (see Table 4.3) is also indicated: CSS = canopy stored seed, SSS = soil stored seed

CSS	Protea: Leucadendron (Protosection Alatosperma?) Aulax Faurea
SSS	Paranomus line - Paranomus, Spatalla, Sorocephalus, Serruria Leucospermum line - Vexatorella, Leucospermum, Diastella, Mimetes, Orothamnus Leucadendron (Protosection Leucadendron?)

TABLE 4.3 Syndromes of seed storage, release and dispersal and seed biology in the southern African Proteaceae. After Jordaan (1944), Brown and van Staden (1973), Brits (1982) and unpublished data

Dormant seed	Nondormant seed
Dispersal	
Seasonal seed release	Seeds retained on parent plant.
Dormant seeds accumulate in the soil.	Seeds accumulate in the old inflorescence of the parent plant.
Restricted dispersal.	Restricted dispersal.
Largely ant dispersed.	Dispersed en masse only after fire.
Seed biology	
2-3 months to mature	More than 3 months to mature

Dormant seed	Months	% Seed set	Nondormant seed	Months	% Seed set
Leucospermum conocarpodendron	3	0-16	Protea repens	7	10-20
Mimetes cucullatus	1,5	0-33	P magnifica	5+	0-4
Serruria fascifolia	2	low	P obtusifolia	7	0-2
[1]Leucadendron argenteum	2,5	70	P caffra	5-6	15
L pubescens	3	>50	Leucadendron salignum	4,5	4-40
			L lanigerum	3,5	low
			L plumosum	3+	0-40

Dormant seed	Nondormant seed
Seed coat hard, sclerified.	Seed coat corky or membranous.
Germination	
Seed coat broken by swelling of cotyledons following hydration.	Seed coat broken by extending radicle.
Hypogeal.	Epigeal.
Decomposition of pericarp.	Release of seed by fire, although some species can or must first germinate in the inflorescence.
Moisture - winter, sustained moisture supply. Low or widely fluctuating temperature as experienced in the soil after a fire.	Moisture - winter, sustained moisture supply. High altitude species may require cold, but temperature is a secondary requirement.
Taxa	
Leucospermum, Diastella, Mimetes, Orothamnus, Vexatorella, Serruria, Spatalla, Sorocephalus, Paranomus, many Leucadendron in the section Leucadendron. Six of the Leucadendron species are myrmecochorous, the rest are atelochorous.	Protea, Aulax many Leucadendron species, including all of section Alatosperma, and Aulax. Many of the Protea species are not actually serotinous (notably the ground proteas).

[1] L argenteum appears to have soil stored seed but may retain seed for up to two years (Jordaan 1944).

I suggest that a simple gene-flow model, similar to the one proposed by Givnish (1981) for *Pinus rigida*, can account for the derivation in the Proteaceae, of serotiny from CSS. The serotinous type would become dominant when, under a particular fire regime, it produces larger numbers of seedlings than the nonserotinous type. Where fires are too frequent for the accumulation of significant CSS reserves, serotiny will be weak or absent. Grassland Proteaceae, which must survive frequent fires, are nonserotinous and mostly resprouters (Beard 1958; Rourke 1972). Where fires occur at intervals long enough for individuals established between fires to maintain or increase population size, serotiny should again be weakly developed. This may be the case in *Protea laurifolia* and *P aristata* which occur in dry fynbos with relatively long fire-free intervals. The predictability of the fire-season and the probability of conditions suitable for germination soon after the fire are also major factors influencing the development and maintenance of serotiny. The susceptibility of CSS plants to fire season and other factors are discussed in more detail below.

HYPOTHESES CONCERNING THE SELECTIVE VALUE OF SEROTINY IN FYNBOS

The hypotheses presented below are interrelated and act in concert.

Predator satiation

Salisbury (1942 in Cavers 1983) postulated that periodic or mast seeding could saturate seed predators and result in the successful establishment of seedlings. This is primarily because the predators cannot increase their numbers rapidly enough, even through immigration and by concentrating on this food source, to consume all the seed before it escapes by germinating. This principle is also the core of the ideas put forward by Gill (1975), O'Dowd and Gill (1984) and Bond et al (1984) concerning serotiny. The effects of fire season and parent density on seedling numbers provide insights into the dynamics of this mechanism.

Fire season

Jordaan (1949, 1965) was the first to recognize the vulnerability of serotinous Cape Proteaceae to fire season: "Van besondere belang in hierdie verband is... die brandvastheid van die sade van soorte met saad reserwes, dit wil sê van soorte wat gedurende hul blomtyd nog sade van die vorige blomtyd, of die vorige blomtye, op die plant het.... *Leucadendron plumosum (L rubrum)*... besit so 'n saadreserwe" (Jordaan 1965). Jordaan (1949) predicted that *Protea repens* would only regenerate successfully after fires in the "safe" season (summer/autumn), because this was the period when mature seed was present on the shrub (Jordaan 1965, 1982). The *P repens* population he studied was weakly serotinous, releasing most of its seed within a year of flowering (Jordaan 1965) and thus having inadequate seed reserves to ensure recruitment after an "out of season" burn.

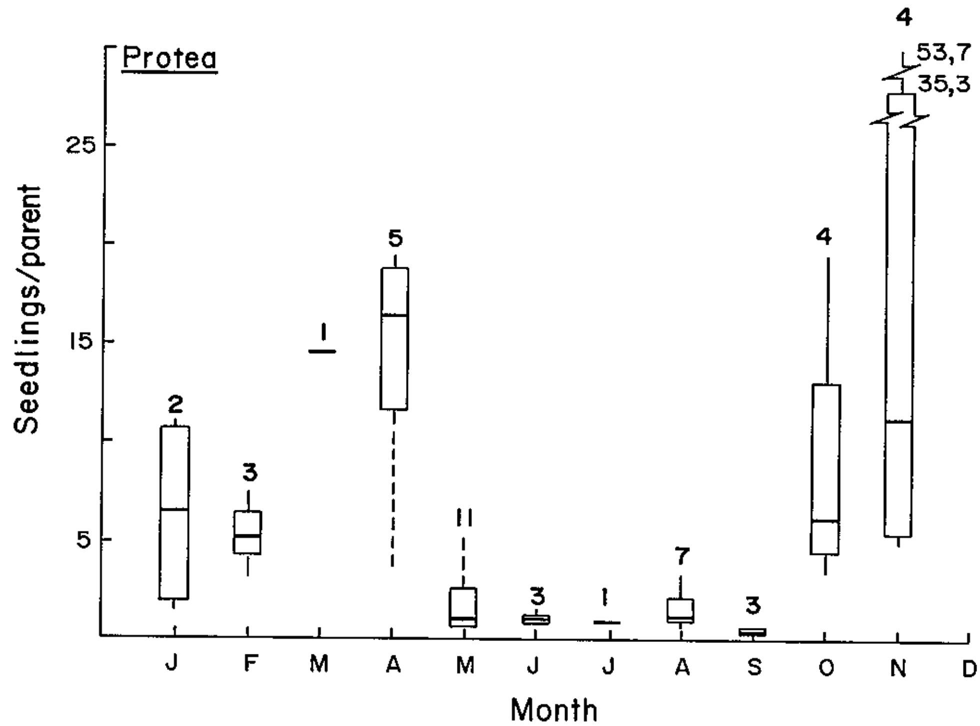
Bond et al (1984) and van Wilgen and Viviers (1985) found that seedlings to parent ratios of serotinous Proteaceae ranged from one or less after winter and spring fires to 20 or more after autumn fires. Bond et al (1984) suggested that fire season affects the success of the predator saturation mechanism. The period of time between seed release and the onset of conditions favourable for seed germination is critical because of the high rates of post-dispersal predation (Bond 1984). The rate of seed predation will decrease with time (Sullivan 1979; S A Botha unpublished data). Bond's (1984) hypothesis also requires germination to be seasonally restricted, either by moisture requirements or by more complex germination cues. Fire season will have no effect on regeneration where predation is negligible or where germination is not seasonally restricted (Bond 1985). Germination is apparently not always seasonally restricted in moist sites as Kruger (1972) found a few Proteaceae seedlings in spring following a September fire at Jakkalsrivier, a south facing humid catchment. Many more seedlings emerged in the succeeding autumn and winter (Kruger 1972).

Both Jordaan's and Bond's hypotheses predict the observed responses, given that the species has a seed production pattern similar to *Protea repens* (Jordaan 1944, 1949) and low reserves of older seed. The viable seed reserves would be more critical for species which have a low level of serotiny or higher rates of seed predation (Coetzee 1984) and loss of viability in the flower head (van Staden 1978; Table 4.4). The present hypotheses cannot account for the abrupt decline in seedling to parent ratios from April to May or the subsequent increase in this ratio in *Leucadendron* during the winter months (Figure 4.1).

TABLE 4.4 Loss of viability in CSS reserves in inflorescences of different Proteaceae, based on Bond (1985)

Taxa		Mean number of viable seed/age class/plant (n=20)		
	Age (yr)	0[1]	1	2
Protea				
aurea	17	4,8	4,4	2,8
eximia	24	3,1	1,4	3,6
lorifolia	20	10,4	10,4	2,8
punctata	28	9,3	9,4	11,9
repens	30	0,7	0,7	0,1
Leucadendron				
album	18	2,0	2,0	1,7
conicum	18	4,2	1,9	1,2
eucalyptifolium	17	11,5	10,2	9,9
rubrum	20	13,0	12,9	2,5
uliginosum	17	6,4	6,4	3,2

[1]Potential number, see Bond (1985).



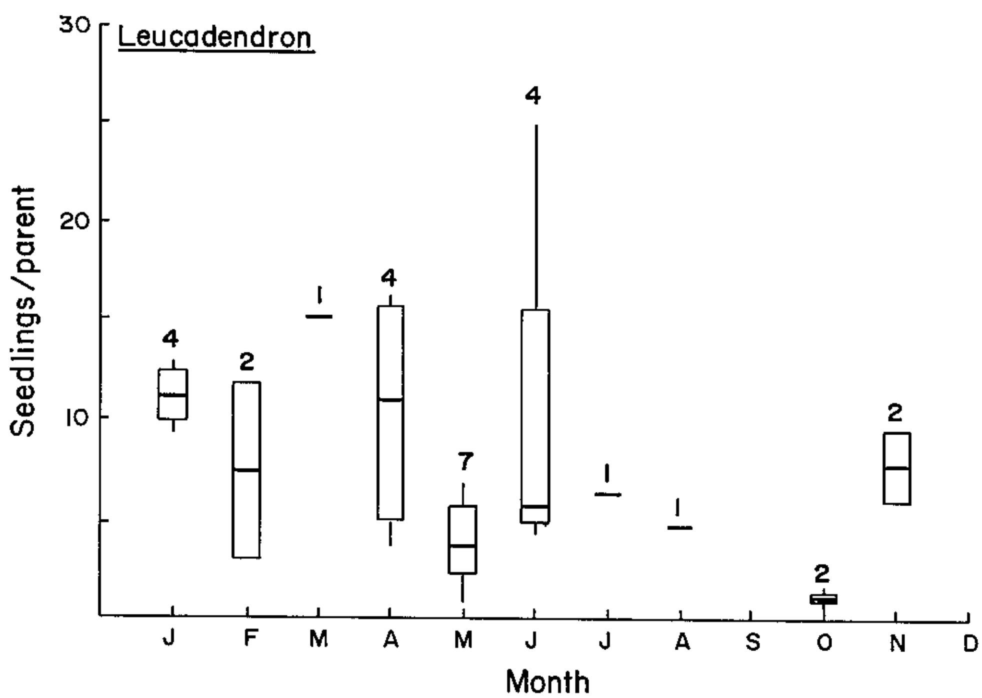


FIGURE 4.1 Seasonal variation in the number of seedlings per parent plant in *Protea* and *Leucadendron* species in the western Cape. The data are summarized by means of box-whisker diagrams: 50% of the values are located within the box and 75% between the ends of the two "whiskers"; the bar across the box is the median value. The sample size for each month is given above it. Data from van Wilgen and Viviers (1985).

Prolonged delays between dispersal and germination, even in the optimal season (O'Dowd and Gill 1984; Le Maitre 1985b) or low post-fire rainfall (Bradstock and Myerscough 1981; Specht 1981) also affect regeneration. Therefore the success of predator satiation depends on both a reliable wet season for germination and a minimum time between seed release and germination. This could explain the prevalence in wet habitats of serotiny in Proteaceae (Midgley 1987) and other taxa (eg *Erica sessiliflora* (Baker and Oliver 1967) and Bruniaceae).

Another possibility is that of rapidly declining seed viability after dispersal (Bond 1984; Cowling and Lamont in press), possibly because of exposure to extreme environmental conditions on the soil surface. Seed released after spring burns will be exposed to high summer soil temperatures.

Parent density

Bond et al (1984) found that seedling recruitment of serotinous Proteaceae was poor at high parent densities, regardless of fire season. Seedling densities in *Leucadendron laureolum* at the Kogelberg are strongly related to both season and parent density (Le Maitre 1985b), although data for *Leucadendron xanthoconus* show that seedling density is not affected by parent density, even at 11 plants per metre square (Figure 4.2). In dense populations the increasing interplant competition will result in a reduction in mean plant size and on the allocation of resources to seed reserves (see Harper 1977). Proteaceae in dense populations have long juvenile periods, few cones and little seed (D C Le Maitre personal observation) so that they will produce few seedlings per parent plant. This relationship may be very important, because the intra-specific competition will increase as the populations age and the individual plants grow larger. The normal decline in inflorescence production and seed stores will then begin at a younger stand age. It also suggests that a high degree of predator satiation is not necessarily optimal in the long term.

Favourable environment

Gill (1981a) and Bond (1984) argue that fire cued seed release allows seed to disperse and seedling establishment in an environment with relatively little competition from other plants for light, moisture and nutrients. This hypothesis is also relevant for species with soil stored seed banks which are cued for post-fire germination (Pierce this volume).

The Proteaceae have large phosphorus reserves in the seed (eg Kuo et al 1982; Mitchell and Allsop 1984) and do not appear to utilize the temporary nutrient surpluses that may be present in the soil (Siddiqui et al 1976) and may even be adversely affected by them (Ozanne and Specht 1981). Cowling and Lamont (in press) found that germination of seeds of four co-occurring *Banksia* species, planted in enclosures, was not greater in burnt than unburnt western Australian scrub-heath. However, nearly all seedlings in the unburnt area succumbed during the first summer after establishment. There are no published data on the post fire soil moisture regime, substrate and radiation requirements for the regeneration of CSS species.

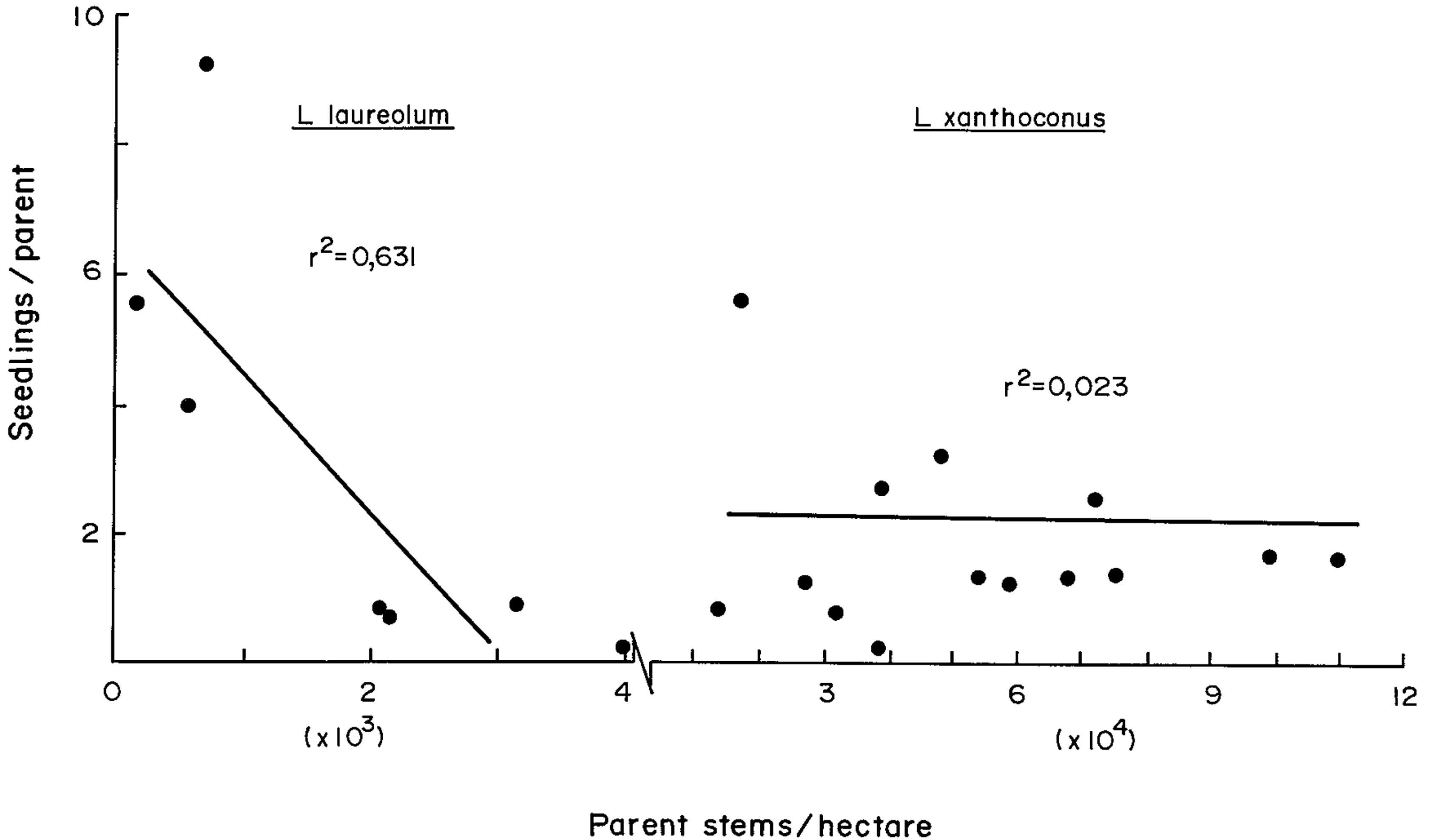


FIGURE 4.2 The effect of parent density on the number of seedlings per parent plant. Data for *Leucadendron laureolum* from Le Maitre (1985b) and *L xanthoconus* from Kruger (1972).

Protection from the inter-fire environment

Breytenbach (1984) argues that the low density of seedlings in mature fynbos is largely due to high levels of post-dispersal predation. Canopy-stored seed is protected from this predation (Kruger and Bigalke 1984). However, this hypothesis does not explain the success in the fynbos of nonserotinous, nonsprouting Proteaceae with no soil-stored seed bank (Midgley 1987). Soil moisture and pathogens are also involved in limiting seed germination and seedling establishment between fires. Critical experiments are required to assess the relative importance of these factors.

Buffer effect of reserves

Seed reserves provide a buffer against fluctuations in seed set, whether inherent or mediated by pollinators or climatic conditions (Gill 1981b; Bond 1984, 1985). The buffer effect also applies to species with soil-stored seed, whether perennials or annuals (see Cavers 1983). This hypothesis predicts that serotiny should be more strongly developed where the probability of seed production in any year is variable or low (Bond 1985). However, Cowling et al (in press) found that degree of serotiny was not correlated with the coefficient of variation of annual seed set among four co-occurring *Banksia* species. An alternative explanation is that erratic seed production may actually reduce predispersal predation by occasionally reducing predator populations to low levels (Ford et al 1979; Gill 1981b). Fluctuations in seed set will reduce infestation levels, relative to constant seed set, because of lags in predator populations growth and longer search times (Forcella 1980; Schmid et al 1984). This could also explain the marked annual fluctuation in flowering and seed set in *Banksia* species (Gill 1981a; Cowling et al in press) and in fynbos CSS species (Table 4.5). The long flowering seasons and varied season of flowering noted for CSS species (Pierce 1984) may allow the plants to reduce predispersal predation by evading insects with seasonally bound life-cycle stages (see Coetzee 1984). Myburgh et al (1974) note that large scale harvesting of inflorescences in *Protea magnifica* resulted in lower infestation levels in a subsequent harvest because the populations of the pests were reduced.

Fire frequency

I have already argued that fire frequency and seasonal patterns have led to the evolution of serotiny in the Cape Proteaceae. The clinal trends in serotiny found in pines (eg Givnish 1981) do not appear to be present in the Cape Proteaceae. Where they occur in western Australian *Banksia* species, moisture requirement levels of serotiny are apparently determined by the success of inter-fire seedling establishment and fire behaviour rather than fire per se (Cowling and Lamont 1985b).

Nonsprouters with canopy-stored seed are sensitive to variations in fire frequency. Recruitment will fail when fires occur before the population has time to build up seed reserves (van Wilgen 1981). Post-fire flower production is usually gradual and the juvenile period for any species may vary with altitude and habitat (Tables 4.6 and 4.7). Serotinous species are relatively short-lived and fires in senescent stands can result in little or no regeneration (Bond 1980). Specht et al (1958) suggest that

TABLE 4.5 Fluctuations in the flowering of some CSS species at Jonkershoek. Nf = no flowering recorded; C = flowered in the current season; C-1 = flowered in the previous season; C-2 = flowered two seasons previously. One hundred plants of each species were assessed

		Number flowering				
	Age (yr)	Nf	C	C-1	C-2	Total
Brunia albiflora	6	40				40
			21			21
				34		34
			5	5		5
Erica sessiliflora	11	3				3
			27			27
				12		12
			58	58		58
Protea neriifolia	8	49				49
			18			18
				20		20
					6	6
			6		6	6
				1	1	1

TABLE 4.6 Post-fire flowering of fynbos CSS taxa. No flowering was recorded in the first three post-fire years. Data, recorded at a range of sites, from Kruger and Bigalke (1984) and Le Maitre (unpublished)

	Sample size	% in flower at a given age (yr)						
		4	5	6	7	8	9	10
Erica sessiliflora	100	0	1	21				
Aulax cneorifolia	20	45	50					
Leucadendron microcephalum	299	0	0	0	0	27	36	
L salicifolium	100	0	1	64	100			
L xanthoconus	100	0	0	5	45			
Protea neriifolia	100	0	0	0	8	12	63	49
P neriifolia	100	0	0	12	21	25		
P lacticolor (moist)	100	1	6	19	85			
P lacticolor (dry)	100	0	0	1	28			
P mundii	100	0	0	1	7			
P stokoei	120	0	0	1	14			

TABLE 4.7 Reproductive maturity of plant populations of fynbos CSS taxa. Data from Kruger and Lamb (1978) and Le Maitre (unpublished). N = sample size

	Age (yr)		% of population with given number of flowering seasons							
		N	0	1	2	3	4	5	6	7
Brunia albiflora	6	100	40	55	5					
B albiflora	10	26	96	4						
Erica sessiliflora	6	100	79	20	1					
Leucadendron gandogeri	11	25	0	48	40	12				
L laureolum	5	60	98	2						
L microcephalum	6	246	13	44	33	10				
L microcephalum	10	227	8	14	16	15	17	18	10	3
L salicifolium	7	100	0	40	59	1				
L salicifolium	12	100	0	2	8	23	28	26	12	1
L xanthoconus	9	100	2	39	43	13	3			
Protea lepidocarpodendron	9	100	50	40	9	1				
P mundii	5	100	93	6	1					
P neriifolia	6	100	87	13						
P neriifolia	8	100	49	44	7					
P neriifolia	11	95	13	37	32	14	3	1		
P stokoei	5	120	86	13	1					
P stokoei	8	119	48	32	18	3				
P stokoei	10	97	30	36	26	5	3			

TABLE 4.8 Observed mortality rates in CSS Proteaceae. Data from Kruger and Lamb (1978) and Le Maitre (unpublished)

	Final age(yr)	Initial No	Observation period (yr)	Mortality (% yr^{-1})
Leucadendron laureolum	25	401	5	8,03
L microcephalum	10	246	3	2,57
Protea coronata	12	107	9	6,65
P neriifolia	11	99	3	1,35
P neriifolia	24	1 150	9	5,01
P neriifolia	39	220	7	8,59
P stokoei	8	120	3	0,28

senescence results from nutrient stress when available nutrients are bound up in wood and litter. Density dependent mortality may also play a role (Kruger 1984), but there is no direct evidence for this in the Proteaceae. Senescence is poorly understood and requires further study (see Manders and Cunliffe this volume). The general pattern in nonsprouting Proteaceae seems to be a low rate of mortality in juveniles and adults, which increases markedly in populations 20 years and older (Table 4.8).

There are data on inflorescence production and seed yields (eg Wiens et al 1983), but none on age specific fecundity. Reproductive output of certain species may vary from site to site (Lombaard 1971; Table 4.9). Although *Protea repens* and *P burchelii* set more seed than *P nerrifolia*, they have higher levels of predispersal predation (J H Coetzee personal communication). In a 28 year old *P neriifolia* stand, 18% of the shrubs had no inflorescences with seed, and 11% had no seed in their inflorescences; 71% of all the shrubs had less than 30 seed (D C Le Maitre unpublished data).

TABLE 4.9 Seed reserves of *Protea* species from different sites. Data for *P repens* and *P burchellii* from Lombaard (1971), Sossyskloof: P Manders (personal communication) and Swartbosch-kloof: D C Le Maitre (unpublished data). The ages for Lombaard's sites were estimated by adding four years to the maximum number of flowering years. Seed data are actual numbers of plump nonpredated seed

Species	Site	Age (yr)	Density (stems/ha)	Cone crop	Inflore-scences/ plant	Seeds/ infl	Seeds/ plant
P neriifolia	Sossyskloof	7	5 000	current	3,8	5,4	20,5
	Sossyskloof	7	3 583	current	1,9	5,5	10,5
	Swartbosch	28	3 575	current	2,5	1,4	3,5
	Swartbosch	28	3 575	total	21,3	1,5	32,0
P repens	Bainskloof	11	-	total	11,0	5,0	54,5
	Paarl	12	-	total	15,2	4,9	75,2
	Stellenbosch	12	-	total	12,7	15,3	194,9
P burchellii	Wolseley	11	-	total	12,0	13,0	156,5
	Paarl	12	-	total	19,3	18,6	359,6
	Stellenbosch	12	-	total	12,4	15,5	191,8

Reproductive failure of nonsprouting CSS species as a result of fire intervals that are either too long or too short, could result in local extinction since dispersal is too limited for long distance replacement within a reasonable time period (Cowling 1987; Manders and Cunliffe this volume). This suggests that the lower limit to historical fire intervals in an area could be estimated from a knowledge of the length of the juvenile periods of the nonsprouting CSS species present. The data in Tables 4.4 and 4.6 suggest that in most cases the minimum interval between fires would have been about 10 to 12 years. Patterns of population senescence in CSS Proteaceae indicate that the maximum fire free interval would have been between 30 and 50 years for communities with those species. However, it is possible that many species may have become locally or totally extinct as a result of an increase in fire frequency during the Holocene, and especially in historical times (Moll et al 1980).

Strategies for nonserotinous species

There are three phenological strategies open to nonserotinous taxa in order to reproduce sexually after fire. One is to have a long flowering season so that mature seed are present during most of the year (eg *Protea nitida*). Secondly, species can be adapted phenologically so that mature seed is available during the fire season (Figure 4.3). Clearly these species would be vulnerable to "out of season" burns. The third applies only to sprouting species where the vigorous post-fire flowering may enable the species to establish seedlings in the relatively open environment. Data are required to confirm this.

The ground proteas

Very little is known about the ecology of the low shrub and ground *Protea* species in the fynbos. Some are able to sprout, none are strongly serotinous and many are rodent pollinated (Rourke and Wiens 1977; Wiens et al 1983). Even less is known about the biology of the *Leucospermum*, *Leucadendron* and *Serruria* species with this growth form. Small mammal pollinated species flower in winter or early spring, when food supplies for small mammals are limited (Rourke and Wiens 1977). This means that mature seed is available during the fire-season. The staggered floret opening in these species and high floret numbers provides some protection from incidental destruction during feeding (Wiens et al 1983). Small mammals also prey heavily on the seed of the ground *Protea* species (J P Rourke personal communication) but there seem to be no predation avoidance syndromes.

SEED DISPERSAL

In *Protea* the trichomes flex with humidity changes and free the seed from the receptacle (Brits 1982). Most of the seed is released within a day of the plant or branch dying (D C Le Maitre personal observation). *Leucadendron platyspermum* appears to be unique in relying on the extension of the radicle of the germinating seed to push the seed out of the cone bract (Williams 1972). Data on the dispersal ranges of the CSS species are not available, but are probably limited (less than 10 m) in the Proteaceae (Manders and Cunliffe this volume) and potentially long range in the small seeded species (Table 4.1). Manders and Cunliffe (this volume) point out that efficient seed dispersal is not necessary where fires create large tracts suitable for recruitment.

SEED GERMINATION

Seed germination syndromes of CSS Proteaceae are related to the storage and dispersal patterns (Brits 1982; Table 4.3). There are no data for ratios of seed shed to seedling emergence and establishment in fynbos but Gill (1981a) gives a ratio of eight seeds/seedling in *Banksia ornata*

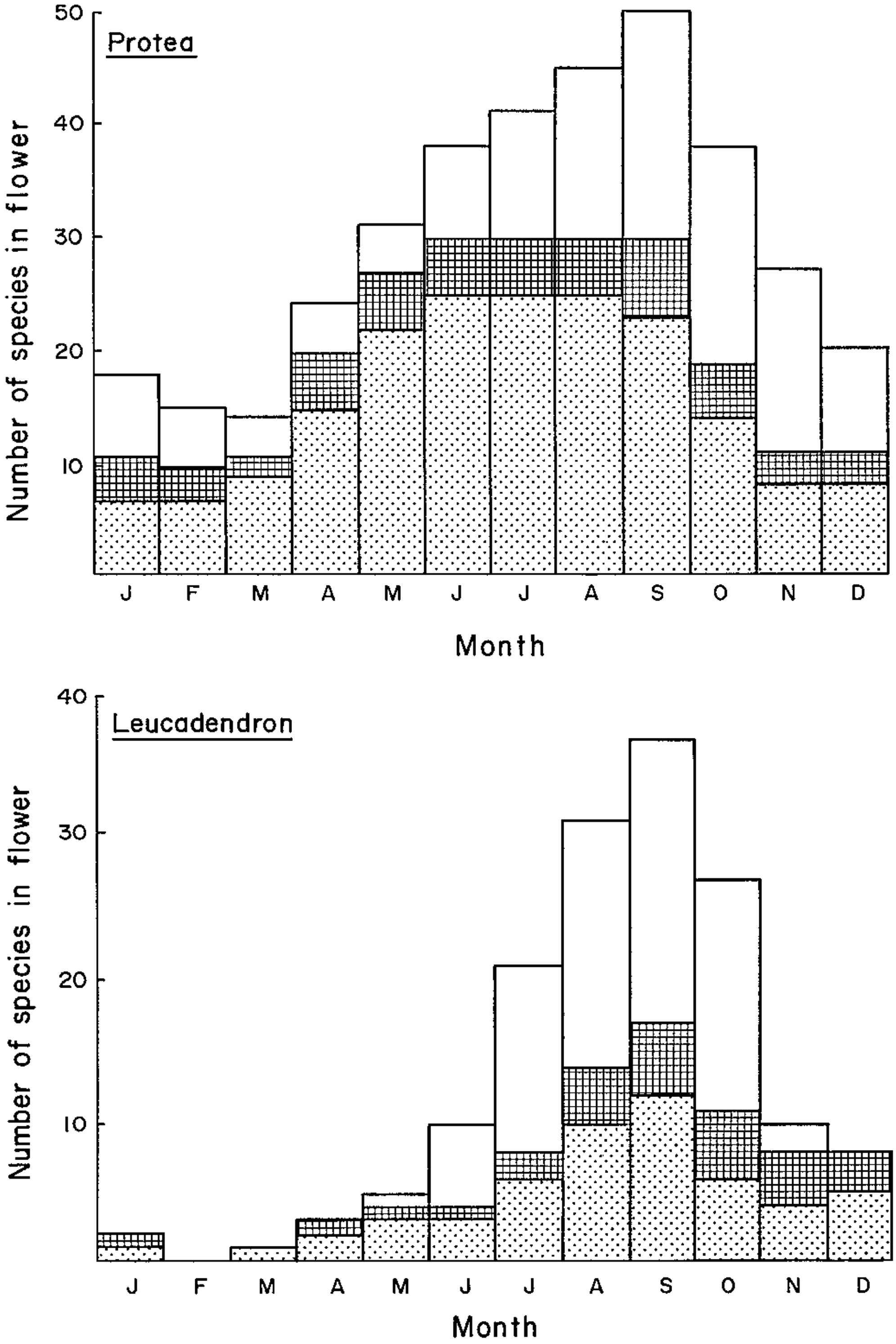


FIGURE 4.3 Seasonal variation in the number of fynbos *Protea* and *Leucadendron* species in flower. Open bars are nonserotinous species; grid bars are serotinous species from the winter rainfall region; and stippled bars are other serotinous species. Data from Williams (1972), Rourke (1980) and Pierce (1984).

nine months after a fire. Seedling numbers were linearly related to the length of the wet season and seedlings took at least six weeks to emerge after the onset of the wet season (Specht 1981). Kruger's (1972) observations suggest that the germination in the field may be relatively rapid in some Proteaceae. Observations in the Cederberg suggest that the emergence of seedlings from seed of CSS species may be less synchronous than germination from soil-stored seed, probably because moisture fluctuations are more marked on the surface than deeper in the soil.

SEEDLING GROWTH

Mortality of seedlings, particularly in the cotyledon stage, is apparently relatively high (Bond 1984). Mortality on south facing slopes may be less than on north slopes following late-autumn or winter burns probably because the seedlings are less well established on the drier, north facing slopes (Bond 1984). Whelan and Main (1979) found that herbivory by grasshoppers adversely affected recruitment in *Banksia* species and that it decreased with distance from the perimeter of the burnt area. Cowling and Lamont (in press) reported high levels of mortality of enclosed seedlings and almost complete mortality of exposed seedlings, of four co-occurring *Banksia* species, during the first summer after an autumn burn. There are no published data on herbivory either during emergence or establishment in fynbos. Post-fire data at the Kogelberg show that mortality in established seedlings is low and not related to density for at least the first four years in *L laureolum* (D C Le Maitre unpublished data). The causes of the local variations in plant density and recruitment within areas burnt in the same fire (Bond et al 1984) are not yet fully understood. Detailed studies on prefire seed reserves, seed dispersal, germination, seed predator behaviour and spatial variations in seedling recruitment are urgently required.

CONCLUSIONS

The primary selective agent in the evolution of serotiny from CSS taxa has been the fire regime, which in turn is determined by the production of fuel and by the climatic regime which controls the fuel moisture and provides an important source of ignition through lightning. The relatively wide, but predictable range in fire frequency found in the fynbos (van Wilgen this volume) has been instrumental in the development of serotiny in at least the Proteaceae. The sensitivity to fire season may be a consequence of a recent (Holocene) expansion in the seasonal occurrence of fires through ignition sources and fuel flammability patterns and a restriction of germination to a seasonal period because of drier moisture regimes in warmer climates. These factors explain why serotiny is weakly developed or absent in areas where fires are rare or frequent and also in areas where rainfall is unpredictable or unreliable. The vulnerability of CSS species to fire-induced local extinction suggests that the complex distribution patterns and disjunctions of many of these species in the Cape mountains may be the result of local fire histories rather than climatic changes on a regional scale and edaphic factors.

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5. DYNAMICS OF SOIL-STORED SEED BANKS IN RELATION TO DISTURBANCE

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INTRODUCTION

Soil-stored seed banks are common in vegetation prone to relatively frequent disturbance (Thompson 1978; Grime 1979). In fynbos, these seed banks have not been studied even though most species probably regenerate after fire entirely from soil-stored seeds. For example most members of the largest fynbos genera - *Erica*, *Agathosma*, *Phylica*, *Muraltia*, *Aspalathus* and *Cliffortia* - are nonsprouters lacking canopy-stored seed. Post-fire seedling recruitment, from apparently soil-stored seed banks, has been observed in a number of fynbos biome communities (Adamson 1935; Levyns 1929, 1935; Martin 1966). Bond and Slingsby (1983) report that many fynbos species have seed which are dispersed by ants to largely subterranean nests, where they are safe from predators (see also Bond and Slingsby 1984; Slingsby and Bond 1985).

This chapter reports on the first attempt to study in detail soil-stored seed banks in fynbos. Preliminary results on the dynamics of seed banks and how they are affected by disturbance, particularly fire, are presented for six small-leaved, nonsprouting fynbos shrubs growing in South Coast Dune Fynbos (Cowling 1984). Reference is made to the dynamics of soil-stored seed banks in fire-prone shrublands elsewhere in the world.

South Coast Dune Fynbos is confined to the calcareous coastal dunes between Stil Bay and Port Alfred. The dunes in this region comprise a mosaic of grassland, fynbos and thicket. On well-drained sands, in the absence of fire, there is a Clementsian succession from grassland through fynbos to thicket (Cowling 1984). The vegetation is maintained by pastoralists in a grassy state by frequent burning and to a lesser extent, bushcutting. Established thicket is relatively fire-resistant and impractical to bushcut. Thus the fynbos cover state which contains several endemics (Cowling 1984) is highly threatened.

The six dune fynbos species (Table 5.1) are being studied near Cape St Francis (see Cowling 1984 for a description of the study area). All are members of genera well-represented in fynbos. Parameters measured in the study include phenology, seed production, granivory, seed banks and germination cues. In addition, seedling establishment and survival after fire and bushcutting are being monitored. The intention is to develop a predictive understanding of the effect of disturbance on recruitment of these species. This information will be of use to pastoralists and conservationists.

EFFECT OF FIRE ON SEED BANKS

The four main components of a fire regime are considered here - season, frequency, intensity and size.

TABLE 4.1 Characteristics of selected dune fynbos species

Species	Family	Distribution	Height (m)	Mode of seed dispersal
Agathosma apiculata	Rutaceae	Riversdale to Port Elizabeth (coastal dunes)	0,8	Ballistic and myrmecochory
A stenopetala	Rutaceae	Humansdorp to Port Elizabeth (coastal dunes)	0,6	Ballistic and myrmecochory
Felicia echinata	Asteraceae	Mossel Bay to Port Alfred (coastal dunes)	0,1	Wind
Metalasia muricata	Asteraceae	Cape to Drakensberg	2,3	Wind
Muraltia squarrosa	Polygalaceae	George to Port Elizabeth	0,8	Myrmecochory
Passerina vulgaris	Thymeleaceae	Cape to Drakensberg	1,5	Unspecialized

Season of fire in relation to reproductive phenophases may be critical for recruitment of nonsprouters with transient seed banks. Fires which occur after the seed bank is depleted, and before the current seed crop has matured, could result in local extinction (see also Le Maitre this volume). Clearly there is a selective advantage in these species having viable seed available shortly before the "normal" fire season (Pierce 1984). Species with persistent seed banks should be more resilient to variations in the season of burn than those with transient seed banks, depending on the levels of post-disposal seed predation (Bond 1984). Fire season could also affect recruitment of species with soil-stored seed banks if the time of burn does not coincide with conditions favourable for germination (Brits 1986) or the survival of seedlings.

Short interval fires could result in the depletion of seed banks. Several successive annual inputs may be essential for the maintenance of critical numbers of seed necessary for successful post-fire recruitment. In this respect, juvenile periods (time required to reach reproductive maturity) and fecundity schedules (age-specific reproductive output) are important in determining the upper and lower limits to fire frequency necessary to maintain adequate seed banks.

The effect of fire intensity and associated temperature rises on the germination of soil-stored seed of fynbos plants has been little studied. Germination of *Agathosma betulina* and *A crenulata* was 80% after dry heat treatment (80°C for 20 minutes) as opposed to 40% success without heat (Blommaert 1972). There are few data on subsoil temperatures during fynbos fires (Van Wilgen this volume). Martin (1966) measured temperatures of 550°C at the soil surface and less than 43°C at 12 mm depth, during a fire in grassy fynbos. In Australian shrubland fires, soil surface temperatures ranged from 90 to 550°C, and subsoil temperatures ranged from 50 to 130°C at 10 mm depth, decreasing to a range of 40 to 70°C at 50 mm depth (Humphreys and Craig 1981). Subsoil temperatures remain elevated for periods of 12 minutes to two hours, and could thus provide a cue necessary for the germination of soil-stored seed.

Fire intensity may also alter soil nutrient levels and microbial populations (Renbuss et al 1973; Warcup 1981; Mitchell this volume) and change the temperature regime of the soil surface (Brits 1986) depending on how much cover is consumed. These fire-induced changes may stimulate germination. In chaparral it has been shown that leachate from charred wood can break dormancy in soil-stored seed (Keeley 1987). Equally important, post-fire conditions may favour seedling growth and survival (Renbuss et al 1973; Cowling and Lamont in press).

Size of burn is important for species with transient seed banks, since small fires would enable rapid dispersal of seed from adjacent unburnt vegetation.

SEED BANK DYNAMICS

Seed input

Seed input is affected by seed production which may vary according to plant age, resource availability (eg moisture), flower predation, fungal infection, pollination success, abortion and predispersal seed predation (Manders and Cunliffe this volume). Seed set provides a measure of initial reproductive success.

The relatively low seed set for two dune fynbos *Agathosma* species (Table 5.2) was apparently the result of flower predation, fertilization failure and abortion. Annual plump seed production per plant was highly different between the species. This value was weighted by density of individuals in the community and expressed on an area basis which allows for more meaningful comparison with soil-stored seed densities expressed in the same way (Table 5.3).

Dispersal and predation

Dispersal modes for the dune fynbos species are given in Table 5.1. Bond and Slingsby (1983) argue that rapid dispersal of myrmecochorous seeds reduces predispersal seed predation on the soil surface. However, examination of soil samples under a microscope revealed numerous seed remnants of myrmecochorous species (unpublished data) indicating extremely high levels of predation either on or in the soil.

A cafeteria experiment was set up with fresh seeds of the six dune fynbos species. The experimental design included: open depots with free access to mammals and invertebrates; depots excluding mammals; depots excluding invertebrates; and a control depot which excluded both invertebrates and

TABLE 5.2 Seed production in 1985 for two dune fynbos *Agathosma* species

	A apiculata	A stenopetala
Seed set[1] (%)	13,9	3,1
Predispersal seed predation (%)	19	22
Plump seed production:		
per plant	3 937	781
m^{-2}	1 444	175

[1]Seed set = 100 x $\frac{\text{No. seeds}}{\text{No. ovules}}$ per inflorescence

mammals. Seed removal was rapid from all three treatments. After six days, removal from the open depot was 100% for most species. Further experiments with depots containing whole *Muraltia squarrosa* seed and seeds from which elaiosomes had been removed showed no significant difference between removals of treated and untreated seeds. These experiments indicate removal rates only, and fail to differentiate between granivory and myrmecochory. Investigation of ant nests for evidence of the latter is needed. However, it is of interest that there was evidence of granivory in the depots accessible to invertebrates only.

Size of seed banks

In most studies, size of seed banks is determined indirectly by counting numbers of seedlings emerging from incubated moistened soil samples. This method assumes that moisture alone is sufficient to stimulate germination of all species. Because of a lack of knowledge of germination requirements, the direct seed count method was employed in the dune fynbos study. Once germination ecology of the selected species is better understood, soil-stored seeds will be tested for viability.

Seed bank densities (seeds m^{-2}) of the dune fynbos species (Table 4.3) were determined with the aid of a microscope from 50 soil cores (50 mm diameter; 50 mm depth) which were randomly sampled in the same community in June 1985 and March 1986.

Consistent with data reported elsewhere in the literature (Pratt et al 1982; Roach 1983; Mallik et al 1984), the results showed high variation in the density of soil-stored seed. In 1985 the per area seed bank to seed production ratios for *Agathosma apiculata* and *A stenopetala* were 0,06 and 0,26 respectively. Preliminary data indicate that these values were lowest for wind-dispersed species.

As there are no other data on fynbos seed bank densities, the only comparative data for fire-prone shrublands are from Californian chaparral and Scottish heathland. Seed bank sizes of the dune fynbos species (Table 5.3) were comparable with the chaparral species *Ceanothus gregii* (0 to 262 m^{-2}) and *C leucodermis* (0 to 83 m^{-2}) (Keeley 1977), but were markedly lower than *Calluna vulgaris* (223 000 ±56 800 m^{-2}) in Scottish heath (Mallik et al 1984).

TABLE 5.3 Soil-stored seed bank densities (seeds m^{-2}) of selected dune fynbos species. n = number of soil cores (50 mm diameter) analysed. Values are means ±SE. Significance levels (Sig) based on Mann-Whitney U test

	June 1985 (n = 51)	March 1986 (n = 55)	Sig
Agathosma apiculata	92 ± 32	269 ± 85	0,001
A stenopetala	46 ± 20	93 ± 38	N S
Felicia echinata	87 ± 23	83 ± 26	N S
Metalasia muricata	10 ± 7	0	N S
Muraltia squarrosa	678 ± 160	796 ± 164	N S
Passerina vulgaris	245 ± 82	130 ± 46	N S

There were significant annual variations in seed densities for one species only. This variation will result in differential establishment patterns, depending on the year of burn (Cowling 1987).

Dormancy, germination and seedling establishment

Certain mechanisms prevent germination until conditions for establishment are optimal. Dormancy patterns, which are highly complex, are summarized by Harper (1959) as follows: "Some seeds are born dormant (innate), some achieve dormancy (induced) and some have dormancy thrust upon them (enforced)" (my brackets). Enforced dormancy may be broken simply by adequate water whereas innate dormancy requires a specific stimulus (eg heat treatment). Dormancy may be induced by many factors, including seed burial. The situation may be further complicated in that combinations of all three dormancy states are common (Silvertown 1982). No data are as yet available on the dormancy characteristics of the dune fynbos species.

Germination of seeds may be initiated by a number of factors including: widely fluctuating diurnal temperatures (eg after post-fire exposure of the soil surface); cold temperatures; dry heat etc (Brits 1986). Some plants produce polymorphic seeds, resulting in within-crop variation in germination cues. Polymorphism may not be genetically fixed - the germination physiology of a seed may be affected by environmental pre-conditioning of the parent plant (Grime 1979; Rathcke and Lacey 1985).

Germination trials on the dune fynbos species are currently being undertaken. Field germination was estimated from seedling counts subjected to different disturbances (Table 5.4). Recruitment was poor in mature vegetation and after bushcutting but was clearly enhanced by fire. It would be of interest to express recruitment as a fraction of the viable seed bank but data are as yet unavailable.

TABLE 5.4 Seedling recruitment (number of seedlings per parent) of dune fynbos in mature vegetation (13 year old) and after various disturbances.[1] Recruitment recorded in 20 x 1 m^2 plots, 10 months after treatment

	Treatment			
	Mature vegetation	Fire	Bushcut	Bushcut and litter removal
Agathosma apiculata	1,50	48,0	0,09	-
A stenopetala	0,26	-	0,15	-
Metalasia muricata	0,00	2,0	1,66	0,00
Muraltia squarrosa	0,00	20,0	0,28	0,00
Passerina vulgaris	0,07	24,0	1,10	0,40

[1] Fire and bushcutting in March except for bushcutting of *Agathosma* species in May.

The timing of germination of soil-stored seeds should ensure suitable conditions for the survival of seedlings. An important consideration is that any cohort of plants emerging from a seed bank may contain genotypes from several different seed crops, and not just from the most recent crop (Silvertown 1982).

Continued monitoring of seedling densities after the fire and bushcut treatments in dune fynbos (unpublished data) confirmed Specht's (1981) statement that fire regime is only one of a set of selective agents acting on plant populations. Post-fire climatic conditions, which can vary stochastically, also exert a strong control on seedling recruitment. The first summer and autumn period after the fire was unusually wet and negligible seedling mortality was recorded. However, during a hot, dry period in March 1986, 24 months after fire, mortality increased dramatically.

DISCUSSION

Although the six dune fynbos species all have soil-stored seed banks and, apparently fire-stimulated germination, they differ in other aspects of their life histories, resulting in differential longevity in the succession from dune fynbos to thicket (Figure 5.1).

Felicia echinata, *Passerina vulgaris* and *Muraltia squarrosa* are pioneer species, having short juvenile periods (Figure 5.1); high seed output (unpublished data) and relatively large seed banks (Table 5.3). All three species are relatively short-lived, showing high levels of senescence and mortality in 13 year old dune fynbos (unpublished data). *Agathosma* species have slightly longer juvenile periods, moderate seed production and smaller seed banks. *A apiculata* is generally associated with fynbos communities transitional to thicket whereas *A stenopetala* is a true fynbos species (Cowling 1984). The former species is longer-lived and capable of substantial recruitment in the inter-fire period (Table 5.4).

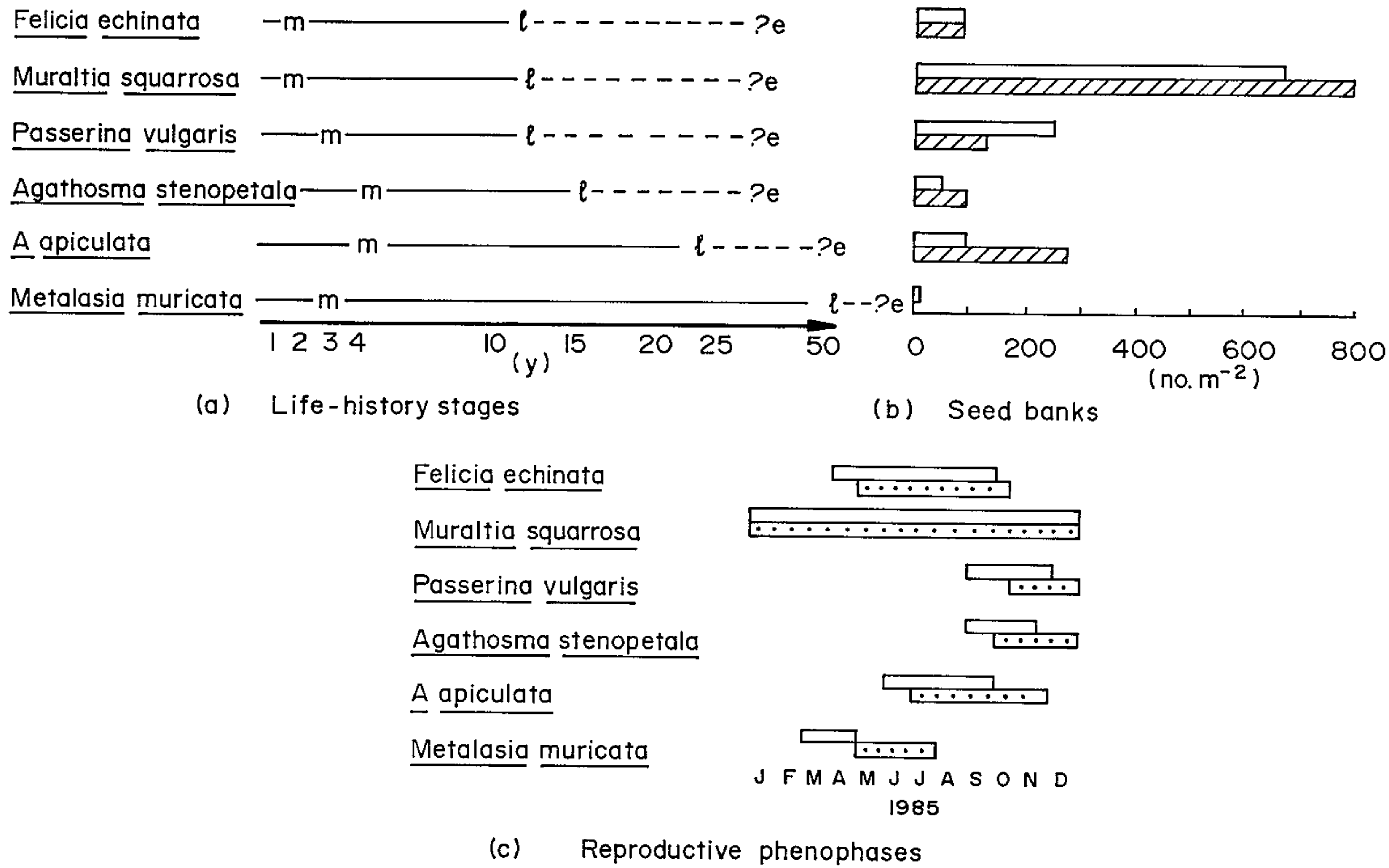

FIGURE 5.1 Summary of life-history characteristics of South Coast Dune Fynbos species. (a) m = maturation period (juvenile period); l = longevity; e = local population extinction - not determined (Noble and Slatyer 1980). (b) open bars = 1985; shaded bars = 1986. (c) open bars = flowering; stippled bars = seed production.

With regard to season of disturbance, *Metalasia muricata* has the longest period between seed production and normal fire season (summer-autumn) (Figure 5.1). Low soil-stored seed densities, high germination success (in vitro) and potentially long-distance wind dispersal (S M Pierce personal observation) and greatest longevity suggests that this species has life history traits similar, in some respects, to pioneer thicket species (Knight 1986).

The data on *M muricata* could be construed to support the suggestion by Martin (1966) that the emergence of *Erica* species some two years after fire, may be a result of the import of seed from adjacent unburnt areas. However, without seed bank data, such ideas are merely speculative. The complexities of dormancy could similarly explain late emergence after disturbance.

CONCLUSIONS

Comprehensive data on viable seed banks and other life history traits together with germination ecology obviate the need to study seed production in detail. The former data provide the necessary information towards predicting recruitment of a species in response to disturbance regimes. However, to reiterate Specht's (1981) statement, disturbance is only one selective force acting on populations - they must also survive other stresses such as stochastically variable drought-induced seedling mortality.

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6. SMALL MAMMAL DYNAMICS IN RELATION TO FIRE

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INTRODUCTION

One of the aims of 1986 fynbos biome annual general meeting, was to determine whether the objectives set by the Fynbos Biome Project, ie "... to gain a predictive understanding of the structure and functioning of fynbos ecosystems ..." could best be achieved by studying demographic processes; describing community patterns; or using both approaches simultaneously. However, in order to achieve this objective, the physical and biotic variation throughout the fynbos biome must be described within space, over time and under all possible disturbance regimes. It is therefore necessary to be able to predict the effect of disturbances at both a small (microsite) and a large scale (landscape level). These effects should also be studied from the suborganismic level (at the level of gene selection), up to community and ecosystem levels.

I will discuss the effect of fire on small mammals and attempt to show whether synecological or autecological studies provide adequate data to come to a "... predictive understanding ..." of small mammal responses to fire. I will also attempt to show that the two approaches address problems at different levels of organization, are not mutually exclusive and should be used in support of one another.

STUDY AREA

The effect of fire on small mammals was assessed in the Groot Swartberg and Outeniqua mountains of the nonseasonal rainfall zone in the southern Cape (Figure 6.1). Table Mountain Sandstones form the major underlying geology and soils are generally low in nutrients (Bond 1981). Fynbos of generally low nutritive status (Joubert and Stindt 1979a,b; Joubert et al 1979; Stindt and Joubert 1979) with Proteaceae and Bruniaceae in the overstorey and Ericaceae, Restionaceae, Rutaceae, Asteraceae and Cyperaceae in the understorey, is the major vegetation type at both study sites (Bond 1981). Fires occur at intervals of between six and 20 years. After fire graminoids (Restionaceae, Cyperaceae and Poaceae) and sprouters recover quickly, but those species dependent on seed resources to recover take far longer and individuals may only mature after five to 12 years. Plant recovery rates are related to rainfall and this is considerably higher in the Outeniqua (400 to 1 200 mm) than in the Swartberg mountains (250 to 800 mm).

METHODS

Small mammals were sampled on grids consisting of five trap lines with 10 traps per line, 10 m between lines and five metres between traps. Traps were placed out for four days and checked once a day in the morning. Elliot and Sherman live traps baited with peanut butter and rolled oats were used on all occasions. Grids were located subjectively in such a way that a single habitat unit was sampled, ie sampling at alpha diversity level. Data for each grid (eg time since last fire) are given in the results.

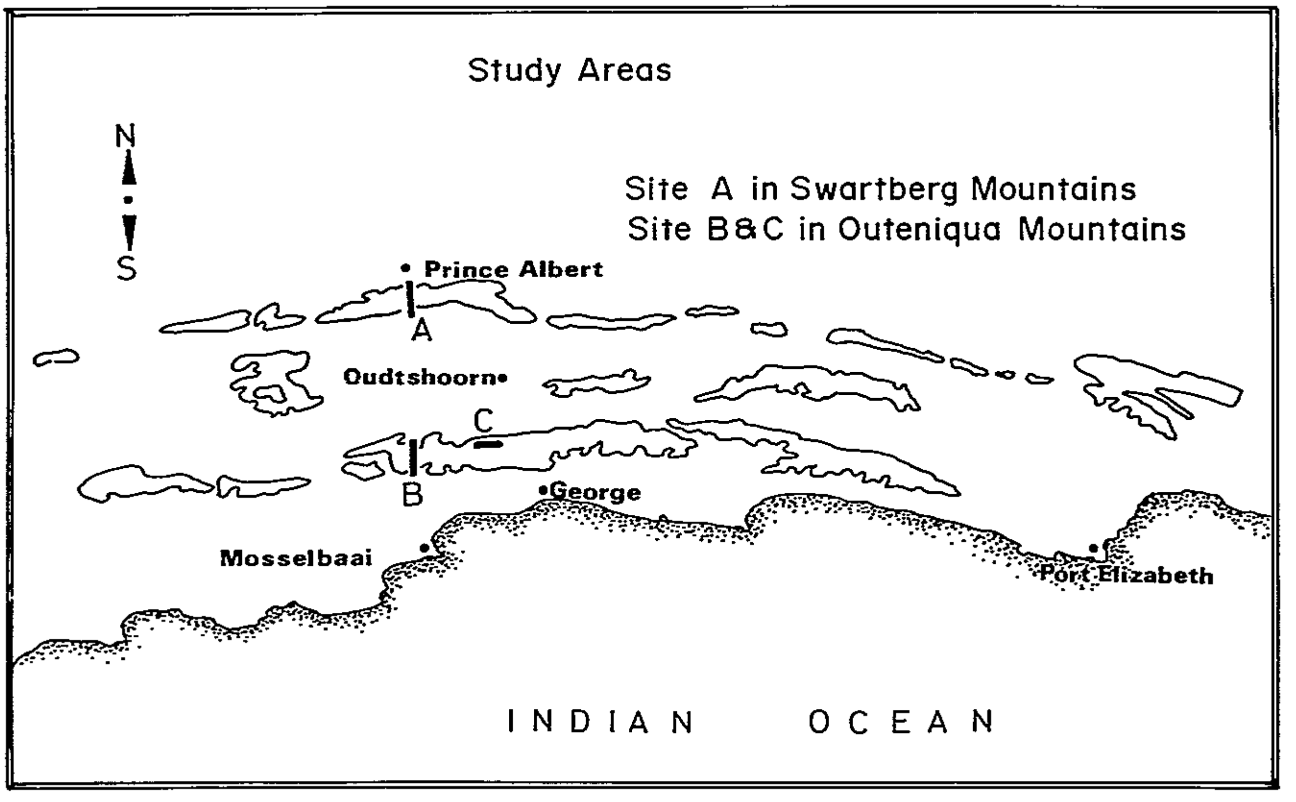


FIGURE 6.1 Map showing the location of the study sites (see text).

To determine whether small mammals are killed or maimed by fire, large areas of newly burnt veld were systematically searched for dead animals.

The potential physical effect of fire on small mammals was assessed by randomly locating dead animals in the study area before the fire and assessing the carcasses directly after the fire. This was done in fynbos that was 22 years old at the time of the fire.

The effects of fire on small mammal community structure was assessed in two ways:

- Trapping stands of different ages within the same habitat unit (coenocline). Location of study areas are given in Figure 6.1 (sites A, B and C).

- Following the recovery of small mammals on a single plot after a fire, with repetitive sampling (three to four seasons) being done before the fire. (Figure 6.1 sites A and C).

It has been shown that fire regime (eg fire intensity) affects the rate of vegetation recovery (Trollope 1978; Breytenbach 1986). The effect of fire regime (and slow recovery of vegetation) on small mammal communities was assessed by relating the recovery of small mammal community structure in sites managed under different fire regimes (Figure 6.1 site C) to that occurring elsewhere in the same vicinity (Figure 6.1 sites B and C) where fire regimes were 'normal'.

Patterns in small mammal community structure were described by ordinating trap data (number of individuals captured per species over a 200 trap night period (Table 6.2)). The Czekanowski similarity coefficient (Campbell 1978) was used in Bray-Curtis ordinations (Shimwell 1971). The subjective selection of end points was avoided by using reciprocal averaging (Orloci 1975) to identify the first two endpoints. Endpoints for the second axis were identified by extracting subjectively an orthogonal axis. Ordination groupings were confirmed by classification of the data using the group average technique (Webster 1979). Successional patterns were analyzed by ordinating post-fire time sequence data on species abundance (Austin 1977, 1980).

RESULTS

Direct effects of fire

Only two dead individuals (*Otomys irroratus, Rhabdomys pumilio*) were found after fire at all study sites. No records were kept of the surface area that was searched for dead animals, but at least 200 ha were searched intensively. Several live *R pumilio,* and *O irroratus* were observed moving about immediately after fires, and were frequently observed moving out of the newly burnt veld to adjacent areas.

There was little fire damage to carcasses located at the Swartberg study site (Table 6.1). Even though very few dead animals were found, the toes, tails and whiskers of small mammals captured in recently burnt veld often showed signs of having been damaged in the fire.

TABLE 6.1 Effect of fire on carcasses of small mammals. N = number of carcasses

Species	N	Whiskers burnt off	Coat singed	Toes burnt off	Tail burnt off
Myosorex varius	6	4	3	4	3
Rhabdomys pumilio	4	2	2	2	1
Praomys verreauxii	2	2	2	0	0
Acomys subspinosus	3	1	0	0	1
Otomys irroratus	1	1	1	1	1

Effect of fire on community structure and composition

Fire modifies composition of small mammal communities considerably. Diurnal species disappear within two or three days after the fire, unless a large amount of unburnt material remains (Table 6.2). After a week or two population numbers stabilize in the immediate post-fire environment. Certain successional patterns emerge over the next 10 to 20 years, before the next fire occurs. Different species show preferences for veld of different post-fire ages (Figure 6.2), and because of this selectivity, changes in community structure can also be followed over time (Figure 6.3). Figure 6.2 is based on data from both Table 6.2 and data in Fox et al (1985). Site 1, the only site in which *Dendromus melanotis* was recorded, is placed in the centre of the ordinal space (ie at the origin) since it differes totally from all other sites, and ideally

TABLE 6.2 Trap data, given as number of individuals captured over the trapping period

Swartberg study sites

Number in Figure 6.3	1	2	3	4	5	6	7	8	9	10	11	12	13
Vegetation age (yr)	0,3	4	8	40	20	20	20	20	20	0,3	1,3	2,3	3,3
Species													
Elephantulus edwardii	0	0	0	0	1	1	0	0	2	4	3	2	2
Crocidura cyanea	0	0	0	0	0	1	0	0	0	0	0	0	0
Crocidura flavescens	0	0	0	0	0	0	0	0	0	0	0	0	1
Myosorex varius	0	2	3	1	0	0	0	0	0	0	1	0	0
Graphiurus ocularis	0	0	0	0	0	0	0	0	0	0	1	0	0
Dendromus melanotis	3	0	0	0	0	0	0	0	0	0	0	0	0
Acomys subspinosus	0	4	3	3	1	2	3	2	5	3	0	4	3
Aethomys namaquensis	0	3	0	0	0	0	0	0	0	14	14	2	3
Rhabdomys pumilio	0	0	0	0	0	0	0	0	4	0	0	0	0
Praomys verreauxii	0	0	0	2	5	0	3	2	1	0	0	0	0
Otomys irroratus	0	2	3	3	0	0	3	3	0	0	0	0	0

Outeniqua study sites

Number in Figure 6.4	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Disturbance state[1]	a	c	e	d	e	a	d	f	b	b	b	b	a	b	b	a	a	a	a	a
Hakea cover (%)	0	90	25	70	45	2	95	85	20	40	60	35	0	35	35	0	0	0	0	0
Vegetation age (yr)	2	4	4	2	7	25	2	1	20	20	20	18	22	19	20	18	15	22	22	22
Species																				
Elephantulus edwardii	0	0	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0
Elephantulus rupestris	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Crocidura flavescens	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Myosorex varius	1	0	0	0	1	0	0	1	1	2	2	0	1	0	0	0	0	0	1	0
Dendromus melanotis	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acomys subspinosus	2	0	1	0	0	2	0	0	1	0	0	0	0	2	1	0	0	1	1	0
Aethomys namaquensis	0	0	3	0	4	1	0	0	0	6	0	0	0	2	0	0	0	3	2	2
Rhabdomys pumilio	9	0	8	13	0	7	7	0	10	11	12	17	7	6	3	7	7	0	0	0
Praomys verreauxii	1	0	0	0	1	0	0	0	0	1	0	2	2	0	0	0	2	0	0	0
Otomys irroratus	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0
Mus minutoides	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Gerbillurus paeba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[1] a = undisturbed; b = Hakea sericea present; c = slashed and standing; e = firebreak (four to six year burning cycle); f = pine and hakea infested site, burnt standing.

represents an outlier on the third axis. The first two ordinate axes represent a clear age sequence. These successional sequences based on species preferences for different veld ages are clear enough to allow the development of certain 'successional classes' viz:

- Early successional species. They appear within the first two to three months after the fire, and persist for a year or two, before disappearing eg *D melanotis*.

- Middle successional refugia species. These species colonize veld some two to three years after fire. When veld is between five and six years old they disappear to a large extent but may persist in refugial habitats eg *Graphiurus ocularis* moves into rocky outcrops at this stage.

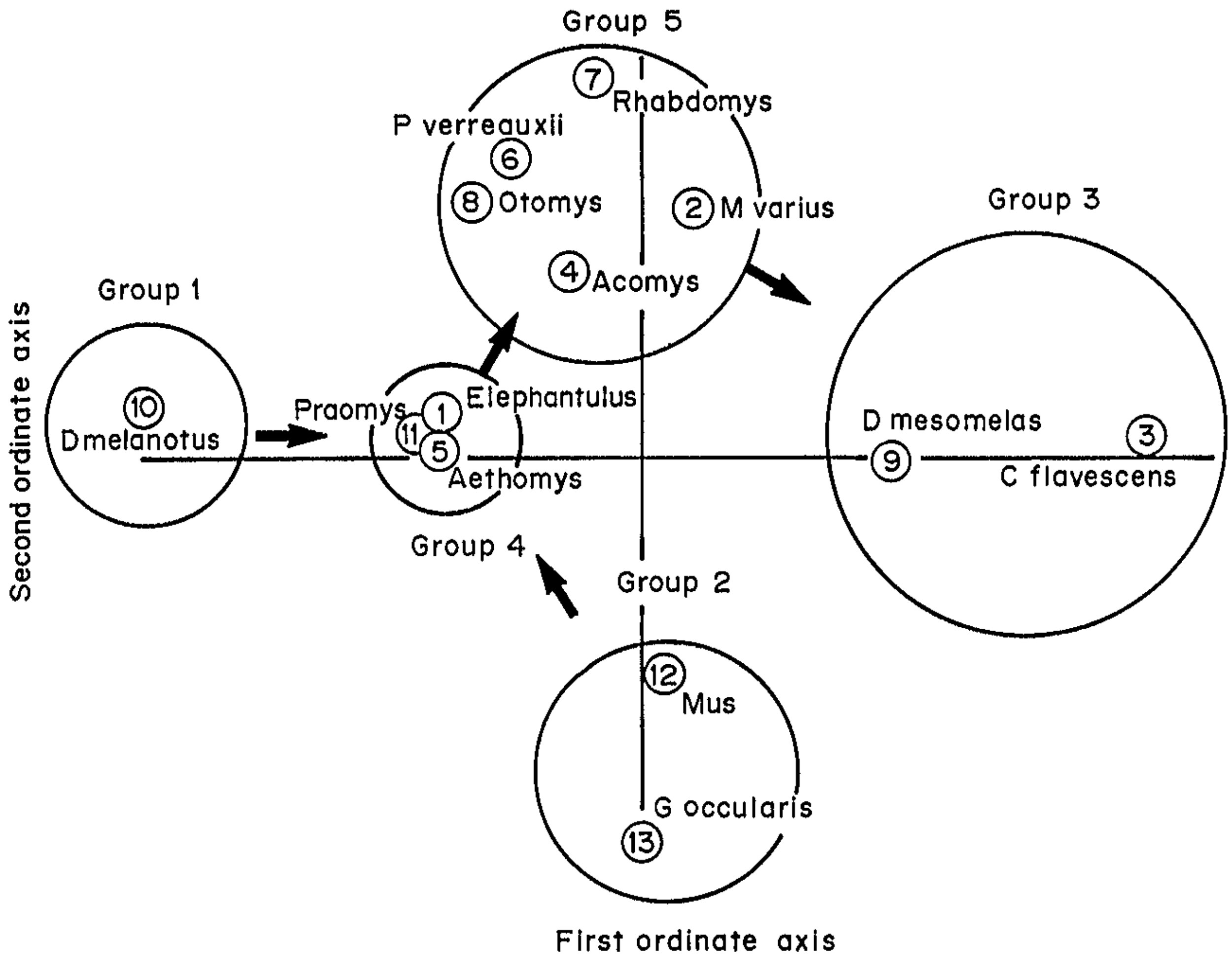
- Middle successional species. These species colonize fynbos some two years after the fire but only persist for a few years before disappearing ie five to six years after the fire. On the mesic slopes of the Swartberg *Aethomys namaquensis* and *Elephantulus edwardii* serve as examples. On the arid slopes they persist for as long as 40 years at which stage the vegetation has already become senescent (Breytenbach 1982).

- Late successional species. Some species only occur in fynbos at least ten to twelve years old. *Crocidura flavescens* and *Dendromus mesomelas* have only been trapped in fynbos older than 10 years and in some drier areas have only been trapped in vegetation older than 30 years.

- Ubiquitous species. Some species appear to be more flexible and may persist between fires eg *Myosorex varius* and *Acomys subspinosus* occur in veld of all ages.

Effect of fire regime

The effect of fire intensity on 'normal successional' patterns was evaluated in the Outeniqua mountains. Veld of different ages, and different treatments were sampled, and compared to sites sampled along an adjoining undisturbed gradient (capture and site data are given in Table 6.2). Small mammal community structure in unburned *Hakea sericea* invaded sites, does not differ from that in uninvaded mature fynbos (Figure 6.4). After fire the recovery of small mammal communities was considerably retarded in *H sericea* sites, where fire intensities could be as much as thirteen times higher than that recorded in adjoining, uninvaded fynbos sites (G J Breytenbach in preperation). Small mammal communities in those sites where fynbos was burnt standing recovered within two years. Those were slashing of *H sericea* took place was arrested at the first stage of succession. The early successional species (*Dendromus melanotis*) persisted even after four years. Two firebreak sites and a pine and hakea infested site that was burned, also failed to recover as rapidly as the uninfested fynbos sites (Figure 6.4; Table 6.2). The effect of increasing fire intensity was to decrease vegetation cover (Breytenbach 1986; G J Breytenbach in preparation), thus making the site effectively more arid in terms of vegetation structure. It is evident from Figure 6.4 that the small mammals show a similar response. The first axis of the ordination reflects a moisture gradient, with site 25 lying in an area that receives some 300 to 400 mm of rain per annum, whilst sites one to 17 receive some 600 to 800 mm per annum. Those communities from sites with a disturbed fire regime, have 'moved' in the ordinal space towards the sites receiving less rainfall (group 1 and group 3).



Swartberg site 2 - Small mammal species

FIGURE 6.2 Ordination of small mammal data in terms of their occurrence in relation to fire. Group 1 = early successional species; Group 2 = mid-successional species; Group 3 = late successional species; Group 4 = ubiquitous species; Group 5 = late successional species. Group boundaries were corroborated using group average sorting (see Methods). Data from Fox et al (1985) and Table 6.2.

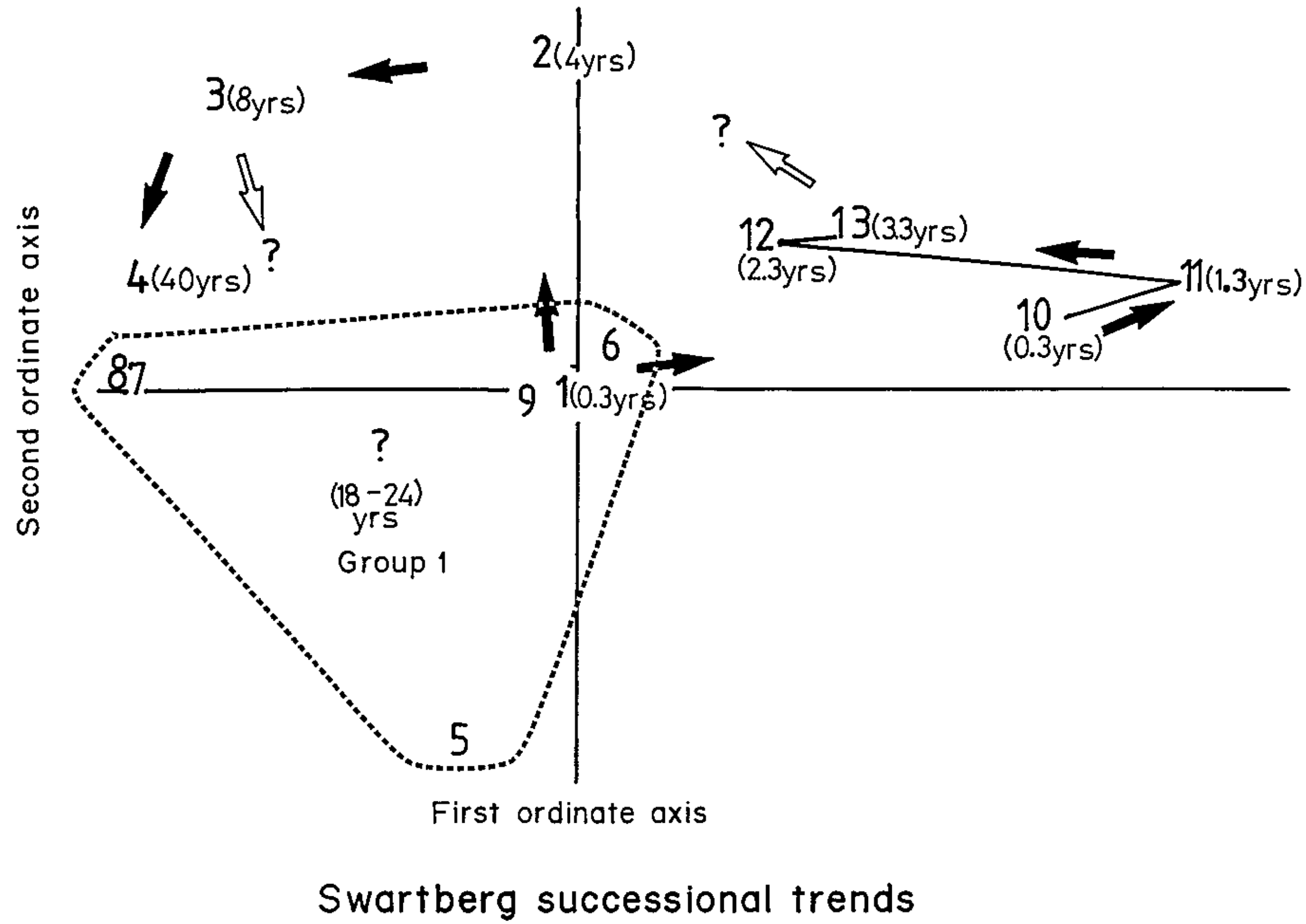
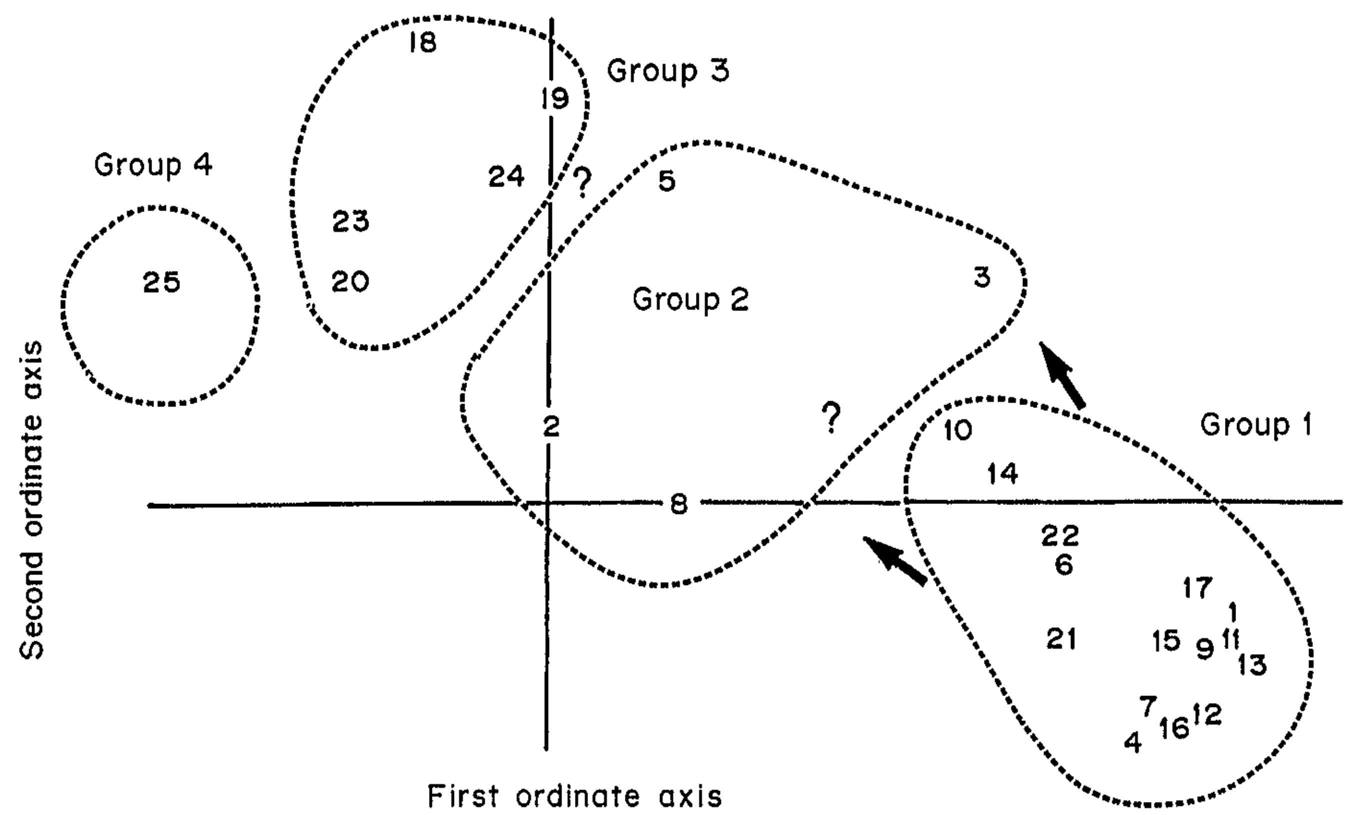


FIGURE 6.3 Ordination of small mammal data in fynbos sites of different ages. Group 1 = single 20 year old site sampled over a two to three year period during different seasons. Successional trends over the first few years after the site was burnt are shown by the trajectory linking sites 10 and 13. Adjoining sites of different ages were sampled and the longer term trends (one to 40 years) are evident in sites 1-4.



Waboomskraal - Effect of fire intensity

FIGURE 6.4 Ordination of small mammal data in sites of different moisture status and subjected to different fire regimes. Group 1 includes sites from a similar position along a moisture gradient in the Outeniqua mountains (see Table 6.2 for an explanation of site numbers) and have all been burned under a 'normal fire regime'. Sites of various post-fire ages, with and without *Hakea sericea* present, are included in this group. Group 2 represent sites where fire regime was changed in some way. Groups 3 and 4 include more arid sites along the moisture gradient.

DISCUSSION

Direct effect of fire

Small mammal populations normally decline after fire (eg Rowe-Rowe and Lowry 1982; Willan and Bigalke 1982) and this has frequently been attributed to reduction of populations by the fire. Reports of animals fleeing from and being killed by fire (Tevis 1956; Lawrence 1966; Komarek 1969) are as common as those reporting low mortality and migration (Howard et al 1959; Komarek 1969; Vogl 1973). I have found very few dead animals after fynbos fires, and only a few of the animals captured after fire show any sign of damage. Studies with caged animals exposed to fire also show that direct effects are not as drastic as one would expect (Lawrence 1966). These data indicate that post fire population decreases can not necessarily be attributed to mortality alone.

It is equally clear that because of the variability in population responses to fire, a predictive understanding will only come once we understand those variables that lead to this diversity of responses: fire intensity, fire season and fire avoidance behaviour must be properly assessed. We also need more data to show whether immediate post-fire population levels have any effect on eventual community structure and recovery of populations.

Effect of fire on community structure and composition

The effect of fire on communities can be assessed by using community descriptors, and most studies discuss fire effects in terms of diversity, equitability, richness, density and biomass (Krebs 1972; Rowe-Rowe and Lowry 1982; Willan and Bigalke 1982; Fox et al 1985). However, these descriptors contain little information on the composition and structure of the data and hence on the communities being evaluated. In this way much of the potential information and insight is lost. I will review previous studies and show how in one case the use of more sophisticated multivariate analyses, increases our understanding through better use of available data.

Fires affect behaviour of animals considerably, and the large changes observed after fynbos fires are probably due to behavioural changes, or migration and mortality after the fire rather than death due to the fire itself. Generally density decreases after fire, remains low (less than 10 animals per ha^{-1}) for nearly two years and then increases. After this, density fluctuates considerably and at times may be lower than what was recorded directly after the fire. In the Groot Swartberg densities in 10 to 20 year old vegetation varied between five to 181 animals per ha^{-1} (Breytenbach 1982). This pattern applies to several mediterranean type ecosystems (Willan and Bigalke 1982; Fox et al 1985). Changes in biomass are even greater as the most common species found in the immediate post fire environments only weigh some five to 20 g (Fox et al 1985). Some of the larger animals (those in the 20 to 110 g size range) only appear two to five years after the fire.

Diversity (<u>H</u>) also decreases after fire and takes nearly three to five years to recover (Fox et al 1985). Equitability is highest directly after fire, decreases up to year three or four after which large fluctuations are recorded (Fox et al 1985).

Recovery rates are a function of the rate at which vegetation cover is re-established (Fox et al 1985). In the Drakensberg grasslands vegetation and small mammal communities recover within the first few months after onset of the rainy season. Numbers and diversity start to decrease after two years which coincides with the time at which live biomass reaches a peak (Rowe-Rowe and Lowry 1982). Trollope (1978) claims that grass growth rates may be retarded for a full growing season after slow moving fires. It is therefore conceivable that small mammal habitat recovery rates could be indirectly affected by fire intensity and more detailed work is required.

The annual rainfall at the Swartberg study sites is only some 400 to 500 mm and diversity, density and equitability of small mammal communities took at least four years to recover (Fox et al 1985). In the Outeniqua mountains rainfall is higher (600 to 800 mm) and diversity, equitability and density of small mammal communities recovered within six months (unpublished data), at least as quickly as those of the Drakensberg grasslands.

In the western Cape (with far drier summers) richness and density reach a maximum after four years (Willan and Bigalke 1982). Density as recorded in a 38 year old stand was higher, but falls within the variation expected for stands older than four years (Breytenbach 1982).

From the above, one could conclude that a three to four year burning regime in fynbos should be sufficient for the maintenance of small mammal diversity, equitability and density at desired levels. I will show below why such a conclusion would be wrong.

Fire modifies composition of small mammal communities considerably. Diurnal species disappear within two or three days unless a large amount of unburnt material is left behind. The role of refugia (Willan and Bigalke 1982) and length of fire perimeter in maintenance and recolonization patterns of small mammal populations cannot be underestimated but will not be discussed here.

The successional patterns and the replacement of species over time was evaluated through multivariate analysis. It is obvious that the abundance of certain species peaks during specific post fire periods. The usefulness of the community approach when studying the effects of fire on small mammals can be illustrated by the following. In the Swartberg, *Graphiurus ocularis* colonizes large areas of three to four year old fynbos and retreats to rocky refugia after five or six years (Fox et al 1985). Channing (1984) studied this species intensively over several years, but failed to notice this phenomenon, and described *G ocularis* as rupicolous. It is possible, but unlikely, that this behaviour is present only in the southern Cape. Nevertheless without using a community approach it is unlikely that this behaviour would have been noted.

In mature vegetation (the period after which all plant species have flowered at least three to four times), there is considerable variation in small mammal species composition (Bond et al 1980; Nel et al 1980; Breytenbach 1982). If the maintenance of community diversity is a major management objective, management regimes should cater for differences in community structure. Here this variation was depicted by subjecting time and spatial sequence data to multivariate analysis (Austin 1980). In the

Swartberg these analyses indicated that only 15 to 17 years after fire does small mammal community structure approximate that of mature vegetation.

Effects of fire regime

The effect of fire intensity on recovery of small mammal community structure was evaluated in the Outeniqua mountains. Fire intensities in areas where *Hakea sericea* was controlled by slashing and burning was nearly 13 times higher than in uninfested fynbos or areas in which *H sericea* was burned standing (Breytenbach 1986) and was used as experimental sites to test for intensity effects. This increased intensity impaired the recovery of vegetation cover through reduction of seed banks and death of resprouting plants. Small mammal community structure in the Outeniqua's normally recovers very quickly but in the high fire intensity sites, succession was halted at the stage where only the early successional species persisted. Fire frequency also had an effect, as the structure of small mammal communities also failed to recover as rapidly in firebreaks and pine infested sites after being burned. This probably reflects on the recovery rate of vegetation. Increased fire intensity and frequency leads to a reduction in plant cover and also results in increased soil erosion rates (Breytenbach 1986; G J Breytenbach in preparation). Further analyses are required, but this study has clearly confirmed the findings of Bond et al (1980) and Breytenbach (1982) that in fynbos communities, small mammal community structure is largely determined by vegetation cover.

CONCLUSIONS

Fire immediately disrupts small mammal communities structure in that animals are killed and the habitat and food resources are changed. The rate at which small mammal communities and populations recover is affected by:

- Rate at which habitats recover, and this is amongst others a function of rainfall, fire regime, herbivory and seed and seedling predation.

- Fecundity of the different species.

- Migration rates.

More data are required on the importance of initial population reduction and the effect of fire patchiness and size on recovery rates.

In order to achieve the objectives of the Fynbos Biome Project it seems that neither a population nor a community approach will be adequate in themselves. Development of a predictive understanding requires inputs that include description and understanding of responses at the species, community and ecosystem levels. Particular attention must be given to intra- and interspecific interactions. There is at present a lack of both correlative and experimental data to show how post-fire changes in vegetation structure and density affect the diversity and density of small mammal communities (cf Bond et al 1980; Breytenbach 1982). In order to assess the effects of various management actions on biota it will be necessary to undertake a broad-based survey (synecological study) to determine which members of the community are affected by the current management regime. Once these have been identified, hypotheses can be developed and tested by using either a broad-based approach, or by doing autecological studies.

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7. FIRE AND FYNBOS ECOSYSTEM NUTRIENT DYNAMICS

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INTRODUCTION

Fire is considered the major disturbance in the fynbos biome. It releases nutrients from the vegetation and litter and may cause volatilization of nutrients and soil erosion (Figure 1). Prescribed burning has been a standard policy of managing the fynbos over the past 15 years. This practice has been based upon the need to reduce fuel loads for wildfire control, maintain maximum yields of silt-free high quality water in mountain catchments, to conserve a diverse indigenous flora and to eradicate invasive plants.

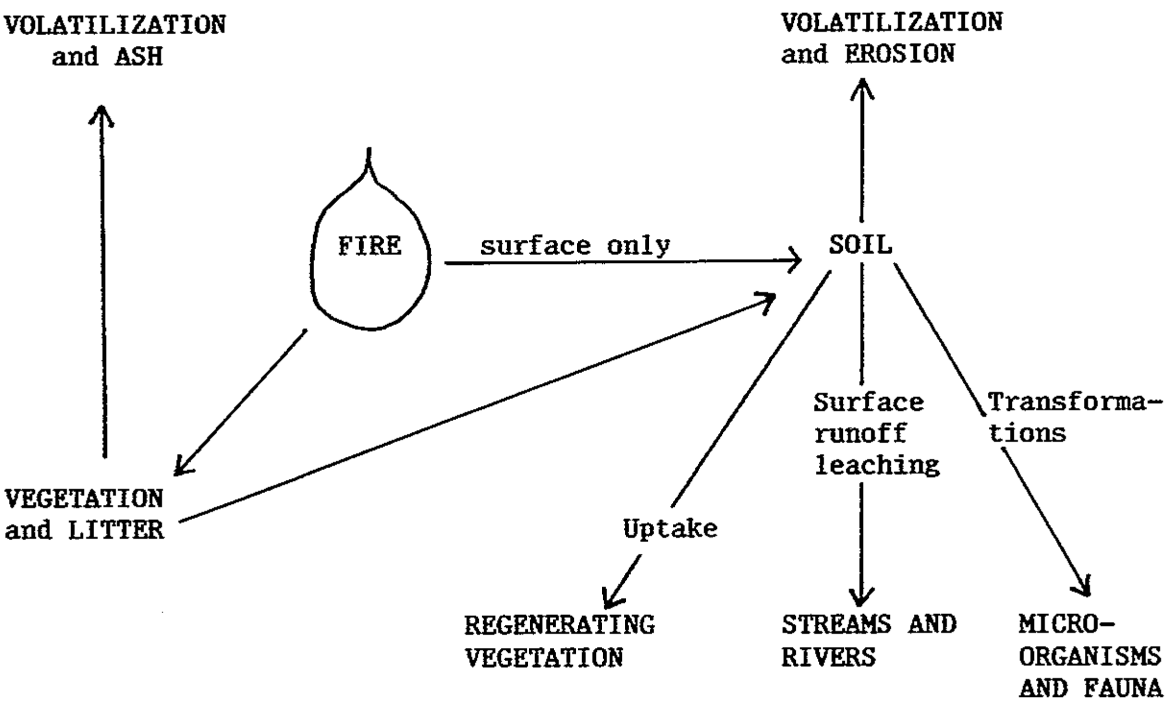

FIGURE 7.1 A flow diagram of the role of fire in the distribution of nutrients in the different compartments of an ecosystem.

CRITERIA FOR IMPLEMENTING PRESCRIBED BURNING POLICY

Size of fuel load is an important criterion for prescribing a burn (Kruger 1977). In mountain fynbos communities, sufficient combustable fuel accumulates four years after a fire (Kruger 1977), and most fynbos burns before it is 30 years old (van Wilgen 1981). Litter production is almost nonexistent in the vegetation during the first four years after a fire (Kruger 1977) but in older stands, litter and standing dead biomass may comprise up to 75% of the total fuel (van Wilgen 1982). However, the overall litter dynamics of the community appear to have been ignored as possible criteria for prescribing burns.

In young stands of vegetation, the litter layer is thin due to a low total annual litter fall (Mitchell et al 1986). In lowland fynbos at Pella, the composition of the vegetation changes with age from a greater proportion of restioids to a combination of proteoid, restioid and ericoid elements and the above ground standing crop and litter layer increase (Mitchell et al 1986). Olson (1963) maintained that the steady state of a vegetation will not occur until its composition, average biomass and litter layer mass have stabilized or reached a dynamic equilibrium. Very little emphasis has been placed on the timing of a burn in relation to when the fynbos vegetation has reached a steady state. In lowland fynbos at Pella, fires are so frequent that the steady state of the vegetation may never be attained (Mitchell et al 1986).

THE ROLE OF FIRE IN RELEASING NUTRIENTS FROM STANDING PHYTOMASS AND THE LITTER LAYER

There is growing evidence that in fynbos, decomposition of proteoid leaf litter and restioid culm litter is very slow compared with similar studies on Californian chaparral and Australian heathland vegetation (Mitchell et al 1986; Mitchell and Coley in press). The release of nitrogen and phosphorus during the decomposition of leaf litter of *Leucospermum parile* is negligible and calcium, iron, magnesium and potassium may accumulate in the litter during the first 18 months of decomposition. Thus, decomposition is probably not as important as periodic fires in releasing inorganic nutrients from the litter layer.

Fire intensity will determine the extent of fynbos biomass consumed and live woody material greater than six millimetres in diameter is normally not burnt even during a moderate to intense fire (van Wilgen 1981; van Wilgen and Le Maitre 1981). It is generally assumed that the release of nutrients from fynbos vegetation during a fire depends upon its age (Kruger 1977) but total nutrient loads also vary from site to site (Table 7.1). Estimates of total nutrients released from mountain fynbos by a fire are about 80 kg ha^{-1} with nitrogen being the dominant element (van Wilgen and Le Maitre 1981), whereas in sand plain lowland fynbos at Kraaifontein, both nitrogen and calcium were the main nutrients in the aboveground plant material (Low 1983).

TABLE 7.1 The total amount of nutrients contained in mountain fynbos at Jonkershoek and Zachariashoek (van Wilgen and Le Maitre 1981) and lowland fynbos at Kraaifontein (Low 1983). Results are in kg ha^{-1}

	Jonkershoek	Zachariashoek	Kraaifontein
Age (yr)	21	12	11
Total aboveground	22 621	7 398	17 310
Nitrogen	159	33	89
Phosphorus	7	1	8
Potassium	72	21	39
Calcium	69	15	195
Magnesium	14	5	13

THE ROLE OF FIRE IN NUTRIENT RELEASE AND BIOLOGICAL PROCESSES IN SOIL

The temperatures of several fynbos fires ranged from 149 to 371°C with a mode at 316°C (Taylor and Kruger 1978). A maximum temperature of 550°C was recorded at the soil surface in a heathland near Grahamstown but this persisted only for 10 seconds and declined to the ambient temperature within 480 seconds (Martin 1966). At depths below 10 mm in the soil, there appears to be a negligible change in temperature. Although the soil environment is insulated against high temperatures during fires, these often result in an elevation of available inorganic elements and pH, and increased soil erosion. Water repellancy, which would reduce infiltration, has been observed in the sandy, lowland fynbos soils. Repellancy may have resulted from the distillation of organic aliphatic hydrocarbons of the burning vegetation, followed by their deposition onto soil particles producing nonwettable surfaces (Cass et al 1984).

During a moderately intense burn of 20 year old lowland fynbos at Pella, total soil phosphorus did not change, but available phosphorus concentrations increased at the soil surface and reverted back to prefire levels within four months after the fire (Brown and Mitchell 1986). Simulated temperature studies showed that 200 to 400°C for 15 minutes caused an elevation of available phosphorus in the soil (Brown and Mitchell 1986). These fire temperature related changes would only occur at the soil surface.

During the same burn at Pella, 66 kg ha^{-1} of nitrogen was deposited as ash (Stock and Lewis 1986). A post-fire ammonium flush occurred at the soil surface but rapidly disappeared within a few days. Soil nitrate levels were not affected by the fire, but an increase in nitrate occurred by nine months after the fire. This accumulation suggests increased microbial activity in the form of nitrifiers during the post-fire period. Nitrogen mineralization studies showed no nitrification at the soil surface due to a sterilization effect by the fire (W D Stock, N Allsopp and O A M Lewis unpublished data). During the post-fire period of 42 days, ammonium and nitrate accumulation was markedly influenced by the moisture status of the soil at 0 to 75 mm depth (W D Stock et al unpublished data).

THE POST-FIRE RELEASE OF NUTRIENTS INTO RIVERS

Van Wyk (1982) has shown that net release of total dissolved solids occurred during the first two floods of the first winter after the burn but there were no marked changes in sediment loads. During the first spate of water after the burn, the pH of water at Jakkalsrivier increased by 1,5 to 2,0 pH units, whereas in other catchments where the water pH is normally about 5,0, no change occurred. van Wyk (1982) concluded that fire may increase water flow out of the catchment but would have a limited effect on nutrient budgets.

FUTURE RESEARCH

Research investigations reviewed here have mainly centred around a few sites in mountain and lowland fynbos. There is considerable evidence that the nutrient status, especially of phosphorus, in mountain and sand plain lowland fynbos is the lowest of all the vegetation categories of the fynbos biome (Witkowski and Mitchell in press). There is a real need to look at the effects of fire on fynbos nutrient cycling dynamics in more detail.

Fire behaviour has mainly been studied in relation to weather patterns, vegetation types and plant population dynamics. It is known that the fuel in older stands of fynbos vegetation is highly flammable. The degree of flammability may also be related to the nutrient status of the ecosystem. However, information on which chemicals affect the flammability of the fuel is very limited.

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