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Succession after fire in selected fynbos communities of the South-western Cape

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Frederick John Kruger

Thesis presented for the Degree of Doctor of Philosophy at the University of the Witwatersrand

Pretoria 1987

I hereby declare that the results presented here are my own work. These have not been submitted in full, or any part, to another university for degree purposes.

Two of my reviews on the topic of this thesis have been included here as Appendices 1 and 2. These arose from work undertaken in the early stages of this project, and for completeness they have been submitted as part of this dissertation. In the case of the paper in Appendix 2 the sections dealing with animals and conservation are not my own work, but all the rest are.

Frederick John Kruger

Pretoria
3 July 1987

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ABSTRACT

Successional changes in the vegetation after fire were studied in several fynbos communities of the south-western Cape Province of South Africa. The study sites were located in the mountains, at altitudes between 300 and 1000 m a.s.l., in areas with winter rainfall regimes and annual precipitation of about 900 to 1000 $mm.yr^{-1}$. Soils are highly leached, derived principally from quartzites. The two main sites were Zachariashoek near Paarl, where summers tend to be rather dry, and Jakkalsrivier east of Grabouw, where summer drought is ameliorated by fog precipitation and cloudiness. Successional changes were followed for intervals of up to 10 yr between fires, as well as for similar periods in vegetation that had been unburnt for 25 yr.

Vegetational changes were analysed by means of repeated floristic assessments on permanent quadrats and point-quadrat sampling of canopy cover composition on these and on larger plots. At Jakkalsrivier, recently burnt and long unburnt vegetation were also compared by paired samples. Demographic trends in populations of prominent shrub species were followed by repeated censuses of tagged samples in unburnt and recently burnt vegetation. Also at Jakkalsrivier, the effects of fire on resources available to plants were examined by sampling soil moisture and soil mineral nutrients, as well as by following trends in xylem pressure potentials in selected species of plants and analysing their foliar nutrient concentrations. Effects of fire on microclimate were tested by comparative studies on burnt and unburnt sites.

All fynbos communities sampled proved to be highly stable in the face of fire. Essentially, the pre-fire species composition was regained in 2-3 yr in every case. Species were added after fire, partly because of the appearance of ephemerals with life histories tied to fire, but

also because of the reappearance of longer-lived plants as well as through the readier detection of species in vigorous vegetative form. The species richness of the regenerating communities tended to be quadratically related to pre-fire biomass, as predicted from current succession theory. Most species in any community (about 70% on average) regenerated vegetatively by sprouting after fire. The relative numbers of species that regenerated germinatively, i.e. the seeders, did not vary in a manner predictively related to community biomass. There were relatively few species with specialised life histories based on reseeding, such as those with canopy-stored seed and ephemerals with presumably specialised requirements for germination. Virtually no recruitment could be found among plants in the older (about 25 yr) vegetation, in contrast with lowland fynbos sites, where recruitment of herbaceous species occurs, and some mountain fynbos sites on more fertile soils, where forest precursors may sometimes colonise.

Canopy redevelopment after fire indicated similar resilience among the different communities, despite variation in regrowth rates. Pre-fire growth-form composition was restored within around 10 yr. Maximum leaf-area indices ranged from about 1,5 to 2,5, although communities on phreatic sites had leaf-area indices exceeding 3,0. There was no evidence for a suppression of the understoreys by overstorey layers, mainly because the latter were sparse despite the abundance of tall broad-sclerophyllous shrubs in certain habitats. This was because the taller shrubs had sparse or slender crowns, or both, and because mortality tended to thin the populations before dense canopies developed. Trends in the composition of the canopy varied among communities. Communities in productive habitats, i.e. in this case on phreatic sites, were dominated in the early stages by a relatively luxurious growth of ephemeral herbs and soft shrubs which declined

within around 3-4 yr. Other sites had very sparse ephemeral cover, the early stages being dominated mainly by Restionaceae, Cyperaceae, and other sprouting herbs, and sprouting and seeding shrubs, which were constituents of the pre-fire canopies. In this respect, the fynbos is clearly distinguished from the California chaparral, for example, where ephemerals tend to dominate the post-fire stages on most sites.

There was no evidence that fire had any effect on the water relations of regenerating vegetation, although stream discharge is known to be increased by fire in these environments. There was tentative evidence, in enhanced foliar concentrations of some mineral nutrients, that regenerating species of climax plants exploited nutrients released in fire. However, any such responses were small, especially in comparsion with responses observed in chaparral, for example. Ephemeral shrubs had much higher concentrations of foliar nutrients overall than climax species, tending to confirm the correlations found in Australian heathlands between plant life-history and nutrient economy. The effects of fire on microclimate were pronounced, especially on the thermal and water vapour regimes experienced by seedlings and sprouts. These extremes did not, however, appear as water stress in regenerating plants. Despite relatively sparse canopies, mature vegetation did reduce light at the ground to levels likely to affect seedling recruitment and survival. Preliminary experiments with a local dominant shrub, Leucadendron xanthoconus, showed a pronounced intolerance of shading and hence that light attenuation by canopies must be implicated in successional processes.

The demographic studies indicated that density-dependent effects were not important in survival of plants. Two species of fire ephemeral shrubs effectively died out within four years, being characterised by markedly higher growth rates than climax species and brief and early

fecundities. Climax shrubs had more or less constant rates of mortality over time, though populations in unburnt vegetation tended to have slightly higher rates of mortality than young populations. Densities of seedling populations were very high, but mortality rates were extremely low.

In summary, it may be said that the fynbos communities studied here are very stable under a given fire regime. Recovery is rather rapid, being apparently achieved within 10 yr. Not much change occurs in older vegetation, but there was a gradual attrition of populations of dominant shrubs, without recruitment, with rare exceptions. Summer droughts in these montane environments are evidently not sufficiently marked for water deficits to play a primary role in succession, so that fire has no effect on plant water relations. Nutrient responses are relatively weak, and masked in the plants by the low rates of metabolism in climax species. Succession after fire is distinguished by the recovery of pre-fire communities, and subsequent inhibition of recruitment. This inhibition is probably through the effects of canopies on microclimate, although the interactions between especially plants and animals have been implicated in succession in other studies.

ACKNOWLEDGEMENTS

This thesis represents part of the outcome of several long-term experiments, as well as the results from new studies. It would not have been possible without the past efforts of several people, and direct assistance in the later stages.

I would like to acknowledge the contributions of staff at the Jonkershoek Forestry Research Centre, who have maintained the system for climate, streamflow, and vegetation monitoring at the sites used in this study, where in some instances the record extends from 1941. For the historical vegetation data at Jakkalsrivier I am indebted especially to Ross Haynes, Theo Stehle, Horace Howe, and Raymond Smith. For the field work during the course of this study I am grateful for assistance from Alan Lamb and especially from Greg Forsyth, who bore the burden of work for ongoing monitoring and assisted considerably with other experimental work and data processing. Dirk Versfeld helped with several aspects of instrumentation and field measurements. My thanks go also to Don Bands at Jonkershoek for the manner in which as Officer in Charge he was able to accommodate my demands on his organisation.

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PREFACE

"When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this! Every one has heard that when an American forest is cut down a very different vegetation springs up; but it has been observed that ancient Indian ruins in the Southern United States, which must formerly have been cleared of trees, now display the same beautiful diversity and proportion of kinds as in the surrounding virgin forest. What a struggle must have gone on during long centuries between the several kinds of trees each annually scattering its seeds by the thousand; what war between insect and insect - between insects, snails, and other animals with birds and beasts of prey - all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees! Throw up a handful of feathers, and all fall to the ground according to definite laws; but how simple is the problem where each shall fall compared to that of the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!"

Darwin (1859:86)

ERRATUM

Page 197 follows directly on page 194 but no text has been omitted.

1. INTRODUCTION

1.1. The fynbos

The Fynbos Biome as a whole includes several sclerophyllous vegetation formations centred in their distribution on the mediterranean and sub-mediterranean regions of the Cape Province. These formations have been classified in several ecological types by Moll et al. (1984). Here, the term fynbos is used to denote the sclerophyllous vegetation of the mountains of the Cape Folded Belt and the coastal sands and limestone hills, with generally highly leached soils or where nutrient deficiencies are otherwise marked. This vegetation is characterised by the presence of tufted aphyllous plants in the Restionaceae. Low ericoid shrubs, often in the Ericaceae, and taller proteoid shrubs are important distinguishing features (Campbell 1985). Campbell (1985) has derived a comprehensive classification of the fynbos communities of the mountains, and further detail may be found there and in Taylor (1978) and Kruger (1979).

Mountain fynbos has attributes of special value to South African society. First, it constitutes a stable vegetation cover in the mountain catchments of the most important sources of water for the agricultural and industrial economies of the region. These montane landscapes provide the scenic backdrop for an area in which tourism is of growing importance, as well as the sites for extensive outdoor recreation. The products of the fynbos, as cut flowers and in other forms, are finding a place of increasing value in the regional economy. Finally, the unique biogeographic and ecological features of the fynbos confer special educational, scientific, and conservation values on the ecosystems. Fynbos must necessarily be managed, because of the need to govern the influence of extraneous factors, such as invasive alien plants, as well as to satisfy human needs, such as to control wildfires. Management requires ecological knowledge and a technology for implementing policies, for example in respect of

controlling invasive plants and applying fire. The study reported here is one of many directed at improving our knowledge of the ecology of fynbos for this purpose.

1.2. Rationale for this study

Ecological succession is defined as the cumulative temporal change in one or more properties of the ecosystem on any particular site (Grime 1979; Miles 1979; McIntosh 1981). These properties include the species composition and physiognomy of vegetation. The changes are directional over a given time period and in the sense that the state of the ecosystem tends away from the initial state. Succession does not include seasonal or other changes over periods shorter than a year. The process does not necessarity terminate in a system in equilibrium.

The process of ecological succession is a fundamental aspect of community ecology. Understanding succession is in turn basic to the rational use and management of natural and semi-natural ecosystems (Finegan 1984). Periodic fire is a widespread factor disturbing many vegetation types of the world, so that the prevalent dynamics of natural communities in such areas are kinds of post-fire or pyric successions and this is especially so in mediterranean-type ecosystems (see, for example, Mooney and Conrad 1977). The fynbos is no exception in this regard. Much of the rationale for the management of natural fynbos communities is based on a largely hypothetical view of the relationship between fire regime, succession, and the maintenance of biotic diversity, and of energy flow and material balance in these ecosystems (e.g. Bands 1977; Kruger 1977). An essential argument in management policy, for example, is that because the intervention of fire is necessary for some plant species to complete their life cycles, it is necessary that the cycle of fire and succession should be repeated in a more or less predictable fashion to allow such species to survive and evolve.

There are very few published studies on succession after fire in fynbos plant communities. Notable among these are reports by Levyns (nee Michell 1922; 1929, 1935a), Adamson (1935), and Wicht (1948). Kruger and Bigalke (1984) have synthesized these studies.

1.3. Theory of ecological succession

1.3.1. Primary and secondary succession in relation to disturbance

In the present context, disturbance may be defined as any external factor leading to partial or total destruction of the plant biomass (Grime 1979). The distinction is drawn between primary succession, where the site is newly exposed or so heavily disturbed that the effects of the past biota are no longer evident, and secondary succession, where the disturbance is great enough to initiate substantial change but where some elements or effects of the biota persist, e.g. in the form of buried seed or an evolved soil profile (Weaver and Clements 1938; McIntosh 1980). Primary succession occurs in fynbos when parent substrates are exposed by topographic processes, such as mass-wastage erosion in mountains, and dune-building at the coast. Such exposures amount to a small proportion of any fynbos landscape.

Processes which denude elements of the landscape differ in the degree of their effects but not necessarily in kind from those leading to primary successions. Disturbance preceding secondary succession may be light or severe, local or widespread, and the succession can vary accordingly. "Much of the persistent controversy surrounding succession stems from the very different starting points of pioneer states following kinds and degrees of disturbance from which the seral sequence begins" (White 1979). Disturbance affects the patterns and mechanisms of subsequent succession. Therefore any study of secondary succession must be specified in terms of the type and quality of the particular disturbance which initiates the process. Vitousek and White (1981), Sousa (1984), White and Pickett (1985) and Grubb and Hopkins (1986) discuss the elements of disturbance regime. Modified slightly, these are as follows:

(a) Size of disturbance. Horn (1981) notes the correlation between size and synchrony and the important distinction between asynchronous, small-scale disturbances and synchronous, large-scale disturbances.

(b) Recurrence interval is the mean return period of

disturbance at a given point in the landscape, and is the inverse of frequency; it is also sometimes useful to recognize regional frequency, i.e. the total number of disturbances in a geographical area during a given period (Sousa 1984).

(c) Rotation or turnover rate is related to recurrence interval but is the average time over which a specified area of the landscape is fully disturbed; certain elements of such an area may be disturbed more than once in this interval.

(d) Magnitude of disturbance has two components, (i) intensity, which is "a physical measure of the force of impact" (windspeed, energy release rate in fire, etc.) and (ii) severity, a measure of the damage to the community caused by the disturbance, e.g. relative proportion of biomass consumed by fire.

(e) Predictability of disturbance is measured by the variance of the period (Sousa 1984).

(f) A disturbance regime is distinguished finally by timing in respect of season.

White and Pickett (1985) also emphasise synergistic effects in this context, for example, the interaction between drought and fire regime. Horn (1981) defines chronic disturbance as disturbance so frequent as to end the lives of most dominant plants (trees); this is a useful relative measure, because different vegetation formations are often characterized by dominants with markedly different life-histories. Fire is a chronic disturbance in forests of Eucalyptus regnans, where it may recur at intervals of centuries (Noble and Slatyer 1981) as well as in fynbos, where it may recur within 10 years or less, since apart from longevity, the life history of E. regnans is much like that of Protea spp. Grubb and Hopkins (1986) draw the distinction between continual and periodic disturbance. Continual disturbance, such as grazing, results in

vegetation that is relatively constant om structure and composition, whereas periodic disturbance causes marked change in these terms.

The kind of disturbance is related to severity; a fire in vegetation is likely to destroy a lesser proportion of biomass than would a landslide, for example. Weaver and Clements (1938) classify causes of disturbances as topographic, climatic (which includes lightning as an ignition source), and biotic.

Problems which arise from the relationships between disturbance, especially severity of disturbance, and subsequent succession, are illustrated by contradictions in Weaver and Clements (1938; pp. 106 et seq.), "Seres [i.e. the successional series] originate only in bare areas or in those in which the original population is partially or wholly destroyed" (p. 106), ".... so .... that pioneers dominate the area" (p.115). They state that fires in grassland "practically never" initiate succession. Nevertheless, they accept the process of recovery in chaparral after fire as being a secondary succession even though the effects of fire are like those in grassland and pyric succession is essentially a process of recovery of species present before fire (Hanes 1971), a process termed "autosuccession" by Muller (1940), Hanes (1971), and MacMahon (1981) and "cyclic succession" by Whittaker and Levin (1977). Therefore, the definition of succession as a process involving pioneers, as required by Weaver and Clements (1938), Connell and Slatyer (1977), McIntosh (1981) and many others, is also a relative one and related to the nature of disturbance.

1.3.2. Mechanisms of secondary succession

1.3.2.1. The sequence of processes involved Clements classified the processes involved in plant succession on newly exposed sites or following disturbance according to the sequence in which they are expressed (Weaver and Clements 1938) and this scheme is still relevant (MacMahon 1981). The processes recognized were as follows:

(a) Migration is the arrival of plant propagules (seeds, fruits, and similar) from outside the disturbed area.

(b) Ecesis includes the phases of germination, establishment and growth to maturity, in invading propagules.

(c) Aggregation is the proliferation of established, reproducing invaders through local dispersal of propagules and their germination, establishment, and growth, or through vegetative propagation and spread. Regeneration after fire through germination from seed surviving on the site or through vegetative means is included in aggregation. "The appearance of each successive stage in succession is brought about by the interaction between immigration and aggregation."

(d) Competition takes effect in the succession as soon as resources become limiting and "... is absent only in the initial stages of succession when the pioneers are still far apart." Competition increases as succession proceeds.

(e) Invasion is the net outcome of migration, ecesis, aggregation and competition.

(f) Reaction is the effect of the plant or stand of plants on the habitat. Reaction is centrally implicated in the classical notion of succession, since it was seen to involve an amelioration of extreme conditions so as to favour late-successional over early-successional species until conditions become more favourable to occupants than to invaders, and the existing community becomes more or less permanent, constituting a climax or subclimax. "Reaction is thus the keynote to all succession, for it furnishes the explanation of the orderly progression by stages and the increasing stabilisation which produces a climax."

(g) Stabilisation is the process marking the culmination of succession and encompassing processes by which conditions favourable to occupying species are maintained and conditions allowing invasion are minimized. It leads to an increase in dominance.

Clements (1916; Weaver and Clements 1938) held that, within biogeographic regions, a uniform climax association would arise despite diverse successional pathways and that succession was analogous to the development of the organism, i.e. involving a fully predictable sequence of developmental phases. These distinguishing features of Clementsian theory have been discredited, on empirical and logical grounds (McIntosh 1980), but the mechanisms identified as operating during succession are broadly valid.

1.3.2.2. Mechanisms governing species' responses to disturbance The relationship between disturbance and community response are discussed in Chapter 4. A useful approach to analysing the plant community with a view to predicting responses is the scheme of plant vital attributes proposed by Noble and Slatyer (1980). This permits the properties of vegetation to be specified so as to allow qualitative prediction of response to a disturbance regime. The method is individualistic, in that it requires information on each of the species of importance in a given stand of vegetation. It is qualitative in that predictions are made of changes in vegetation state as reflected in the presence of absence of species rather than in changes in their relative abundances. Finally, it is analytic in that predictions of vegetation response are deduced from the information gathered about constituent species, and no induction is logically possible.

Three main groups of vital attributes are recognised:

(a) the method of species arrival after, or persistence during a disturbance;
(b) the ability of a species to establish and grow to maturity in the developing community; and
(c) the time taken for the species to reach critical life stages.

Method by which a species presists on the site of disturbance Distinction is drawn between species whose populations are killed by disturbance and replaced by migration ((a) :D-species), and those which survive on site in some form or another. Of the latter, some

survive by means of regeneration from seed or other propagules and these are classified in the following categories:

(b) S-species: those which survive from stores of seed, normally in the soil, which persist longer than the parent plants,

(c) G-species: as for S, but where the stores are exhausted by the germination event, and

(d) C-species, where seed is available while mature plants exist on the site and is normally stored in serotinous organs in the canopy of the plant.

Among species which regenerate vegetatively the following additional categories were recognised:

(e) V-species, which sprout and form juvenile shoots,

(f) U-species, which sprout to form reproductively mature shoots if mature at the time of disturbance, and

(g) W-species which are unable to sprout as juveniles but sprout to form mature shoots if disturbed when mature.

Noble and Slatyer were able to show that just 10 such patterns are likely to be encountered among plants, some of these being rare.

Species may have vegetative and germinative methods of persistence in combination. Additional categories needed to accommodate combinations that may allow a qualitatively different response in species were the following:

(h) Δ-species, where the D and the U or the D and the W characteristics are combined,

(i) $\sum$-species, where S and U, S and W, or G and U are combined,

(j) Γ-species, where G and W are combined.

Conditions for establishment Distinction is drawn between tolerant (T) species, able to establish and grow to maturity at any time in secondary succession, intolerant (I) species, which can establish only under the conditions immediately following disturbance, and species unable to establish immediately following disturbance, requiring modification of conditions by pioneers (R).

These two forms of vital attributes occur in real, "natural" combinations amounting to a maximum of 14 distinct "species types" or "behaviour patterns", each denoted by a two-letter combination.

Life-stage parameters In the scheme, species must be characterised by the time required after disturbance to pass through or attain three stages; these periods are:

(a) m, the time taken to reach reproductive maturity;
(b) l, the longevity of the species population within the community; and
(c) e, the time taken to reach local extinction.

This scheme reduces the information required for qualitative modelling of the effects of disturbance on vegetation to a necessary and sufficient minimum. This parsimonious scheme provides a useful framework for the comparative analysis of secondary succession in vegetation.

1.3.3. The Connell-Slatyer models of plant succession

Connell and Slatyer (1977), dealing with succession as a process of compositional change, synthesised the diverse observations on patterns of plant succession in terms of the dominant interspecific interactions likely to be involved in secondary succession. The initial disturbance opens the site to colonists including or consisting entirely of "early-successional" i.e. pioneer species, which require recent disturbance for invasion. Different patterns of

secondary succession may follow and Connell and Slatyer proposed that any observed pattern may be accounted for in terms of effective mechanisms by one of three models.

The facilitation model includes Clementsian succession. Only pioneers are able to colonise the disturbed site. These species modify the site to the detriment of their own recruitment and in favour of other invaders and so on in relay until stability is achieved, when the final dominants do not favour invasion and are able to replace their populations. This was called the "relay floristics" model of succession by Egler (1954).

In the other two models any available species is able to colonise the disturbed site, and modification of the site is not a requirement for further development. These include Egler's initial floristics model, but also accommodate cases where species may enter the sere later, without requiring the death of plants of species already present or any other interaction. In the tolerance model the initial colonists do not modify the site to the benefit or the detriment of later invaders. The initial flora may or may not contain late-successional species, and late-successional species are able to invade at any time. "The sequence of species is determined solely by their life-history characteristics". However, the outcome of the sequence reflects a competitive hierarchy among species, with the most tolerant, or competitive, species finally dominating (Horn 1981). The third, inhibition, model describes cases where the species which establish after disturbance act to inhibit subsequent establishment or suppress the growth of any colonists.

Connell and Slatyer maintained that secondary succession would proceed in every case to a stage when patterns of recruitment would be dominated by regeneration in gaps as adult plants died asynchronously, and when further invasion may or may not occur (but not in the facilitation model), depending on the available flora.

The facilitation model would be rejected if field studies of a secondary succession show no sequential replacement of species or, similarly, that late-successional species are encountered among

initial colonists: in such cases, either the second or the third model would be valid. If sequential replacement occurs either the first or the second may be valid and then experiments are required to test whether facilitation operates. "Necessary and sufficient evidence in support of [the tolerance model] would consist of observations or experiments showing that invasion and growth to maturity of later species neither require conditions produced by earlier species [the facilitation model] nor are inhibited by them [the inhibition model]... Evidence supporting [the latter model] consists of observations that early species suppress the establishment of later ones, inhibit their growth, and reduce their survival" (Connell and Slatyer 1977).

Grubb and Hopkins (1986) argued on the basis of results from various studies that a more comprehensive classification of dominant successional processes was needed. In addition to tolerance, they recognised (a) enablement, where establishment of late successional species was impossible without the effects of pioneers, (b) facilitation, where the rate of establishment of late successional species was increased by the effects of pioneers, (c) inhibition, where pioneers decreased the rate of establishment on thier successors, and (d) exclusion, where pioneers prevented establishment of later species entirely.

1.3.4. Succession and ecosystem processes The initiating disturbance releases resources, transforming a more competitive to a less competitive environment. The question of resource dynamics during succession must ultimately be resolved at the level of the whole ecosystem. Odum (1969) extended succession theory to include ecosystem processes and set out a conceptual model which included changes in community energetics or carbon flow, community structure, aspects of the life-histories of the species involved, and nutrient cycling. Broadly, he argued for succession to a climax where the site was occupied by fully niche-differentiated species with maximum resource-use efficiencies, low net productivity and community respiration, complex food chains, and tight, highly conservative nutrient cycles. He argued for a trend towards homeostasis, expressible in measures of the degree of internal symbiosis, relative

stability, entropy levels, and information content. Odum's extended notion of the climax community has suffered the same critique on theoretical and empirical grounds as that of Clements, but he firmly established ecosystem concepts in succession theory.

Ecosystem processes in succession have received prominence through the work synthesized by Bormann and Likens (1979). These studies dealt with secondary ecosystem succession including direct observation of development of hardwood forest after clearfelling and computer simulation of development beyond the period of observation. The open disturbed site had considerable dead organic matter available for decomposition, while relatively little live vegetation was available to trap energy and nutrients and consume water. The ecosystem rapidly released carbon, nutrients and water. This was designated the "reorganization" phase. In the next, the aggrading phase, the ecosystem accumulated biomass, evapotranspiration losses increased markedly with growth of vegetation, and rainfall energy and erodibility of substrate decreased. Consequently, streamflow outputs and hence outputs of dissolved and suspended materials declined. Also, greater quantities of materials were sequestered in biomass, and internal nutrient recycling was enhanced. The ecosystem accumulated materials. The transition phase was a variable length of time during which total biomass declined and trends that marked the aggrading phase were reversed. This was followed by the steady state, several hundred years after clearfelling, when total biomass fluctuated about a mean and stabilised at a level less than in earlier phases, net ecosystem production was zero, and nutrient imports and exports were in balance. The authors suggested that this steady state was dynamic and comprised a mosaic of patches in different states following small-scale disturbance - a "shifting-mosaic steady state". This model was called the Biomass Accumulation Model.

Vitousek and White (1981) provide a conceptual framework for the dynamics of nutrient availability during succession. Using phosphorus as an example, they show how the major trend is set by the process of pedogenesis during primary succession. Total phosphorus in the system declines progressively with time but the fractions of phosphorus in parent material, as soil organic phosporus, in the

biomass, in occlusion on soil particles and unavailable to plants, and in equilibrium with the soil solution and available to plants, do not change monotonically. Trends in phosphorous fractions and processes of nitrogen fixation and nitrification interact.

"The net result of these processes is a system relatively deficient in nitrogen early in soil development, one with N and P in near equilibrium, maximum production, and the largest amount of nutrient cycling in the middle, and with substantially decreased nutrient availability late ...". They speculate that disturbance early in this sequence, when nitrogen is limiting but phosphorous is not, will favour leguminous and analogous colonists. Disturbance in the middle of the sequence can lead to a large release of nutrients and a highly productive environment, but disturbance will effect little release of nutrients late in the sequence, when nutrient limitation is general and the system is dominated by internal plant nutrient cycles and other tight cycles.

Vitousek and Reiners (1975) have suggested how the successional course in net primary production can determine patterns in the mass balance of ecosystems (see also Gorham et al 1979). Low phytomass and leaf area indexes immediately after disturbance reduce the evapotranspiration component of the hydrological cycle and increase stream flow. Decomposition of organic material and increased movement of water out of the system in the liquid phase results in high leaching and maximum net rates of nutrient output but nutrients, water and light are fully available to plants and net primary production and phytomass increases rapidly. With recovery of the vegetation, plant uptake of nutrients and greater evapotranspiration reduce leaching so that net nutrient export falls to a minimum. Later losses of nutrients increase as net primary production slows and equilibrate with inputs when net production reaches zero. This model is essentially similar to that proposed by Bormann and Likens (1979).

1.3.5. <u>Resource-use patterns during succession in relation to life-histories and ecophysiological of species and changing availibility of resources</u> Disturbance destroys vegetation and simultaneously affects the availibility of resources. Subsequent

succession is partly the outcome of the fact that pioneer and late-successional species differ in their life-histories, partly because the identity and quantities of resources change in time, and partly due to the onset of or changes in the interactions among species. Research on succession must clarify the nature of these underlying mechanisms.

The theory of r and K selection is relevant. This predicts that species subject to selection through density-independent mortality as a result, for example, of disturbance, will evolve traits that maximise intrinsic growth-rates (r-species), and concomitantly maximise reproductive effort, while those subject to density-dependent mortality, i.e. suffer little disturbance, evolve traits that maximise competitive ability and thus the capacity to retain a site once occupied - the K-species (Pianka 1978). Succession may then simply be seen as a progression from communities dominated by r-species to others dominated by K-species, as the natural outcome of underlying demographic patterns. Grime (1979) proposes a primary three-part classification of plants by life strategies, which expands the notion of the r-K continuum: ruderals, competitors and stress-tolerators. Subordinate categories provide for intermediates, such as stress-tolerant competitors. Again, once the demographics of plants in each category are known, successional patterns may be predicted from a knowledge of how the flora of a site is constituted in terms of strategy-types.

Bazzaz (1979) and Grime (1979) review the demographic and ecophysiological traits that characterize strategy-types in the context of succession. They identified contrasting suites of characters, including those typifying the germination physiologies of pioneer and climax plants, the photosynthetic capacities of the two forms, water relations, resource-use efficiencies, and carbon balances. Grime (1979) considered that processes of succession involved interactions the competitors, the ruderals, and the stress-tolerators. Their relative roles would vary depending on the intensity of stress and the intensity of disturbance in the habitat.

Tilman (1982, 1983) has explained partitioning of the habitat among

sympatric plant species in terms of resource consumption ratios. Plants consume the same resources of light, water and mineral nutrients but species differ with regard to their optimum ratios of nutrient availabilities. Therefore, insofar as there is spatial or temporal heterogenity in the ratios of available, limiting resources so there will be a corresponding diversity of species. The physiology of species in the successional sequence should reflect changes in these ratios. Changing patterns in spatial heterogeneity of this kind, i.e. in resource availability and resource ratios, may also affect the incidence and patterns of interaction between species and hence the patterns of coexistence (Price 1984).

Vegetation dynamics has been implicated as a factor determining community species diversity. Huston (1979), for example, argues that, by and large, communities are continuously successional because of disturbance histories or fluctuating conditions and consequently do not reach equilibrium where species' displacement occurs to leave an assemblage only of those that are fully niche-differentiated; there is a measure of competitive displacement but the rate of displacement depends on the population growth rates of the constituent species (productivity of the site) and the frequency of disturbance; other factors being equal, an intermediate frequency of disturbance will maintain highest diversity. Connell (1978) also presents an "intermediate disturbance hypothesis", but in his argument diversity is greater at intermediate frequencies of disturbance because high frequency allows only r-species, low frequency only K-species, whereas the intermediate regime allows both to co-exist.

Whittaker and Levin (1977) examine a comprehensive hypothesis to explain species diversity in communities and consider small-scale "microsite" heterogeneities and superimposed effects of environmental fluctuation and succession to be major determinants of diversity, although they felt development of theory must wait on more rigorous study of representative cases.

1.4. Conclusion: research needs in the fynbos

Succession theory has evolved to take account of empirical data and to

explain and predict community change in terms of the traits of the biotas involved and how they interact with underlying mechanisms.

The theory has its origins in the temperate Northern Hemisphere, and especially in forest ecology, sometimes limnology, though Clements and his colleagues were admittedly comprehensive in their accounts of succession in North American biomes (Weaver and Clements 1938). Latterly, theoretical treatments have explicitly incorporated tropical forest and marine ecosystems, especially coral reefs and intertidal zones (Connell and Slatyer 1977). Where succession theory has failed to accommodate given successions, or to provide the understanding needed to predict the consequences of a given disturbance regime in a given biome, an analytic approach could provide a specific solution to the case in question. The Noble-Slatyer scheme is an example of the analytic approach. Analyses of this kind will provide indispensible information about succession in natural communities, but no basis for extrapolation beyond the cases at hand.

Although the scheme provided by Clements for the processes of succession is generally useful, there is important variation among different habitats or vegetation types. Grime (1979) has proposed a model which predicts different successional pathways, in terms of changes in composition of species with different ecological strategies (competitors, ruderals, and stress-tolerators), in habitats with contrasting potential productivity. The different pathways are the outcome of variations in the relative roles of competition, stress and disturbance in the contrasting habitats. Grubb and Hopkins (1986) have placed the processes of recovery, or types of resilience, in two classes, <u>in situ</u> resilience, where regeneration is from sprouting of surviving plants or germination from presistent seed banks, and resilience by migration, where regeneration depends on dispersal of plants to the disturbed site from outside. These views of the processes underlying succession need to be unified, to provide a sound basis for predicting the course of change following different kinds of disturbance in different kinds of ecosystems.

In fynbos and its ecological analogues, fire provides a relatively predictable disturbance regime. Resources, especially of water and

nutrients, are often severely limited. Studies of pyric succession in these ecosystems are necessary to provide the knowledge required for a robust theory, or at least for the derivation of a comprehensive set of theories. One may determine from a study of these pyric successions whether the process is uniform and orderly, and whether the processes involve interactions between species or whether they are neutral in this respect. Opportunity exists to isolate the role of resource availability, and to determine the consequences of changing availability of resources over time. One may test explicitly whether or not competition is the mechanism which drives the succession, and how competition would weigh against other mechanisms such as herbivory and predation, or against competitively neutral population processes. Successional changes in ecosystem function can therefore be quantified and contrasted with those observed in the limited number of ecosystems that have been studied in this respect.

The study reported here was designed to contribute to aspects of the necessary understanding of pyric succession in fynbos by meeting the objectives of (a) improved description and quantification of pyric succession in fynbos and (b) analysis of mechanisms underlying pyric succession.

2. PYRIC SUCCESSION IN SCLEROPHYLLOUS SHRUBLANDS OF MEDITERRANEAN-TYPE ECOSYSTEMS

Regions with a mediterranean-type climate are marked by cool winters when precipitation occurs and soil moisture levels are high, warm springs when precipitation is low but soil moisture levels are still high, and warm to hot summers when precipitation is low and soils are dry. All these regions are marked by frequent fires in the vegetation, except perhaps in the case of the matorral in Chile (Mooney and Conrad 1977).

General features of the effects of fire on the sclerophyllous shrublands of the mediterranean-climate regions of the world and of the succession following fire have been reviewed by Kruger (1983). There are features in common among all or most of these shrublands, but also important differences. The factors which determine the differences and the similarities have been identified only in the broadest terms. One such factor is the variation in soil fertility, with variations in the water balance being secondary (Specht et al. 1983). Here, comparisons are drawn between fynbos and Australian heathland, which are similar in nutrient status, as well as with California chaparral, which has substantially more fertile soils (see, for example, Specht and Moll 1983). Although pyric succession has been studied in other shrublands, in the Mediterranean Basin and in Calluna heathlands, for example, the comparisons drawn here suffice to identify the major features of the pyric successions and of the views about the underlying mechanisms.

2.1. California chaparral

2.1.1. Fire regime Fires in the chaparral of Southern California have a fairly long recurrence interval of perhaps 30-40 yr but with a large variance (Keeley 1982; Kruger 1983). Vegetation which has escaped fire for 60 years or more is evidently not unusual. As in other mediterranean-type ecosystems, the upper limit to fire frequency

is determined by primary productivity, plant form, and the rate of accumulation of dead material (Kruger 1983; Christensen 1985). In chaparral, large fires apparently do not recur readily within 15-17 years, although smaller fires may recur earlier if grasses are abundant (Kruger 1983). The fire season is quite markedly restricted to late summer and autumn, mainly by seasonal variation in fuel moisture content but possibly also by seasonal fluctuation in the concentration of ether-extractable organic compounds in foliage (Christensen 1985). Fire intensities are high, and fires usually consume most of above-ground biomass, creating deep ash beds. There have been no specific studies of the differential effects of fire regime or of components of the regime on chaparral, although Horton and Kraebel (1955) have recorded low seedling recruitment after spring fires relative to autumn fires.

2.1.2. Principal features of the succession On most substrates, fire is followed by rapid regrowth of herbaceous species, many of which were absent in their vegetative form before the burn. These herbs may constitute a cover of 30 to 80% in the first year, depending on physiography and precipitation received (Sampson 1944; Keeley et al. 1981; Zedler 1981). Thereafter, abundance declines markedly but cover in the third year would amount to 5-30%, while ephemeral subshrubs such as Lotus scoparius, having germinated in the first season, would at this stage constitute 10-60% or more. Seedlings of these species do not establish again before the next fire. As discussed later, this is either because germination is inhibited through factors associated with the canopy, such as the altered light and soil temperature regimes, or allelopathic effects (Keeley et al. 1985) or because seedlings are eliminated by herbivores. Of these species, as with longer-lived shrubs, those which regenerate from seed do so mainly from seed stored in the soil on the site (Sweeney 1956; Hanes 1977; Zedler 1981; Keeley et al. 1981, 1985; Keeley 1987).

Regenerating shrubs recover pre-fire levels of canopy cover, usually around 50%, by five or up to 7-9 yr after fire (Hanes 1977; Keeley et al. 1981). Biomass accumulation rates (live) decline to zero at about 40 yr (Specht 1969; Black 1987). Further development involves the

growth of persistent shrubs and mortality among some seeders, so that canopy cover is at a maximum 20-40 yr after fire but tends to decline gradually thereafter. The cover of herbs declines in direct proportion as the canopy cover of shrubs increases (Westman 1983). Certain species of shrub are relatively long-lived (see below) and survive without recruitment but on cooler poleward slopes recruitment of species such as Quercus dumosa, Prunus ilicifolia, and Rhamnus ilicifolius may occur and initiate a gradual process of change to a hypothetical oak woodland (Patric and Hanes 1964; Hanes 1977; Zedler 1981).

Reid and Oechel (1987) have analysed the patterns of photosynthesis and transpiration associated with a series of chaparral stands ranging in post-fire age from about one to 85 years (see below) to evaluate possible changes in canopy processes that may be associated with successional change. They found no significant relationship between stand age and the rates of photosynthesis per unit leaf area, nor any evidence of physiological decline with age; they suggested that the factor underlying the change in biomass accumulation rate during succession was the increasing relative cost of maintenance respiration associated with a declining ratio of foliage to supporting and other tissue (cf Black 1987).

Generally, therefore, chaparral stands enter the so-called senescent phase at about 40 yr after fire when some dominant shrubs (e.g. Ceanothus spp.) may have died out, biomass accumulation rates are near zero, and recruitment does not occur (Hanes 1977; Reid and Oechel 1987).

Hanes (1971) has called this cycle of fire and subsequent recovery of the vegetation autosuccession, because the disturbance is followed immediately by the regeneration of the species which dominated the stand prior to the fire.

2.1.3. Plant life histories and regeneration after fire Kruger (1983) has summarized available data. The ephemeral species include mostly annuals and seeding chamaephytes or sub-shrubs. A few species

of geophytes and hemicryptophytes may be found. The longer-lived shrubs include many species of seeders, but any single stand may contain only a few, perhaps three, such species. About 1-10 species of sprouting shrub may be found within the stand.

The canopy of mature vegetation may be dominated by seeders in some cases, or by sprouters in others. Variation in the relative contribution of seeders and sprouters has been ascribed to variations in water balance (Hanes 1977), but also to fire history, with long fire periods purportedly favouring seeders (Keeley 1977a; see below).

Closer analysis of the dominant shrub flora in terms of life-history traits by Zedler (1981) showed a diversity of forms. Of the 18 species he considered, three were obligate seeders, dependent entirely on seed for regeneration after fire with no or very low recruitment between fires. Adults had moderate to great longevity. Among the other species he identified a group of five "sprouter-seeders", where established plants had low to moderate mortality in fire, recruitment after fire was low to moderate (though higher for Adenostoma fasciculatum), and adult longevity was moderate to great. Species of the sage scrub, such as Eriogonum fasciculatum, were variable in their survival of fire, had high recruitment after fire, moderate to high recruitment between fires, and were relatively short-lived. A final group of non-seeding sprouters, such as Quercus dumosa, had nil to moderate mortality in fires, virtually no recruitment after fire, great longevity, and low to moderate recruitment between fires.

Reproductive output in seeding shrubs varies markedly from year to year, apparently in response to rainfall, but soil seed pools are apparently always sufficient for regeneration after fire (Keeley 1977b; Keeley and Zedler 1978; Schlesinger et al. 1982). Seeding shrubs regenerate from dormant seed in the soil as relatively sparse to moderate populations of seedlings after fire, ranging from about 0,5 to 10 individuals per square metre (Horton and Kraebel 1955; Schlesinger and Gill 1980). Several field studies have indicated that about half of seedlings may die, and that mortality is density-dependent (Horton and Kraebel 1955; Schlesinger and Gill

1980). Kummerow et al. (1985) measured 90-92% mortality in the first year, with initial densities of $78.m^{-2}$. The net outcome was a population density about the same as that recorded in other studies in the chaparral. Subsequent mortality among established plants may be more or less constant, though in Ceanothus megacarpus, the age-specific mortality rate may fluctuate before settling down to a constant rate (Schlesinger and Gill 1980). Montygierd-Loyba and Keeley (1987) have extended the observations on C. megacarpus by analysing patterns of mortality in a 55-year-old stand. They found that mortality had occurred at a more or less constant rate. Projection indicated that the population would survive until 100 years. Mortality occurred mainly among smaller plants, indicating that intraspecific competition, rather than population senescence in the sense of Leopold (1961), was responsible for the mortality.

Nevertheless, many seeding shrubs, especially in the genus Ceanothus, do not survive beyond 20 to 40 years after fire (Horton and Kraebel 1985; Hanes 1971, 1977; Black 1987). However, several species have considerable longevity, maintaining vigour and reproductive output at high levels up to a century or so. Keeley (1975) has documented longevity of around a century for some members of Ceanothus in the section Cerastes. In this respect, for example, Keeley and Keeley (1977) could find no difference between a 23-year-old and a 90-year-old population of Arctostaphylos glauca.

Schlesinger and Gill (1980) quantified the log-linear relationship between shrub biomass and density in pure or nearly pure stands of C. megacarpus. The slope of the line was -1,23, substantially less steep than the expected value of -1,50. They ascribed this relatively weak response to density to the plasticity of growth in the shrubs, so that smaller individuals, instead of becoming suppressed and dying, simply maintain a slender leafy crown in the canopy while lower branches die (see also Keeley and Keeley 1977).

The dominant sprouter of the chaparral, Adenostoma fasciculatum, has a complex life-history. Mortality of established plants in fire is often high and there is normally fairly abundant recruitment of

seedlings. Further, the mortality among established plants in the interfire period is often significant, to the point that long fire periods have been invoked to explain the relative dominance of long-lived seeders in many chaparral stands (Keeley 1977, 1986).

Plant species in the chaparral may be grouped broadly in terms of "demographic patterns" that correlate with germination behaviour (Keeley et al. 1985; Keeley 1987). The differing life histories of these groups, summarised in Table 2.1, determine the process of pyric succession in the chaparral.

2.1.4. Changes in species richness Increases in plant species richness inevitably occur after fire, sometimes threefold (Kruger 1983). There are few data to indicate trends during pyric succession but Westman (1981) observed for the coastal sage formation adjacent to chaparral that there was a recovery in species richness with the immigration of tolerant herbs about halfway through the succession, with species being lost again subsequently.

2.1.5. Resource economy during pyric succession

2.1.5.1. Soil moisture and the water balance Chaparral occurs in zones with mean annual rainfall ranging from about 300 mm to 1000 mm. Increasingly favourable water balance is correlated with increasing leaf-area index, so that transpiration is maintained at about 200 $mm.yr^{-1}$. The specific composition of the dominant shrubs also tends to change along the moisture gradient. Moister sites tend to have a greater diversity of shrubs, with broad-leaved species of Arctostaphylos (Ericaceae), Ceanothus (Rhamnaceae), and Quercus (Fagaceae) often being prominent (Hanes 1977). Many of the species of this so-called hard chaparral are seeders. More xeric sites tend to be dominated by Adenostoma fasciculatum (Rosaceae; chamise), a facultative seeder-sprouter. This variation may be expressed along geographic gradients, or locally on slopes of contrasting aspect (Miller and Poole 1979).

Chaparral soils reach moisture contents of 20% in winter but are

invariably markedly droughted in summer (Schlesinger and Gill 1980; Miller and Hajek 1981). As noted above, the density of chaparral canopy increases with increasing precipitation, so that there is seldom a surplus of soil moisture for drainage (Poole et al. 1981).

Table 2.1. Classification of plants in chaparral on the basis of shared demographic characteristics. Groups distinguished share distinct germination behaviours. After Keeley (1987) and Keeley et al. (1985).

Demographic group	Germination behaviour
Opportunistic annuals	polymorphic seeds; non-refractory seed colonise gaps, refractory seed stimulated by factors associated withe fire; seed widely dispersed.
Fire annuals	seed markedly dormant, long-lived; germination strongly cued by factors associated with fire (heat, charate, etc.); local dispersal only
Herbaceous perennials	no dormancy, not inhibited by vegetation canopy
Ephemeral suffrutescents	seed somewhat polymorphic, mostly strongly dormant; germination cued by fire, as above; local dispersal
Coastal sage shrubs	no seed dormancy, no innate germination requirements, brief period of viability; recruitment in second season after fire from new seed crop or in canopy gaps; widely dispersed
Obligately sprouting shrubs	as for coastal sage, but no post-fire recruitment, only in canopy gaps; widely dispersed
Obligate seeding shrubs	seed have great longevity; stimulated to germinate by heat shock of fire or charate or both; local dispersal
Facultative seeder-sprouters	relatively short-lived seed (?), dormant; germination stimulated by heat

Consequently, soil moisture contents rise after removal of the canopy. This is often seen in enhanced moisture status of regenerating plants (Radosevitch et al. 1977; Oechel and Hastings 1983; Reid 1985), though not always in shrub seedlings (Schlesinger and Gill 1980). Because surface soil layers dry rapidly from the late spring onward, the responses of plants to the increased soil moisture after fire depend on their rooting habits. Year-to-year variation in drought subsequent to fire has been observed to affect seedling mortality markedly (Horton and Kraebel 1955). Year-to-year variation in soil moisture strongly regulates herb regrowth, as discussed earlier. Competition for water between herbaceous, especially grass, seedlings and shrub seedlings has also been shown to adversely affect survival in the latter (Schultz et al. 1955; Bond, personal communication, 1985). Shrub seedlings may be eliminated by such competition (Schultz et al. 1955).

Kummerow et al. (1985) have experimentally manipulated regenerating vegetation, water and nutrients to examine effects on survival of seedlings of Adenostoma fasciculatum and Ceanothus greggii. Treatments did not affect survival but growth of seedlings was favoured by removal of herbaceous vegetation (65% cover) and irrigation, not by removal of resprouts or by application of nutrients. The trends of evapotranspiration and water stress during succession in chaparral are complex. Leaf-area index increases progressively for a period after fire. Schlesinger and Gill (1980) quantified conditions in an age series of chaparral dominated by Ceanothus megacarpus, from six to about 20 years old. Leaf biomass increased progressively with age, so that the leaf-area index grew from 0,8 at six years to 1,6 at 21 years. Pre-dawn plant water potentials in 6-yr-old stands decreased from about -0,94 MPa in late spring to about -8,5 MPa in autumn; in 21-yr-old stands they decreased from -0,48 to about -2 to -3 MPa over the same period. They were intermediate in a 13-yr-old stand. Summer pre-dawn water potentials were linearly related to plant size in the six-year-old stand, with values down to -12,0 MPa recorded in small plants. High mortality was recorded in shrub populations during the interval from five to 15 years after fire (Schlesinger and Gill 1978). Schlesinger and Gill (1980) reasoned that water was a more critical resource in the young stand than the older,

despite the lower leaf area and hence transpiration in the former, because the deep root systems of the older plants allowed exploitation of a larger reservoir of soil moisture. Drought is frequently implicated in the mortality of established chaparral shrubs (e.g. Mooney and Hobbs 1986).

Reid and Oechel (1987) recorded little water stress in regenerating shrubs in recently burnt chamise chaparral. Pre-dawn potentials in summer were about -0,5 MPa, as compared to about -3,0 to -5,0 MPa in vegetation unburnt for 11 years. Water potentials registered in older stands ranged from about -0,5 to -1,5 MPa. Transpiration rates followed the same trends, with highest rates per unit leaf area in the youngest stands These patterns correlated with canopy density, which increased from the recently burnt to the 11-yr-old stand and decreased in older stands.

Although there have been several investigations of plant water status in relation to pyric succession in chaparral, there have been few definitive studies of the role of drought in determining mortality of seedlings in the first year (Kummerow et al. 1985).

2.1.5.2. Mineral nutrients Chaparral soils on the whole are moderately leached, and substantially richer in mineral nutrients than are the soils of fynbos and Australian heathland (Specht and Moll 1983). Fertilizer experiments have indicated that the mature vegetation is limited by both phosphorus and nitrogen (Hellmers et al. 1955; McMaster et al. 1982). Althought total soil nitrogen levels are high, only a small proportion is mineralizable (Gray and Schlesinger 1981).

Most fires substantially enhance soil nutrients through ashfall and by affecting mineralization processes (Rundel 1983). For example, substantial enhancements to available nitrogen may occur, depending on fire intensity and soil moisture conditions (De Bano et al. 1979; Dunn et al. 1979). The nutrient flush has been implicated in the abundance of herbaceous vegetation in the first several years after fire, though such a dependence is apparently subordinate to effects of soil moisture (see earlier). Regenerating shrubs show enhanced levels of

mineral nutrient content (Rundel and Parsons 1980; Oechel and Hastings 1983) and this, rather than enhanced water status, has been argued to be responsible for the higher carbon gains and growth rates recorded for regenerating shrubs (Oechel and Hastings 1983). Thus, sequestration of limiting nutrients in biomass (cf Black 1987), litter, and recalcitrant soil compounds could be implicated in pyric succession.

Schlesinger and Gill (1980), using foliar nutrient concentrations in Ceanothus megacarpus, found no evidence of increased stress with advancing age, up to 21 yr. Marion and Black (1987) have analysed the patterns of change in nitrogen and phosphorus in a series of sites on relatively uniform soils, selected to represent chaparral stands varying in post-fire age from four to 85 years. Substantial and statistically significant changes were documented, with available nitrogen increasing up to about 50 years and then declining. This was associated with an increase in total soil nitrogen up to 50 yr, but the total soil nitrogen and the fraction of the total that was potentially mineralisable declined with age after 50 yr. Foliar concentrations of nitrogen correlated with trends in the soil. Thus there was an aggradation of nitrogen up to 50 yr and a degradation from 50 yr onward. Total soil phosphorus levels did not change significantly, but available levels and foliar concentrations declined logarithmically with stand age. They suggested that available data on nutrient accumulation in biomass and litter (e.g. Specht 1969; Black 1987) tended to support the hypothesis that these trends were owing to sequestration rather than biological factors affecting mineralisation such as allelopathy (cf. Christensen 1985). Reid (1985) corroborated this with data from older stands.

2.1.5.3. Light Schlesinger and Gill (1980) recorded a negative linear relationship between leaf biomass, and hence stand age, and irradiance below the canopy in Ceanothus megacarpus. Light levels in 6-yr-old stands were reduced by about 20-50%, and in 21-yr-old stands, by about 60-90%. On bright days, levels in older stands were as low as 200-400 $\mu mol.m^{-2}.s^{-1}$. Relative growth-rates and root:shoot ratios in C. megacarpus seedlings were markedly reduced at light levels below 400 $\mu mol.m^{-2}.s^{-1}$ (Schlesinger et al. 1982). Oechel and Lawrence

(1979) detected net photosynthesis in chaparral shrubs only at levels above about 400 $\mu mol.m^{-2}.s^{-1}$. Therefore, increased shading would necessarily play a role in succession, though Schlesinger et al. (1982) reasoned that in established cohorts this competition would not affect mortality, but rather plant form. McPherson and Muller (1967) have shown experimentally that shading by canopies of Ceanothus species can eliminate other shrubs by light competition.

2.1.6. Allelochemicals Secondary compounds in the foliage of several shrub species of the California chaparral have been shown to be toxic to plants of herbaceous species, in that the substances may inhibit germination of seed or growth of plants or both, and cause mortality (Westman 1983, and references cited therein; Christensen 1985; Keeley et al. 1985). Whether these phytotoxins have allelopathic effects, i.e. whether shrubs exclude all or some of the understorey herbs by this means, is controversial because field experiments have not often succeeded in isolating the effects of phytotoxins from those of other factors associated with the canopy, such as light attenuation, and of herbivores which shelter under the canopy. Nevertheless, allelopathy is at least sometimes significant in determining the interactions between overstorey shrubs and understorey herbs (Westman 1983; Christensen 1985; Keeley et al. 1985).

In contrast, it is now known that chemical stimulation of germination by charred wood is an important cue in the case of herbaceous fire ephemerals as well as ephemeral subshrubs (Keeley et al. 1985) and certain shrubs (Keeley 1987). The full role of allelochemicals in pyric succession has yet to be determined.

2.1.7. Interactions between plants and animals A diverse and relatively abundant small-mammal fauna is found in mature chaparral (Wirtz 1977; Fox et al. 1985). These rabbits and rodents substantially reduce the abundance of herbaceous plants in mature stands (Westman 1983). There is a marked pyric succession in this small-mammal fauna. Dominant species of mature chaparral vanish after fire, but are replaced rapidly and abundantly by others, which are then gradually replaced by the former (Wirtz 1977; Fox et al. 1985).

An effect on plant succession must be anticipated. Mills (1983) found that rabbits reduced seedling populations of shrubs by 25% for Adenostoma fasciculatum and 43% by Ceanothus greggii (see also Kummerow et al. 1985). However, this was on a burn two hectares in extent, and pressure from herbivores sheltering in surrounding unburnt vegetation may have been greater than would normally be the case. Later, Mills (1986) showed experimentally that small mammals increased mortality of Ceanothus greggii and Adenostoma fasciculatium significantly during first two years after fire, from about 45% to 94% for the fomer species and from 67% to 92% for the latter. Once more however, the experiments were conducted on a small burn (2,5 ha).

2.2. Pyric succession in Australian heathlands

2.2.1. Fire regime From the meagre information available, Kruger (1983) suggested that Australian heathlands experienced fires at relatively short and regular periods, probably in the order of 6 - 10 or 20 yr. The seasonality of fire was unclear. Beard (1984) considered the kwongan, i.e. the heathlands of Western Australia, as being fire-prone, i.e. with fires recurring at intervals between one and 20 yr.

Regarding fire regime, there have been no studies of the effects of varying fire intensity on Australian heathlands. Similarly, there have been few explicit studies on the effects of varying fire periods. McMahon (1984a) has analysed patterns of vegetation structure in relation to fire history. Marked reduction of recruitment occurred with fire periods of four years or less, which eliminated the obligate seeder, Banksia ornata. The density of Banksia recruitment increased as fire periods increased beyond 10 years, but other seedling recruitment did not increase similarly. Because the reproductive potential of a stand of vegetation varies with season and because subsequent environmental conditions vary predictably by season, the timing of fire in this respect is important. Seedling recruitment among all species as well as that in Banksia ornata was at a maximum after fires in summer and early autumn, and at a minimum after winter fires (McMahon 1984a). Cowling and Lamont (1987) have documented variation in relative

recruitment of Banksia seedlings which correlated with the season of burn. High recruitment was found after autumn fires, and low recruitment after the spring fire, the ratio of daughter to parent plants being twice as great in the former case.

2.2.2. Plant life histories and regeneration after fire Specht (1981) and Bell et al. (1984) have summarised data on the gross patterns of survival of fire by plants in Australian heathlands. About 70-75% of species in any stand of vegetation regenerate vegetatively by sprouting from underground rootstocks or other surviving organs. The balance are obligate seeders.

Bell et al. (1984) classified plants of Australian heathland in a comprehensive scheme which incorporates mode of regeneration and kind of life history. The categories they used are described in Table 2.2. They have classified 152 species from the heathland of a sandy habitat north of Perth according to this scheme, and their information is summarised in Table 2.3. The diversity of forms thus defined is striking.

An important set of plant traits in relation to seed regeneration, obligate or otherwise, is that governing the fate of seed after ripening. A feature of Australian heathlands (and South African fynbos) is the prominence of shrubs which store seed in cones or similar organs in the canopy, i.e. so-called bradysporous or serotinous species, a form which is absent from other mediterranean-type ecosystems except in conifers (Kruger 1983). In the kwongan sample analysed by Bell et al. (1984), not less than 29 of 31 obligate seeders and 10 of 67 long-lived sprouters possessed this habit.

There has been little explicit plant demographic work in Australian heathlands (Kruger 1983). Specht et al. (1958) measured populations of the obligate seeder Banksia ornata in vegetation of different ages after fire and the data indicated high mortality rates in young populations after fire, and very low rates in old populations, indicating that this species did not senesce. Recently, Cowling and Lamont (1987) and Cowling et al. (1987) have conducted

Table 2.2. Categories of response to fire recognized for plant species in the kwongan (heathland) of Western Australia by Bell et al. (1984)

Primary Category	Sub-category	Description
Fire ephemerals	Monocarpic, polycarpic	Fire-stimulated, sometimes fire-obligate germination, growth, early maturity, life-spans of 3 months to 4 years
Obligate seeders		No capacity for vegetative regeneration; life-spans potentially less than 15 years and growth cycles terminated prematurely by fire
Sprouters	Obligate vegetatively reproducing sprouter	Vigorous vegetative multiplication, virtually no seed regeneration, clonal populations
	Facultative sprouter-seeder	Variable vegetative regeneration; but usually poor, some or even abundant seed regeneration
	Auto-regenerating long-lived sprouter	Abundant vegetative regeneration; seed regeneration adequate to replace parent mortality

detailed demographic analyses of serotinous species of Banksia, with the emphasis on reproductive output and on recruitment.

2.2.3. Succession Fire is followed by regeneration of all plant species within the first 12-24 months (Specht et al. 1958; Kruger 1983). The initial stand is usually sparse, with variable but relatively low densities of seeding ephemerals and longer-lived shrubs. In moist habitats, however, regeneration is dense and seedling recruitment low (see below). In these respects, and in all others, the process of succession closely fits the model presented for fynbos in Table 2.3 (Specht et al. 1957; McMahon 1984b).

Table 2.3. Frequency of different species in different fire-response categories in a list of 152 from sandy habitats in heathlands north of Perth. See text. From Bell et al. (1984).

Fire-response category	Frequency of species within growth-form categories							
	Annual herbs (therophytes)	Geophytes	Herbaceous perennials (hemicryptophytes)	Chamaephytes	Shrubs and trees (phanero-phytes)	Aerial para-sites	Stilt plants	Total
Seeders								
Regular ephemerals	5	-	-	-	-	-	-	5
Fire ephemerals	10	-	-	4	1	-	-	15
Obligate seeders	-	-	2	10	14	1	4	31
Sprouters								
Facultative seeder-sprouters	-	-	5	8	2	-	-	15
Autoregenerating long-lived sprouters	-	12	16	16	23	-	-	67
Obligately vegetatively reproducing sprouters	-	9	4	2	3	-	-	18

2.2.4. Changes in canopy cover Specht and colleagues (Specht and Morgan 1981; Specht and Moll 1983) have analysed geographical patterns in the projected canopy cover of mediterranean sclerophyllous vegetation of Australia and South Africa. Within the heathland environment, projected canopy cover was found to vary as a function of the annual moisture index, i.e. the ratio of estimated actual evapotranspiration to potential evapotranspiration. Specht and Morgan (1981; see also Specht et al. 1983) adduced data indicating a negative linear relationship between overstorey and understorey layers. During pyric succession, maximum canopy cover is reached within 3-5 yr after fire. The succeeding trend was such that the relationship between overstorey cover and understorey was negative and linear, and total projected canopy cover remained more or less constant until senescence set in.

In regions with about 500-800 mm of rainfall, maximum canopy cover achieved in heathland is around 70-75%. Specht et al. (1957) and Bell et al. (1984) have analysed samples of heathland of different ages in relatively dry environment and shown how canopy has recovered fully within 10 years after fire. Russell and Parsons (1978) analysed recovery on a mesic site at Wilson's Promontory on the South-Eastern Coast of Australia and found full recovery within about five years after fire.

Specht and colleagues (Specht and Morgan 1981; Specht and Moll 1983) argued for a competitive interaction between the overstorey and the understorey layers of the canopy. In Australian heathlands these were seen to increase together until about 3-5 yr after fire, whereafter the understorey was progressively reduced so that there was a negative linear relationship between understorey and overstorey canopy cover.

2.2.5. Changes in species richness Plant communities of Australian heathlands are invariably richer in species, at least in their vegetative form, in the years immediately following fire and richness tends to decline progressively with continued absence of fire (Specht 1981; Kruger 1983; Bell et al. 1984). For example, Specht et al. (1958) reported a gradual decline from 36 species immediately after

fire to 10 at 50 years after fire. McMahon (1984b) reported similar results, though there was no decline between 30 and 50 years. In Western Australian heathland, Bell et al. (1984) found the same overall trends, but increases in richness after fire were relatively small and declines were gradual.

Specht (1981; Specht and Moll 1983) has attributed the decline in richness to the competitive exclusion of the understorey species by the developing overstorey and reports linear and negative relationships between overstorey projected canopy cover and community richness. The losses do not continue once the overstorey becomes senescent, but there is no recovery (Specht et al. 1958; McMahon 1984b). However, the higher the proportion of sprouters in the stand, the smaller the increment in species richness after fire and the more gradual the subsequent decline (Specht 1981).

2.2.6. Resource economy during pyric succession

2.2.6.1. Soil moisture and water balance Aside from dense myrtaceous thickets in special habitats, such as calcareous dunes, the proportion of the biomass of heathlands consisting of sprouters increases with increase in foliage projective cover and hence with increasingly favourable water balance (Specht 1981). The rapid recovery of sprouters after fire tends to exclude seedlings.

Competition for water plays an immediate role in structuring communities. Dodd et al. (1984) have documented the seasonal progression of plant water potentials in shrubs of the kwongan (heathland) near Perth, in an area receiving about 800 mm of rain per year. They found pronounced differences between species, depending on rooting habit, as for chaparral. In shallow-rooted species, pre-dawn and midday potentials declined to below -6 MPa in mid-summer. Species with tap-roots to about 3 m and widespread laterals declined to below about -4,0 to -6,0 MPa. Species with deep tap roots and few laterals (sprouters) hardly declined below -2,0 MPa. Water stress in shallow-rooted species was strongly affected by the moisture content of the top 1 m of soil, but in deep-rooted species the level of stress depended on whether roots reached the water table or not.

Specht (1957b) estimated the water balance of burnt and unburnt heathland at Dark Island by periodic direct sampling of soil-moisture stores and detected substantial and significant increases in soil-moisture contents of soils on burnt sites. He concluded that there had been a reduction in evapotranspiration from the burnt sites. However, the relative role of competition for water as opposed to competition for other resources as well as other factors determining pyric succession has not received explicit attention.

Specht et al. (1958) and Specht (1981) have emphasized the role of soil moisture in governing seedling abundance and establishment at Dark Island heath, drawing the distinction between the effects of winter drought and those of summer drought. Nearly tenfold variation in seedling numbers was found in burns of different years, and this was evidently related to winter droughts. Survival of seedlings of all shrub species as well as those of Banksia ornata varied two- to fourfold respectively and was directly related to the duration of the wet season, i.e. of the period during which soil moisture contents exceeded the arbitrary level of 4%, subsequent to the fire.

At the same site, Specht (1957a) noted but did not quantify that extreme droughts induced a higher mortality in established shrubs in stands unburnt for 5, 10 and 12 years than in young plants of the same species on a recent burn, thus tending to confirm the more marked influence of soil moisture deficits in the mature and maturing vegetation.

Dodd et al. (1984) have also recorded population responses to unseasonal drought in the kwongan of Western Australia, and found that mortality reduced the frequencies of individuals in shallow-rooted seeding species which tolerated wetter sites, whereas the frequency of similar species which tolerated drier sites remained stable or increased in response to drought. Species with deep or spreading roots did not respond to the drought. This suggested a shifting competitive hierarchy, depending on soil moisture availability.

2.2.6.2. Mineral nutrients The soils of Australian heathlands are markedly impoverished of phosphorus and nitrogen as well as certain

micro-nutrients, more so than most fynbos soils (Specht and Moll 1983). Specht et al. (1958) have quantified the progressive sequestration of mineral nutrients in phytomass and litter as pyric succession proceeds. Several fertilizer experiments have served to indicate substantial and significant responses of heathland plants to added phosphorus, and sometimes of a secondary response to added nitrogen (Groves 1981). Growth responses of dominant shrubs were limited to relatively low levels of addition. Added nutrients increase growth rates but also shorten life-cycles of dominant shrubs (Heddle and Specht 1975; Groves 1981). But enhanced levels of soil phosphorus cause tissue necrosis in established plants and mortality in seedlings, evidently because uptake by the plant proceeds despite diminishing growth responses so that an imbalance of nutrients occurs and tissue concentrations of phosphorus rise to toxic levels (Ozanne and Specht 1981).

Pate and Dell (1984) have analysed nutrient pools in above-ground biomass of 10-year-old heathland at Eneabba north of Perth, with dead and live matter amounting to 1500 $g.m^{-2}$. Simulated burning of the material indicated that soil pools would be increased by fire to the extent of 2,5% for nitrogen, 5% for phosphorus, 56,9% for potassium, 15,9% for calcium, and 13,4% for magnesium. Their analysis indicated that the nutrients released would have been sufficient to meet the demand for plant growth during 18 months after fire. They drew attention to differences among plant forms in their patterns of growth and nutrient uptake. Fire ephemerals, with high relative growth-rates and superficial fibrous root systems accumulated nutrients to exceptionally high levels of tissue concentration, evidently having the capacity for rapid utilization of nutrients in the upper soil horizons. Dominant species had large reserves of nutrients in their seeds (sufficient for a year of growth or more - Barrow 1977), slow-growing seedlings, extensive proteoid or other specialized root forms, and deep tap-roots, both the latter being established in the first year of growth. These latter forms evidently did not require the nutrients from ash-fall, which were probably depleted within one year.

Siddiqui et al. (1976a, 1976b) have calculated for a sand heath in

eastern Australia that the releases in fire were sufficient to double the concentrations of plant-available phosphorus in the soil. Laboratory trials showed such concentrations to inhibit the growth of or to kill seedlings of Banksia species. This was not found among seedlings in the field after fire. Evidently, uptake by roots and micro-organisms rapidly reduced concentrations of phosphorus in soil solutions or the laboratory procedures induced higher uptake of phosphorus by the seedlings than was the case in the field. Longer-lived shrubs have diverse morphological and physiological adaptions to low levels of mineral nutrients, and often have specially effective mycorrhizas (e.g. Lamont 1982). In the field these shrubs apparently grow relatively independently of environmental fluctuations in nutrients.

The overall picture for heathlands is of a flora adapted in different ways to low but variable nutrient availabilities. In the simplest model, no competition occurs in the nutrient-rich post-fire environment because short-lived plants and hemicryptophytes capture nutrients rapidly whereas longer-lived members of the community rely on internal resources (Pate and Dell 1984). Later, the greater biomass and the sequestration of nutrients induce a competitive environment, where longer-lived plants would respond to addition of nutrients.

2.2.6.3. Light No experimental work has been done to evaluate the role of competition for light in heathland succession but Specht et al. (1958) believed that shading by overstorey plants causes mortality among at least some understorey plants.

2.2.7. Interactions between plants and animals Animals may play a role in the pyric succession by determining reproductive potential through pollination, pre- and post-dispersal predation upon seeds and other propagules, and reduction in vigour by herbivory. The course of succession after fire may be affected by predation upon seedlings.

Cowling and Lamont (1987) have documented variations in post-fire recruitment of Banksia, which correlated with the season in which fire

occurred. Experiments showed how pre-dispersal predation on the seeds in follicles by itinerant flocks of cockatoos could govern the availability of seed for regeneration after fire. Post-dispersal predation on seeds released after a spring fire was evidently responsible for lowered recruitment, and this was evidently by vertebrate predators.

As a rule, Australian heathlands like other mediterranean shrublands are even-aged, with no significant recruitment of cohorts in the plant populations after the first season or two following fire (Kruger 1983). Definitive studies to determine the causes of this have been few. However, Whelan and Main (1979), working in sclerophyllous woodland of Western Australia, found relatively abundant germination under the canopy, but that seedlings were rapidly consumed by orthopterans and others invertebrates, so that no effective recruitment occurred. The effect of fire in moderating such predation is evidently crucial in allowing regeneration of the community, in some cases at least. Cowling and Lamont (1987), however, ascribed observed mortality in seedlings of Banksia species in unburnt vegetation to the effects of seasonal drought.

2.3. Pyric succession in fynbos

2.3.1. Fire regime Kruger (1983) and Kruger and Bigalke (1984) have summarised such data as were available on the fire regime in the fynbos. Fires tend to recur at intervals of 10 to 40 yr, with variable seasonality. Van Wilgen (1984) has analysed fire seasonality for different regions in the fynbos. Fire seasons are concentrated in the late summer and autumn in the south-west and interior, but have weak seasonality in the southern coastal region. Data from field and computer simulations indicate that fynbos fires have lower intensities than those in chaparral (Van Wilgen et al. 1985).

2.3.2. Plant life histories and regeneration after fire Data for selected stands summarised by Kruger (1983) and Kruger and Bigalke (1984) indicate a suite of plant life histories in fynbos like those in Australian heathland and not like those in chaparral. Kruger

(1983) has postulated from available data that obligate-seeding shrubs show marked senescence, i.e. have a Deevey Type I survivorship curve (Pianka 1978), which contrasts with information from other mediterranean shrublands.

2.3.3. Succession The processes of pyric succession in fynbos have been dealt with in fuller detail in Kruger and Bigalke (1984). Few published measurements of successional change are available for fynbos. Kruger (1979) and Kruger and Bigalke (1984) have summarised published data, observations and experience. This descriptive summary is presented in Table 2.3, as modified by Bond (1980). This model requires verification for different fynbos habitats, and will need an environmental component to allow for prediction of the courses of succession in different areas, if indeed they are different. It will need also to be amplified to accommodate the effects of variation in fire regime, which may modify pyric succession substantially (e.g. Kruger 1984; Kruger and Bigalke 1984).

2.3.4. Changes in canopy cover Data in Specht et al. (1983) indicate that canopy recovery during pyric succession is slower in fynbos than in Australian heathland. These authors postulate the same relationships between overstorey and understory as in Australian heathlands.

2.3.5. Changes in species richness Adamson (1935) found the fynbos community to be richer shortly after fire than where fire had been absent for some time. He found that species richness increased progressively during the first four years or so after fire, to a maximum which presumably would have declined thereafter. Most observers postulate post-fire increases in richness which decline progressively thereafter (Kruger and Bigalke 1984).

2.3.6. Resource economy during pyric succession

2.3.6.1. Soil moisture and the water balance Evidence is available from controlled catchment experiments of increases in stream discharge following fire (Bosch et al. 1984), from increased drainage of soil water as a result of reduced evapotranspiration. Effects can often be short-lived, disappearing within a year (Van Wyk 1982).

Table 2.4. Phases in the pyric succession in fynbos. After Kruger (1979). Periods are approximate and differ from area to area.

Phase	Period after fire (years)	Characteristics
Immediate post-fire	0-1(2)	Seed germination, vegetative regeneration of almost all species. Various geophytes (Cyrtanthus spp., Orchidaceae, etc.) and most annuals reproduce only in this phase.
Youth	1-4(5)	Graminoid herbs, sprouting shrubs dominate. Canopy cover approaches pre-burn levels. Sprouting shrubs become reproductively mature; most fire ephermerals set seed and die.
Transitional	4-10	All plants reach reproductive maturity. Tall shrubs emerge from the canopy and adopt ascending branch habit. Remaining fire ephemerals die.
Mature	10-30	Tall shrubs reach maximum height and full, rounded form, and maximum reproductive activity. Seeding low shrubs begin to die. Litter accumulation and reduction in low herbaceous biomass. Virtually no seed germination.
Senescent	30-60?	Mortality of seeding shrubs accelerates. Foliage reduced to tufts at tips of branches, crowns become open. Litter and dead shoots continue to accumulate. Tall shrubs collapse with branches drooping downwards. Rare seed regeneration in open spaces.

Few studies have been directed at the effects of fire on the soil-moisture regime as such (Kruger and Bigalke 1984). Neither Levyns (1929) nor Wicht (1948) could detect enhanced moisture levels in surface soils (upper 150 mm) following fire. Wicht (1948) found constantly higher levels of soil moisture at a depth of 610 mm, but these were masked by variability in the data so that the differences were not statistically different. Levyns (1929) sampled through the year following burning. Wicht (1948) sampled at the end of summer, 44 days after fire, possibly before sufficient rain had fallen to sustain any differences.

2.3.6.2. Mineral nutrients Up till 1984, little evidence had been found of direct effects of fire in fynbos on mineral nutrients in the soil (Kruger and Bigalke 1984). Van Wyk (1982) had documented increased ionic concentrations in streams from burnt catchments, relative to those of unburnt catchment (see Chapter 6).

In coastal fynbos of sandy soils at Pella, North of Cape Town, Stock and Lewis (1986) found that a fire in November caused 6,6 g $N.m^{-2}$ of nitrogen to be deposited in ash. However, total soil nitrogen levels, though enhanced initially, declined rapidly to pre-fire levels by the following mid-winter. The fire caused an approximate doubling in ammonium levels in the surface 200 mm, but this persisted only a fortnight or so. Nitrate levels were enhanced slightly, i.e. by 1-2 g $N.g^{-1}$ soil, for about nine months. Some effects on total nitrogen were evident at deeper levels a year after fire. The authors suggested that these patterns arose from changes in nitrogen mineralization in the soil. Stock et al. (1988) conducted incubation studies which showed that, despite an increase in potential net mineralizable nitrogen with increase in successional age of the fynbos at Pella, the actual rates of mineralization were similar for pre- and post-fire soils. They suggested that increased levels of nitrate found after fire were owing to ashfall and to improved mineralization in the moister soils, as well as a temporary surplus because of low demand from the regenerating vegetation. Brown and Mitchell (1985), also working in fynbos at Pella, found enhanced levels of plant-available phosphorus which they ascribed to ashfall, enhanced

mineralization rates, and, possibly, enhanced microbial action. The effect persisted for about four months, and the enhancement was about six-fold.

2.3.6.3. Light No substantial studies of the effects of plant canopies on light have been undertaken in fynbos (Kruger and Bigalke 1984).

2.3.7. Interactions between plants and animals Bond and Breytenbach (1985) have shown how predation by small mammals on seed and seedlings can substantially affect plant recruitment in fynbos. Conversely, dispersal of seeds of certain species by ants is important in ensuring adequate recruitment, and disruption of this process by whatever means could substantially affect plant populations (Bond and Slingsby 1983). The small-mammal predators are evidently responsible for the major differences in plant recruitment that may follow on fires in different seasons of the year (Bond et al. 1982; Van Wilgen and Viviers 1984). Clearly, interactions between plants and animals and successional relations in these interactions must play an important role in structuring communities. The relative effects in pyric succession of competition for resources, herbivory and predation, and inherent plant life-histories have yet to be elucidated. At Jakkalsrivier, however, observation over a long period had not given evidence of direct effects of herbivores on vegetation structure during any given cycle of pyric succession, and trapping had revealed very low densities of small mammals (R. C. Bigalke and S. Lewis, personal communication). This aspect was therefore not addressed in the study reported here.

2.4 Synthesis

In many respects, the ecological effects of fire have been best studied in the chaparral of California than in the other two regions analysed here. This is particualrly so in regard to certain aspects of demography and of plant ecophysiology. Because of this, any synthesis of the topic will tend to be biased somewhat toward our knowledge of chaparral.

The less frequent and more intense fires of the chaparral, together with more frequently limiting soils moisture regimes than in Australian heathland and fynbos, appear to effect larger releases of resources post-fire. Possibly because of this, the plant species of any given habitat are mostly ephemerals, completing their life cycles in the first decade or so after fire. A handful of long-lived shrubs persist, and have relatively great longevity, up to a century or so in the case of seeders. The heathland and fynbos communities include about the same diversity of life histories, but ephemerals are relatively rare, and long-lived seeders absent or nearly so. This may reflect the differences in fire regime - fires being more frequent, less strongly confined to season, and less intense than in chaparral - as well as different levels of limitation by water and nutrients, and less pronounced pulsing of resources as a result of fire. There is sufficient evidence that both plant life-histories and the effects of fire on resources and hence on competition and other interactions among species, underlie the processes of pyric succession. Their relative roles have yet to be properly determined.

3. DESCRIPTION OF STUDY SITES

3.1. Jakkalsrivier

3.1.1. Location and topography The Jakkalsrivier catchment, 157,5 ha in extent, is situated at 34°09' south latitude and 19°09' east longitude, on the Lebanon State Forest (Fig. 3.1). It lies on the southern slopes of the Groenlandberg range, about 12 km east of Grabouw. Kruger (1974) has described the physiography of the site in detail. The catchment has a high relief, with altitudes ranging from about 650 m to nearly 1200 m over about 2 km (Fig. 3.2). The predominant aspect is south-westerly. Average slope is about 45% but about 20% of the land has slopes exceeding 60%. Nevertheless the area is not deeply dissected.

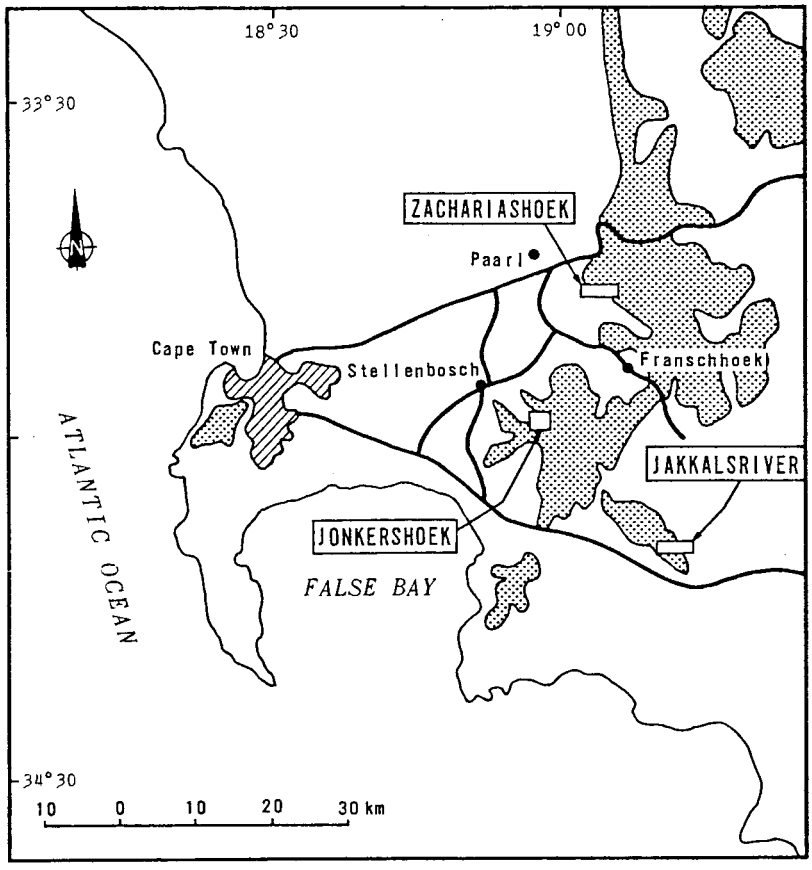


Figure 3.1. Map showing location of the study sites.

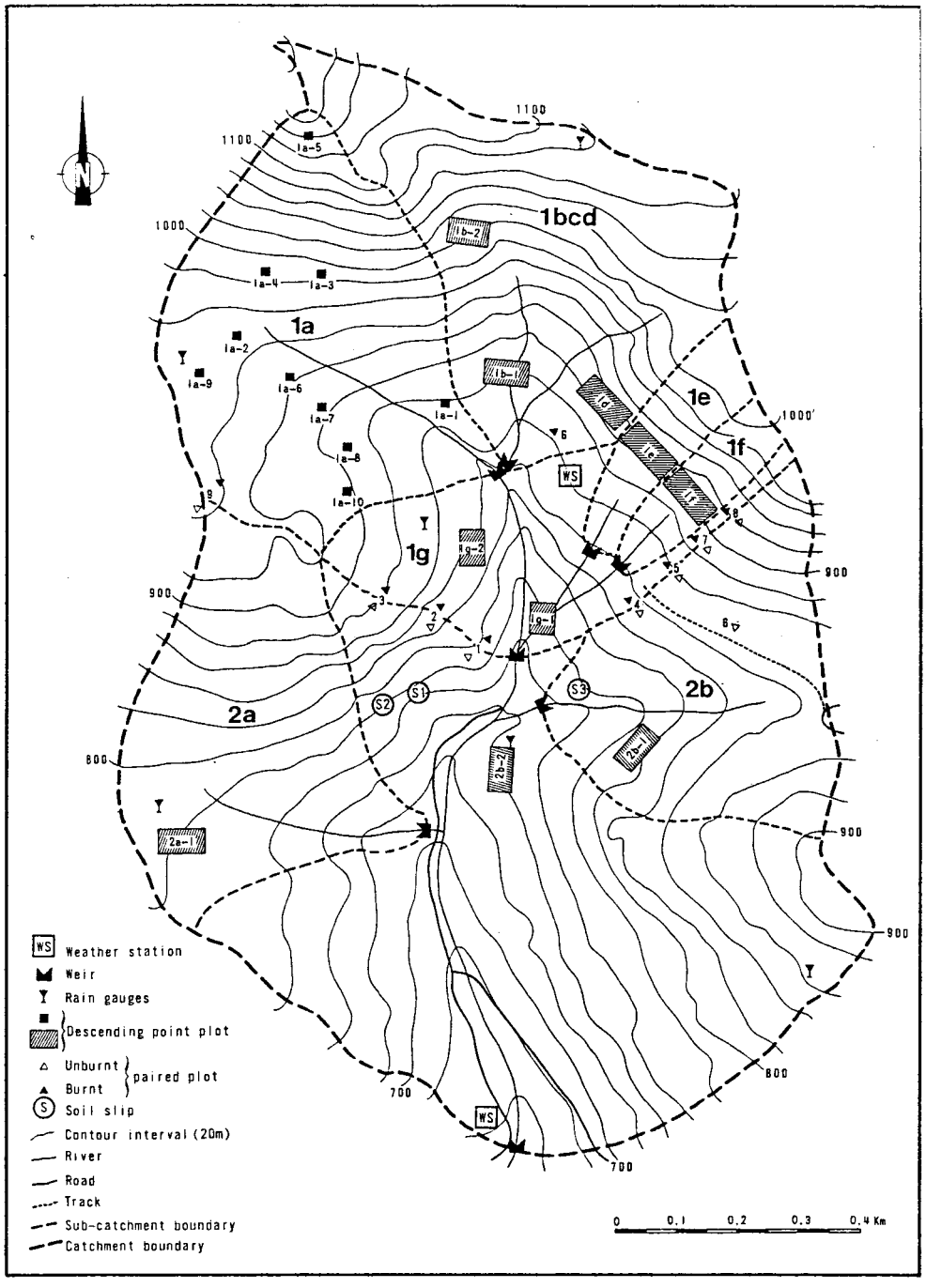


Figure 3.2. Map showing the principal topographic features of Jakkalsrivier as well as sample and study sites mentioned in the text. Sub-catchments labelled 1a to 1g receive experimental burns, 1e and 1f on a 5-year cycle and the rest on a 10-year cycle. Catchments 2a and 2b and the remainder of the area have been protected against fire since December 1958. Filled squares show locations of sites where the vegetation has been monitored since 1969 by means of point-quadrat samples of 250 points each, and hatched rectangles, those monitored by means of 1000-point sampled (see Chapter 5). Location of paired quadrats in the gradient sample (Chapter 4) are shown by triangles, open symbols indicating quadrats in vegetation not burnt since 1958, and filled symbols those in vegetation burnt in 1980.

3.1.2. Geology and soils The geological formations are those of the Table Mountain Group. Quartzites of the Peninsula Formation are overlain by tillites of the Pakhuis Formation, a band of siliceous shale in the Cedarberg Formation, and then quartzites again of the Nardouw Formation.

Parent material is the primary determinant of soil form. On the shale band, on smaller shale lenses in the quartzites, and on drift material from these, one encounters sandy loams with yellowish- or reddish-brown B horizons. On the quartzites, soils are grey sands or coarse sands, sometimes sandy loams. Depth, degree of soil development, moisture status, and leaching status vary according to slope position. Soils derived from shales contain more clay and nutrients than those from quartzites. Nutrient status of quartzite-derived soils correlates strongly with organic carbon content (Kruger 1974). Soils are acid, with pH of water solutions ranging between 3,5 to 5,0.

3.1.3. Climate and hydrology

The general climate of Jakkalsrivier is cool-temperate, humid and windy. The climate is classified as Csb in the Köppen (1931) system, in the moist mediterranean category, and as transitional mediterranean in the Gaussen system (Bagnouls and Gaussen 1957). Alternating passage of southerly cyclones and the South Atlantic anticyclones determine the weather and the climate of the site. Both of these weather systems follow a more northerly track in winter and a more southerly one in summer. Cyclones are more frequent in winter and bring cool moist air off the southern oceans, rain, and high gusting winds.

Anticyclones arise from subsiding air and may be warm and dry but often entrain relatively moist air which when orographically lifted can reach condensation point. On the mountains, anticyclones are characterised by steady strong winds, relatively high temperatures, and precipitation usually as fog, sometimes as rain. Intervening weather, especially after a cyclone, may be relatively calm and clear

and ground frosts may occur in winter. When anticyclones dissipate and a cyclone advances the pressure fields cause a gradient from interior to coast; this often draws warm dry air off the sub-continental plateau, which is adiabatically heated as it flows to lower altitutes. Turbulent flow over the mountain often causes strong, gusty winds. These are the so-called berg wind conditions, which induce anomalously high air temperatures and low lumidities.

Because the alternation between weather systems is more-or-less irregular despite a seasonal cycle, the climate does not have strong seasonal definition. Thirty-six per cent of rain falls in the summer half-year, and 24% in the spring months of September-November. Absolute maximum temperatures are high at almost any time of the year (Table 3.1), though the average temperature is moderate.

The measured rainfall of some 860 $mm.yr^{-1}$ is relatively low for a site at this altitude in the region. Equivalent sites 20-40 km to the west would receive twice this amount of rain or more (e.g. Wicht et al. 1969). Precipitation from intercepted mist is a frequent occurrence, even when no rain falls, especially in summer (Kruger 1974). This precipitation has not yet been measured in a meaningful way but could be a substantial input to the water balance (Kruger 1979). The winters are not cold. Frost occurs infrequently and irregularly, and snow falls about once a year or less on average. Cold days occur when maximum temperatures are a mere 5-10oC, but these are not accompanied by freezing night-time temperatures.

Jakkalsrivier is an extremely windy site, with the highest mean wind-speed of all south-western Cape stations where wind is recorded at 2 m above ground (Kruger 1974). No completely calm days are experienced. Mean daily wind-speed varies little through the year; the annual average is 3,5 $m.s^{-1}$ (Table 3.1). Mean daily maximum windspeeds exceed 7,0 $m.s^{-1}$, and absolute maxima, measured as the speed for a 10 km run, range from 25 to 38 $m.s^{-1}$ (Table 3.1).

Cloudy conditions limit the duration of bright sunshine to an average of 54% of the potential, ranging from a minimum of 41% in July to a maximum of 62% in February (Table 3.1).

Table 3.1 Climate averages at the main meteorological station, Jakkalsrivier situated at an altitude of 655 m. Arranged according to the hydrological year, which begins on 1 April.

	A	M	J	J	A	S	O	N	D	J	F	M	Year
Solar radiation													
Screen temperature (°C)													
(1968/69–1981/82)													
Mean daily maximum	19,8	16,3	14,9	14,1	13,9	15,4	17,8	20,1	21,9	23,2	23,4	22,4	18,6
Mean daily minimum	10,8	8,5	7,2	6,3	5,9	6,5	8,0	9,6	11,0	12,0	12,6	12,1	9,2
1/2 (max. + min.)	15,3	12,4	11,0	10,2	9,9	11,0	12,9	14,9	16,5	17,6	18,0	17,2	13,9
Absolute maximum	33,5	29,5	26,9	26,0	26,4	19,5	32,8	37,0	34,0	36,0	36,0	35,8	37,0
Absolute minimum	3,0	0,0	0,0	0,0	-0,6	-1,2	2,1	3,3	4,0	0,0	6,2	4,1	-1,2
Rainfall (mm) (1968/69–1981/82)	58,1	82,9	86,7	113,1	132,9	77,2	78,2	47,2	54,6	44,7	40,6	43,1	859,3
Wind velocity ($m.s^{-1}$) (1968/69–1981/82)													
Daily mean	3,5	3,6	3,8	3,7	3,6	3,4	3,4	3,4	3,4	3,3	3,6	3,6	3,5
Daily minimum	1,2	1,0	1,3	1,1	1,2	1,0	1,2	1,2	1,5	1,3	1,3	1,3	1,0
Maximum for 10-km run	29,2	26,2	31,4	26,0	28,4	25,9	25,5	35,1	31,4	28,4	35,1	28,4	35,1
Daily duration of bright sunshine (hr) (1968/69–1978/79)	4,8	3,8	3,3	3,7	4,0	4,8	6,0	6,6	7,2	7,8	6,9	6,0	5,4
Daily A-pan evaporation (mm) (1968/69–1978/79)	3,1	2,3	2,1	2,4	2,4	2,9	4,0	4,6	5,7	6,0	5,4	4,1	3,7

Potential evapotranspiration is indicated by an annual mean A-pan evaporation of nearly 1400 $mm.yr^{-1}$. This is about 70% of that recorded for lowland sites such as Cape Town.

3.1.4. Vegetation The vegetation of the catchment has been described by Kruger (1974). It is classified as Acock's (1953) Veld Type 69, Mountain Fynbos. The following major categories of vegetation were detected in the prior phytosociological study:

(a) Phreatic communities : microphyllous evergreen scrub:

(i) Berzelia lanuginosa-Leucadendron salificifolium community

(ii) Brunia alopecuroides-Restio bifidus community.

(b) Communities of upper cool, steep slopes, mainly microphyllous evergreen dwarf scrub.

(i) Willdenowia sulcata-Thamnochortus pulcher community

(ii) Willdenowia sulcata-Erica brevifolia community

(iii) Willdenowia sulcata-Klattia partita community

(c) Communities on shale soils: mesophyllous evergreen broad sclerophyll scrub.

(i) Tetraria bromoides-Erica plukenetii community

(d) Communities of hot dry sites, mainly microphyllous evergreen dwarf scrub.

(i) Staberoha cernua-Restio tenuissimus community

(ii) Staberoha cernua-Phylica lasiocarpa community

(iii) Erica corifolia-Restio egregius community

(iv) Leontonyx spathulatus-Roella incurva community

(v) Crassula coccinea-Prismatocarpus schlechteri community.

These categories reflected, first, the dominant effect of parent material, in that the Tetraria bromoides - Erica plukenetii community was confined to soils derived from shale and tillite. Site water balance was inferred to be the next most important factor. Categories sorted well along a gradient defined by altitude and relative solar radiation index or were distinguished by their association with phreatic sites along streams and on raised bogs.

The fynbos at Jakkalsrivier falls within the Proteoid, Ericoid, and Restioid Mountain Fynbos types determined by Campbell (1985).

3.1.5. History of research and experimental treatment

The Jakkalsrivier catchment was set aside as an undeclared reserve within the Lebanon State Forest in 1950, after having been incorporated as demarcated State Forest in 1945. Before this it was used as seasonal pasture by farmers of the district, but grazing appears to have been light since the stock trails, terracing and other signs associated with grazing by domestic stock are absent. Research began with instrumentation of streamgauges and weather stations in 1966. Strict control of fire, invasive plants and any other unduly disturbing factors followed. The vegetation of the catchment was burnt accidentally in December 1939, February 1947 and again in December 1958 (Kruger 1974). The experimental programme laid down treatments including complete exclusion of fire from vegetation last burnt in December 1958, 5-year burning (about 10% of the area), and 10-year burning cycles (Fig. 3.2). Burns were applied in September, November and early December 1969, March 1970, October 1974, March 1975, October 1979, and March 1980, as appropriate.

3.1.6. Intensive study sites

Four sites were chosen for intensive study in this investigation (Fig. 3.3, Table 3.2), to supplement the information from long-term studies over a wider range of sites (Fig. 3.2). Logistic considerations dictated that these should be reasonably close to a road, so that ideal sites could not be chosen. One of the sites, called the control, was placed in vegetation last burnt in 1958. It was close to the 'mesic' site within the area subject to experimental burning, was physiographically similar, and bore vegetation similar in physiognomy and composition. This site did not have a soil similar to that of the mesic site (Table 3.2). Though both sites were dominated by Leucadendron xanthoconus and understoreys comprised mainly Restionaceae the floristic composition differed. But practical

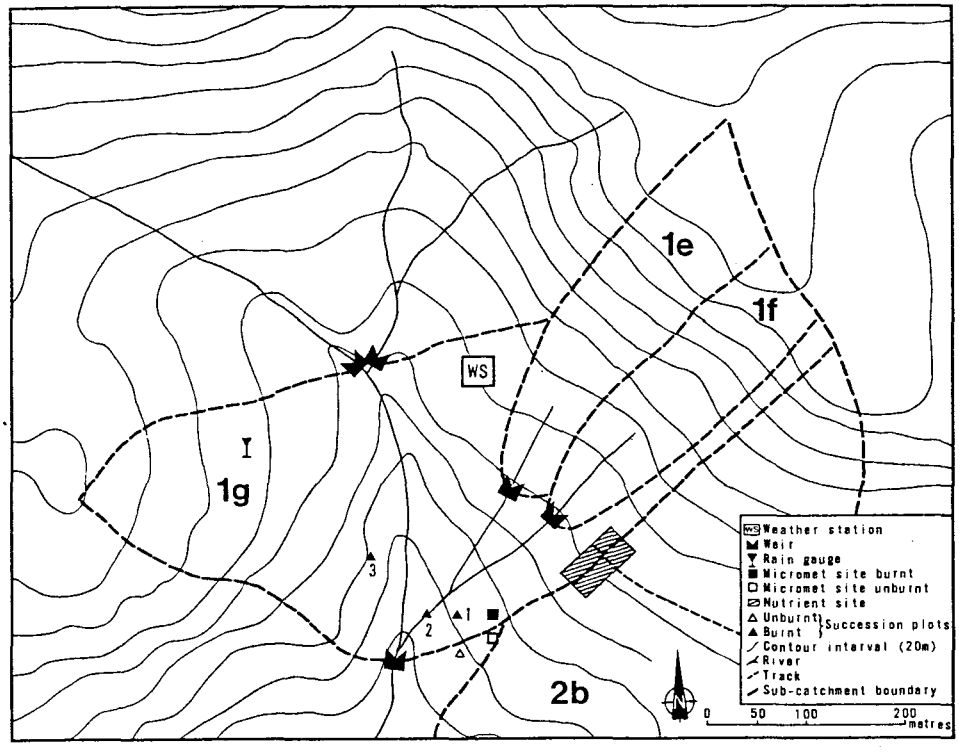


Figure 3.3. Location of sites used in the intensive study at Jakkalsrivier. Triangles indicate the position of permanent quadrats (see Table 4.2; Chapter 4). Squares indicate the location of micrometeorological studies (Chapter 5). The hatched rectangle indicates the site where soils and climax plants were sampled for comparative analysis of mineral nutrients, and for check measurements of plant water potentials (Chapter 5).

difficulties did not allow for an alternative. The other three sites were all located in vegetation burnt experimentally in December 1969 and March 1980. The first, the mesic site, was selected to represent the broad-sclerophyllous fynbos dominated by Leucadendron xanthoconus. The second, the phreatic site, was selected to represent tall narrow-sclerophyllous fynbos dominated by Bruniaceae and typical of streamside, phreatic habitats. The third, the dry site, was typical of low ericoid fynbos on shallow soils. Details of these sites are presented in Table 3.2.

Soil pits were excavated at each plot and the profiles were described and classified by standard procedures (G. Schaefer, personal communication; Table 3.2; Appendices 3.1-3.4). Bulk samples were taken from each horizon, except, in some cases, the saprolite horizons, by trowelling from each of the four faces of the pit. These samples were air-dried, passed through a 2-mm sieve, and despatched to the Citrus Exchange Leaf Analysis Service for analysis by the techniques described in Appendix 3.7. Results of the chemical analyses are tabulated in Appendix 3.5. Aliquots of the bulk samples were analysed for textural classes at the forest soils laboratory at the Saasveld Forestry Research Centre. Samples were also taken by means of an impact core sampler for determination of bulk density by normal gravimetric techniques. These results are summarised in Appendix 3.6.

The relationships between soil moisture content and soil water potential were determined by the pressure plate technique. Initially, sieved subsamples from each horizon were mixed and measured off into rings of 55 mm diameter and 10 mm deep, placed on the porous pressure plates. These were soaked overnight and then drained, before placing them in pressure chambers. Standard procedures, as recommended by Soil Moisture Equipment Corporation, were then followed in establishing an equilibrium moisture content at a given chamber pressure and measuring the resultant gravimetric moisture content. Replicates indicated that this technique frequently gave unacceptable discrepancies. The analysis was therefore repeated using cores replicated three times for each horizon and pressure. Cores were obtained in the field and taken intact to the laboratory to be placed

Table 3.2 Characteristics of the permanent quadrats at Jakkalsrivier.

	"Control" plot 2b	1g-1	1g-2	1g-3
Apparent character of the moisture balance	mesic	mesic	phreatic (riparian)	dry
Altitude (m)	770	770	770	770
Slope (%)	31	35	35	65
Slope azimuth (o)	216	236	238	92
Parent material	Quartzite	Shale & tillite drift	Mixed colluvium	Quartzite
Soil depth, mm	700+	500	700+	340+
Soil water-holding capacity, mm	24	54	204	24
Maximum "available" plant water, mm	18	26	108	12
Vegetation category after Kruger (1974)	Transitional Staberoha cernua-Phylica lasiocarpa	Tetraria bromoides-Erica plukenetii	Berzelia lanuginosa-Leucadendron salicifolium	Transitional Staberoha Phylica lasiocarpa
Mean height of predominant shrub layer (m) before fire	1,5	0,5-1,0	1,9-2,2	0,4-0,6

Table 3.3 Water-holding capacities, Jakkalsrivier soils. See text for details.

Site	Hor	Depth (mm)	Per cent rocks	Bulk density ($g.ml^{-1}$)	Soil moisture constants (% dm)		Profile water capacity			
					Field capacity (ψ soil = -0,033 MPa)	Permanent wilting point (ψ soil= -1,5 MPa)	At field capacity ($g.m^{-2}$)	(mm)	Available to plant ($g.m^{-2}$)	(mm)
Control: 2b										
	A	130	0	1,03	7,83	2,40	10484	10,5	7271	7,3
	E	190	0	1,3	3,96	0,90	9781	9,8	7558	7,6
	R/S	530	85	1,3	3,30	0,60	3410	3,4	2790	2,8
Totals for profile							23676	23,7	17619	17,6
1g-1	A	160	2	0,91	16,8	10,4	23972	24,0	9132	9,1
	B_1	160	1	1,00	10,8	5,56	17107	17,1	8300	8,3
	B_2	130	0	1,00	5,52	2,00	7176	7,2	4576	4,6
	B_3	70	5	1,50	5,52[a]	2,00[a]	5506	5,5	3511	3,5
Totals for profile 25,5								53761	53,8	25519
1g-2	A	300	0	0,95	26,4	12,60		75240	75,2	39330
39,3										
	E	450	0	1,35	12,1	3,38		73508	73,5	52974
53,0										
	B	250	0	1,24	17,7	12,5		54870	54,9	16120
16,1										
Totals for profile							203618	204	108424	108,4
1g-3	A	100	2	1,03	16,6	9,60	16756	16,8	7066	7,1
	E	50	2	1,2	4,76	1,56	2799	2,8	1882	1,9
	C	350	80	1,2[a]	4,76[a]	1,56[a]	3998	4,0	2688	2,7
Totals for profile							23553	23,6	11635	11,6

[a] Not measured: values assumed to be the same as for the overlying horizon.

Table 3.4 Nutrient pools ($g.m^{-2}$), Jakkalsrivier soils. See text for details.

Site	Hor	Depth (mm)	Per cent rocks	Bulk density ($g.ml^{-1}$)	Size of nutrient pool ($g.m^{-2}$)											
					Tot N	Tot P	Av P	K	Ca	Mg	Na	Zn	B	Mo	C	Organic matter
Control: 2b																
	A	130	0	1,03	33,7	4,02	0,536	1,07	9,37	2,81	1,34	0,0482	0,1205	0,0402	1393	2410
	E	190	0	1,30	13,8	5,68	0,741	0,74	2,96	0,99	1,23	0,1235	0,1482	0,0864	272	494
Totals for profile					47,6	9,70	1,277	1,81	12,34	3,80	2,57	0,1717	0,2687	0,1266	1664	2904
1g-1	A	160	2	0,91	117,9	10,70	0,428	3,71	13,41	4,85	4,00	0,0214	0,1427	0,0485	4024	6949
	B_1	160	1	1,00	75,4	8,71	0,317	1,90	5,54	3,33	2,53	0,0618	0,1267	0,0475	1093	1885
	B_2	130	0	1,00	25,5	6,50	0,260	1,17	2,47	1,82	1,56	0,0182	0,0832	0,0650	429	728
Totals for profile					218,7	25,91	1,005	6,78	21,43	10,00	8,09	0,1014	0,3526	0,1610	5546	9562
1g-2	A	300	0	0,95	359,1	16,53	2,565	8,26	18,24	11,68	10,26	0,2622	0,2850	0,0997	9462	16302
	E	450	0	1,35	255,1	33,41	3,037	5,47	12,15	7,29	7,90	0,1215	0,4252	0,2005	6379	10996
	B	250	0	1,24	208,3	13,33	3,410	3,41	6,82	2,79	4,65	0,2449	0,1860	0,0930	6696	11253
Totals for profile					822,6	63,27	9,012	17,1	37,21	21,76	22,81	0,6286	0,8962	0,3932	22537	38551
1g-3	A	180	2	1,03	137,4	4,54	1,454	5,45	31,61	18,35	5,09	0,0963	0,1999	0,0563	7195	12391
	E	160	65	1,20	13,2	1,21	0,134	0,27	1,95	0,94	0,40	0,0087	0,0470	0,0423	370	638
Totals for profile					150,5	5,75	1,588	5,72	33,56	19,29	5,49	0,1050	0,2469	0,0987	7565	13030

on the pressure plate without further disturbance. This technique gave less variable results at pressures of about 0,5 MPa and less. However, values obtained at 1,5 MPa often varied erratically, and some were obviously wrong, with moisture contents higher than those recorded for 0,5 MPa for example. In such cases soil-moisture retention constants for 1,5 MPa were determined by extrapolation of the hyperbolic regression fitted to values obtained for pressures up to 0,5 MPa, or by extrapolation of hand-fitted curves, whichever gave the more acceptable result. Values for the soil-moisture constants are given in Table 3.3.

Soil physical data together with profile descriptions were used to calculate the water-retaining capacities of the individual profiles, as well as storage capacity for plant-available moisture (Table 3.3). Nutrient concentrations from chemical analyses were used with bulk density measurements and profile depths to calculate soil mineral nutrient pools (Table 3.4).

The deep profile at plot lg-2 has by far the greatest water capacity, retaining 204 mm at field capacity, with about 108 mm available to plants. The dense B_{2hs} horizon, with high silt and clay content, acts as a pan (Appendix 3.3) and this, together with the streamside location, results in nearly perennial wetness through the profile. This profile also contains the greatest pools of mineral nutrients (Table 3.4), and organic carbon contents equal to the highest recorded for any profile other than in tundra and marshes (Schlesinger 1977). The shallow rocky profile at plot lg-3 has the lowest water-holding capacity of all four, less than half of that of the "mesic" site at lg-1. The capacity of plant-available water of 11,6 mm is sufficient for about 3-5 days of evapotranspiration at potential rates (Table 3.1). Nutrient pools are lower than those for the other two sites in the burnt area. The profile at the control site, though relatively deep, has a rather low capacity to store water because of the low organic matter content in the A horizon, its coarse texture, and the rocky saprolite horizon. Nutrient pools are small, because of low concentrations, especially in the strongly leached E horizon.

3.2. Zachariashoek

3.2.1 Location and topography

The Zachariashoek site was located in research catchments situated near Paarl in the south western Cape Province at 33°48' South latitude and 19°02' East longitude (Figure 3.1). This area includes three main sub-catchments, Kasteelkloof (324,5 ha), Zachariashoek (287 ha) and Bakkerskloof (356,4 ha). Six- and 12-year burning cycles are applied in Kasteelkloof and Zachariashoek respectively, while Bakkerskloof is protected from fire. Van der Zel (1974) has described the experiments and the site. Van Wilgen and Kruger (1981) have summarised the fire history of the area.

The catchments are situated on a broken plateau which rises abruptly from the valley of the Berg River, with a mean altitude of about 675 m.

3.2.2. Geology and soils

Rock strata of the Table Mountain Group (Cape Supergroup) underlie the catchments. These comprise the Peninsula Series of quartzites, a thin band of tillites (the Pakhuis Series), a 200-m thick band of shale of the Cedarberg Series, and the Nardouw Series of quartzites. The strata are not strongly folded.

Soils in this area vary from organic podzols of the La Motte form through to shallow lithosols of the Mispah form. In the area selected for study soils are mainly well-drained, frequently dry, acid sands and lithosols of the Cartref, Clovelly, Glenrosa, and Mispah forms.

3.2.3. Climate

Climate at Zachariashoek is controlled by essentially the same synoptic-scale phenomena as at Jakkalsrivier.

Mean annual rainfall for the 15 years ending March 1984 varied from about 980 mm to 1600 mm, depending on altitude. On the plateau where the vegetation was monitored for this study the mean rainfall was

about 1000 to 1300 mm. General experience in the field suggests that fog precipation is less important than at Jakkalsrivier.

The climate at Zachariashoek has been described by Van Wilgen and Kruger (1985). There is a brief summer xerothermal period. The winter, from April to September, is perhumid. Mean daily wind-speed varies from around 3,2 $m.s^{-1}$ in March to about 4,9 $m.s^{-1}$ in June. Northerly and north-westerly winds are most frequent in the winter half-year, with speeds often exceeding 10 $m.s^{-1}$. In summer, south-easterlies predominate, with speeds mostly between about 4 and 11 $m.s^{-1}$ (Van Wilgen and Kruger 1985).

3.2.4. Vegetation

The sites included in the sample were located in a zone dominated by the Staberoba cernua-Chondropetalum paniculatum tall mid-dense herbland community identified by Van Wilgen and Kruger (1985) (Figure 3.4). This category of vegetation occupies about 70% of the catchments, occurring on soils with low water-retaining capacities varying from shallow lithosols to deep sands. It falls into the mesic restoid fynbos sub-series defined by Campbell (1985). Canopy cover in well-developed stands varies from 50 to 95%, and the canopy is dominated by tufted evergreen herbs of the Restionaceae and Cyperaceae about 1,0 m tall. Sclerophyllous shrubs up to 5 m tall occur sparsely; lower (0,40 to 1,0 m) narrow-leaved shrubs are more common. Prominent mid-high herbs are Chondropetalum paniculatum and Hypodiscus argenteus (Restionaceae), and Tetraria involucrata (Cyperaceae). Prominent low herbs are Restio filiformis, Tetraria ustulata, and Elegia parviflora (Restionaceae). Details are available in Van Wilgen and Kruger (1985).

3.2.5. History of research and experimental treatment

The Zachariashoek Experimental Catchments forms one of several research areas established by the Department of Environment Affairs (Forestry Branch) for studies on mountain catchment ecosystems. These areas were selected for experiments to test the effects of various management options (such as veld burning and afforestation) on water

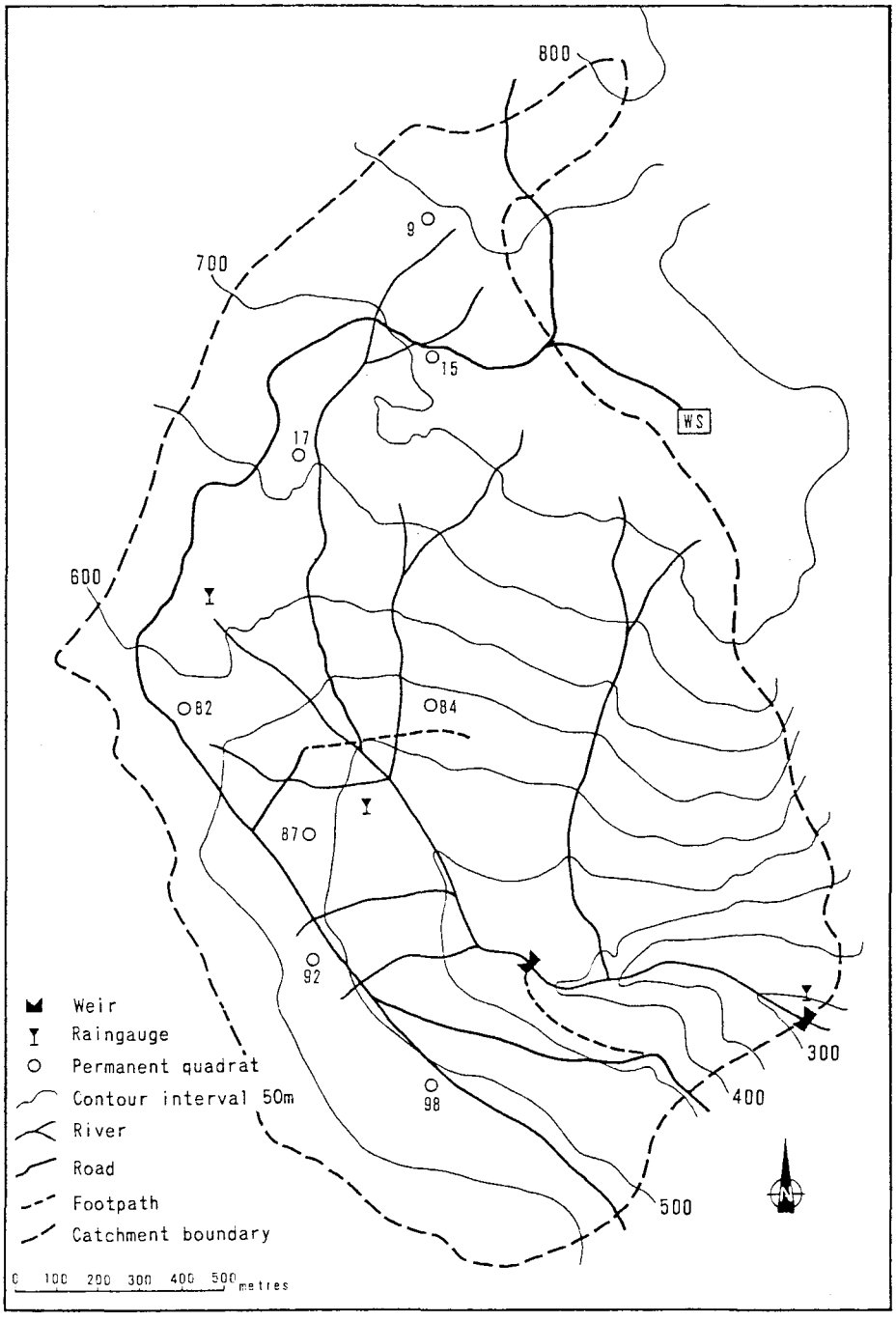


Figure 3.4. Location of permanent quadrats at Zachariashoek used in this study. See Chapter 4.

yield, water quality and on the biota. The options chosen at Zachariashoek are late spring (November) burns at 6-year (short) and 12-year (moderate) intervals and protection from fire. Late spring burning, although not currently encouraged, was initially advocated as being suitable for mountain fynbos, as such burns would occur after the period of maximum growth and flowering among plants. This would supposedly be less damaging to the natural community than earlier burns, while nevertheless occurring when soil and litter were likely to be moist and therefore not adversely affected by the fire (C.L. Wicht, pers. comm.). A preliminary description of the physiography and climate of the area and of the experimental design is given by Van der Zel (1974). Van Wilgen and Kruger (1981) provide further details of the history of the area.

4. RESPONSES OF PLANT SPECIES AND PLANT COMMUNITIES TO FIRE AT JAKKALSRIVIER AND ZACHARIASHOEK

4.1. Introduction

This chapter is an analysis of the natural history of the fynbos plants of the study areas, specifically in relation to fire and especially at Jakkalsrivier. The purpose is to describe the plant communities as they are constituted by species, differing in their traits, which collectively govern the responses of communities to a single fire and, by inference, to fire regime. At the same time, changes after fire in community properties such as species richness and composition in terms of species, life-forms, and guilds, are quantified and used to test hypotheses about the general features of pyric succession in fynbos. The data are then explored to derive further hypotheses. The approach is essentially analytic and reductionist, in that the aim is to describe and predict the response of vegetation to fire regime by referring to the properties of its constituent species.

The recovery of a stand of vegetation after fire or other disturbance may be predicted if certain attributes of the species it includes are known. These attributes, or traits, are ones which determine the reproductive or re-establishment potential of a given species at the time of fire, and the course of its life cycle after regeneration until the next disturbance. Wicht (1945), for example, listed four modes of survival found among fynbos plants. The first three involve survival and regeneration of plants by regrowth from soil storage organs, sprouting from rootstocks, and sprouting from protected dormant buds on stems and branches. The fourth mode involves regeneration from seed where the parent population is killed. Various authors have reviewed the biology of plant survival and regeneration after fire and derived simplified schemes to depict the limited array of attributes involved (e.g. Gill 1975, 1981; Frost 1984). Noble and Slatyer (1980, and earlier papers) have used such information to derive an analytical system in which the response of the plant

community can be expressed fully in terms of a limited number of vital attributes, as discussed in Chapter 1. With this information it is possible to deduce the effect on the composition of the stand of any given fire regime and express this as explicitly derived vegetation replacement sequences. Kruger (1984) reviewed briefly the significance of such vital attributes in South African biomes and has used this scheme in a preliminary analysis of certain fynbos stands. Cowling (1984) has analysed responses to fire of a fynbos community of the Eastern Cape in this way. Few complete analyses of fynbos stands are available. They are needed both for interpretation and prediction of the effects of fire in fynbos.

Published information on patterns of change in species composition and richness in fynbos communities following fire have been reviewed by Kruger and Bigalke (1974) (see also Kruger 1983). Aside from work by Adamson (1935), Levyns (1935, and earlier), and Wicht (1948) there have been no detailed evaluations of such changes in fynbos. Descriptive studies are needed upon which to base hypotheses for experimental studies of the processes underlying successional change in fynbos.

The temporal changes after fire in samples of vegetation at Jakkalsrivier and Zachariashoek were analysed to test the hypotheses explicit or implicit in the conceptual model offered by Kruger (1977, see also Kruger and Bigalke 1984, and Table 2.4) to describe post-fire succession in fynbos.

For mediterranean-type ecosystems, Specht and colleagues (Specht and Morgan 1981; Specht et al. 1983) have developed generalised models to relate physical environmental controls to plant productivity and variations in species richness. In the present context, the relevant aspects of these models are (a) that successional change is accompanied by displacement of plants in the understorey by those in the overstorey such that the sum of the foliage projective covers remains constant, (b) species richness decreases linearly with increasing foliage projective cover. This implies that species richness decreases with increasing productivity and that although the rate of loss of species with pyric succession is a function of

overstorey recovery, the initial richness is a function of initial cover (or biomass). According to this theory, foliage projective cover of the overstorey is determined by water balance and is also related to the constitution of the vegetation in terms of species which seed and those which sprout after fire: the higher the overstorey foliage projective cover, the higher the proportion of sprouters in terms of biomass (Specht 1981). This Specht argues is owing to intense selection against seedling populations in the competitive post-fire conditions which would prevail where regrowth after fire is rapid. Because seeding species are lost as succession proceeds, this implies that the increment in species numbers after fire would be low in highly productive environments, and high in less productive environments.

Campbell and Van der Meulen (1980) have analysed patterns of species richness in fynbos at Jonkershoek. They found that species richness declines with post-fire age and that the decline was relatively greater in fynbos which attained the greater biomass. These declines were owing largely to changes in richness of lower strata, and hence the greater losses of species occur where a tall shrub overstorey develops than otherwise. This lends support to Specht's theory.

More generally, Huston (1979) has argued that species richness in a given community is a function of the degree to which species have been displaced by others in competition, that the higher the rate of competitive displacement the lower the richness, and hence that species richness is a function of both the growth rates of species constituting the community and the frequency of disturbance (by implication, of "disastrous" disturbance in Harper's (1977) terms). Richness depends on a condition of disequilibrium, because at equilibrium there is full competitive displacement and only niche-differentiated species may co-exist. From such arguments, Huston predicted a relationship between richness and frequency of disturbance ("population reduction") which would be hump-shaped. Where the frequency of disturbance is low to intermediate, species richness would be similarly related to growth rates. Connell (1978) argued from r-K theory for similar generalizations. Tilman (1982, 1983) has proposed a general theory of resource competition in

communities which treats space among other factors as a resource. Availability of space is affected by productivity and hence recovery rate and disturbance frequency; this theory also predicts that species richness (alpha diversity) is related to to disturbance rate and productivity in the form of "hump-shaped" curves .

For fynbos, Bond (1983) has found some support for these relationships. This topic was addressed at Jakkalsrivier by examining the relationships between pre- and post-fire richness and certain indices of productivity and recovery rate. Analysis of vital attributes is then used to aid in the interpretation of results, and prediction of the effects of alternative regimes.

Thus, the response of the fynbos community to fire is likely to vary according to the pre-fire biomass of the stand, and hence productivity.

Succession after disturbance other than fire was also investigated at Jakkalsrivier by examining vegetation on sites exposed by soil slips caused by an exceptionally heavy rainstorm in January 1980, when 300 mm of rain fell in 24 hours. The data were compared with those from burnt sites to determine whether patterns of succession differed.

In summary, the hypotheses to be tested in this study were the following:

(a) fynbos vegetation is stable in composition under a regime of fire with a frequency in the "normal" range, i.e. with 10-40 years between fires (Kruger 1979);

(b) the initial floristic composition model of succession applies;

(c) species richness declines over time after fire, as fire ephemerals disappear and recruitment is inhibited by the established canopy.

(d) the flora involved in the initial recovery of vegetation

on exposed soils was the same as that involved in pyric succession, and

(e) the vital attributes of species recolonizing exposed soils were the same as those occupying burnt sites.

A preliminary evaluation of possible long-term changes in vegetation under a more-or-less stable fire regime was also undertaken by repeating a vegetation assessment made in an experimental catchment at Jonkershoek by R.S. Adamson in 1948.

4.2. Methods

4.2.1. Assessments on permanent quadrats on burnt sites Composition of sample stands of vegetation was assessed on 5x10 m quadrats. The conventional quadrat for floristic analysis of fynbos is 10x10 m in size (Werger et al. 1972; Cowling 1984) but a quadrat of 5x10 m contains most of the species to be found in the larger one (Werger et al. 1972).

Quadrats were marked permanently, by means of short iron stakes at each corner and a creosoted wooden pole at a position offset 2 m from the bottom right-hand corner of the quadrat. Each quadrat could therefore be easily relocated. The boundaries of the quadrat were defined by nylon cords drawn tight between the corner stakes. Each assessment was therefore fully repeatable, though boundary lines were sometimes affected, for example, by the growth of shrubs or termitaria.

Nine such units were selected from a grid of 103 permanent quadrats at Zachariashoek, near Paarl. This grid serves for the long-term monitoring of vegetation change in the catchment experiment there (Van Wilgen and Kruger 1981, 1985). The quadrats were selected for accessibility and to cover a range of sites in the area (Chapter 1). Three quadrats were selected at Jakkalsrivier, one to represent a "mesic" situation, one a "xeric" situation, and one a phreatic site (Chapter 1).

Quadrats were assessed in October-November of each year, except in 1978, when work was delayed until the last week of December. Though climatic conditions vary from year to year, late spring is usually a good season for censusing plants in fynbos because ephemerals are normally fully developed and deciduous geophytes have not yet died back.

All quadrats were assessed immediately before burning, when the vegetation was 12 years old at Zachariashoek and 10 years old at Jakkalsrivier, and then reassessed at one, two, four and five years after fire at Zachariashoek, and one, two and three years at Jakkalsrivier.

Quadrats were subdivided in quarters, each of which was thoroughly searched for plant species. When the list was completed the relative importance of each species was estimated visually using the Braun-Blanquet cover-abundance categories (Shimwell 1971). In 1982, however, the Jakkalsrivier quadrats and quadrat 84 at Zachariashoek were subdivided by a 1x1 m grid, and the species were carefully inventoried for each one-square-metre subquadrat. At this stage, all juvenile plants could be identified and the systematic search of the grid ensured a good reference data set for composition and richness.

A portable herbarium collection was used to aid identification of problematic species in the field. Where field identification was not possible, scrap collections were matched with named specimens in the herbarium at the Jonkershoek Forestry Research Centre. Some specimens were referred to the National Herbarium for naming. In the first season after fire many species could not be identified beyond the level of genus or family, because they were unfamiliar in the juvenile form. In such cases, specimens of seedlings or sprouts were retained and identified by matching with older plants in the following season. Also, sprouting species not identified initially, but which survived the fire and could be positively identified in the following season, were later added to the initial list.

4.2.2. Traits of plant species At the end of the survey, the characteristics of each species in regard to survival of fire and other life-history features were determined so as to allow specification of vital attributes (Noble and Slatyer 1980; see Chapter 1) . Regeneration mode (vegetative or generative) was established for each species by reference to herbarium material collected expressly for this purpose over the 10 years prior to the study. Notes were also made during field assessments. Species at Jakkalsrivier where regeneration mode had not been established by the end of the study were inspected finally on 15 September 1984. Life stages (see below) were not determined for the Zachariashoek flora because the relative inaccessibility of this site precluded sufficiently frequent observation.

Determination of critical life stages was tentative in most cases. Age of first flowering, recorded as the year in which an estimated 10% or more of the population flowered for the first time, was established from field notes. Where information was not recorded, herbarium specimens were inspected. Special efforts had been made to collect specimens as and when each species came into flower after the burns of the late sixties and seventies, so that these collections gave reasonably reliable estimates. Except in species which flowered within 24 months after fire, age at reproductive maturity was taken to be one year older than that of flowering since many species require substantial periods of after-ripening before seeds are viable (Levyns 1935; Jordaan 1949).

Most fynbos plant species which regenerate from seed have their seed dispersed over short distances (e.g. Wicht 1948; Bond 1980; cf Hopkins and Griffin 1984). This was assumed for the species in this study unless there was evidence to the contrary. In the Noble-Slatyer (1980) system this meant that few species were classified as "D" species in terms of the vital attribute group relating to the method of persistence through a disturbance, i.e. where survival was through dispersal of seed from unburnt populations. Simple tests showed easily which seeds were effectively transported by wind and which not, but some species were classified by inference (see below).

Species which relied for survival on seed stored on-site were easily identified in cases where seed was retained in protective structures on the plant, e.g. in the Proteaceae and Bruniaceae; these all had vital attribute C and seeds were assumed to have a short life after dispersal.

No information is available on the longevity and germination behaviour of seed in the soil. Here, larger-seeded species, for example in the Fabaceae, were assumed to have long-lived seed, (is in the order of 50-100 yr) and those with small seed (e.g. Ericaceae), relatively short-lived (i.e. in the order of 5 years - cf Levyns 1935b). In every case, soil seed stores were assumed not to be exhausted by post-fire germination, i.e. such species were all assigned vital attribute S and none G.

The second group of vital attributes recognized in the Noble-Slatyer system was that which relates to the conditions required by a species for establishment and growth to maturity. Intolerant (I) species were here taken to be those in which germination and establishment occurred within the first 24 months after fire and not after. Species which appeared later, but whose propagules could be assumed to be freely available at all times, were assumed to require amelioration of the site during succession (R species). Tolerant (T) species would be those found to establish and grow at any stage.

Life-spans of individuals of longer-lived species, i.e. living longer than 10 years, were also not known and had to be guessed.

In addition all species were classified in the types of response to fire recognized by Bell et al. (1984) (Table 2.2), to allow comparison with Australian heathland. Fire-ephemerals, however, were classified as including species which lived to about 10 years, but in greatly diminished numbers and with low vigour.

4.2.3. Survey to assess fire recovery along a productivity gradient at Jakkalsrivier Statistics on the floristic responses of communities to fire at Jakkalsrivier were obtained by a quadrat survey of

vegetation over a range of habitats. A random sample of matched pairs of quadrats was taken so as to represent the vegetation on either side of the catchment boundary, so contrasting vegetation 2,5 years old with vegetation unburnt for 24 years, but otherwise matched in habitat. One member of each pair was placed in the burnt vegetation, and the other in the unburnt, each four metres away from the boundary. If one of a pair did not match the other well in substratum, slope and aspect it was shifted until this was achieved. In one case, the quadrat pair was deliberately placed to represent a phreatic site. In another case, an additional quadrat was included to represent 24-year-old vegetation burnt in 1980. A sample of 10 paired observations was finally obtained, which included altitudes from about 800 to 980 m, contrasting aspects, and both shallow and relatively deep soils (Fig. 3.2).

Quadrats 2x2 m in size were used in this sample, because this size gives a good measure of alpha richness, relatively free of the effects of habitat patchiness (Wicht 1948; Bond 1983). Each quadrat was divided into eighths, in each of which the species were listed and the height and canopy cover of the vegetation estimated.

4.2.4. Analysis of flora on soil slips The soil slips which occurred in 1980 were confined to the unburnt portion of the catchment, and were found on slopes of about 65%. The mass movement of debris cleared paths of about 10-15 m wide. At the heads of the slips the soils were often stripped away, exposing the C horizon, or bedrock. The debris shifted from the heads of the slips also stripped away soil surface horizons lower down the slope although sometimes only the vegetation or only the canopy of the vegetation was affected this way. Stony colluvium was often deposited en route. The result was that the physical features within a soil slip were often complex, representing different kinds and degrees of disturbance.

These sites were sampled in November 1982 by selecting units representing different degrees of soil loss and comparing them with adjacent, undisturbed vegetation. Sample units were again 2x2 m quadrats. All species found in the quadrats were classified and identified as to whether they were colonists of the exposed habitats

or survivors of the disturbance. The mode of regeneration was noted. Cover-abundance of individual species and mean canopy cover and height were estimated for each quadrat. Sample units were classified according to degree of disturbance, distinction being made between sites where the soil was churned and colluvium (rubble) deposited, those where the vegetation canopy was stripped away, and undisturbed sites. Sites where soil had been cleared to the C horizon were not sampled but lists of the few plants found on such sites were made.

4.2.5. Repeat of the transect sample established by R.S. Adamson at Jonkershoek in 1948 R.S. Adamson, assisted by several students, sampled a transect of vegetation in the Abdolskloof experimental catchment on 23 September 1948, 2,5 years after fire. This catchment, which is underlain by Cape granites, Klipheuwel shales, and metamorphic rocks, is clothed in fynbos vegetation varying in structure from a low heath to tall broad-sclerophyllous shrubland. It has been burnt since 1941 according to a randomised schedule, with intervals ranging from four to seven years and seasons from September to April.

The transect was 20 yards long and consisted of two 1-yard-wide belts two yards apart running parallel. All species were recorded in every second quadrat of one square yard in the belts. Percentage canopy cover was estimated for each species in each quadrat, to a minimum level of 1%. Species with less cover were recorded as present. This quadrat could be relocated almost exactly from field notes and from photographs. The procedure was repeated on 17 August 1981, about 12 months after the last burn.

4.3. Results

4.3.1. Patterns of species richness in relation to fire

4.3.1.1. Species lost after fire In the permanent quadrats at Jakkalsrivier the number of species recorded before fire ranged from 49 to 60 per quadrat. Of these all but one, six and four reappeared at plots 1g-1, 1g-2, and 1g-3, respectively. The pre-fire

cover-abundance rating of each of the 11 species lost after the burn was either rare (i.e. only one small plant in the plot) or not numerous and certainly with less than 0,1% cover, i.e. the maximum cover-abundance rating was +. Three species were unidentified geophytes, and may therefore have reappeared unrecognized after the fire. Three were obligate seeders. One of these, Protea neriifolia, occurred in the plot on the phreatic site, outside its normal habitat range. The other two, Chondropetalum hookerianum and Erica longifolia, were single individuals also occurring outside their normal habitat range and evidently merely incidental records. The remaining species were sprouters and although recorded as single or few individuals they would normally have been expected to regenerate, as was abundantly evident in the immediate vicinity. Three of the nine sprouters and both of the seeders survived fire in one or more plots other than that in which they disappeared.

At Zachariashoek, between three and seven species disappeared from each of the nine permanent quadrats assessed, except that no species were lost from permanent quadrat no. 9. The mean number of species lost was 4,11 per quadrat, 7,7% of the mean number of species recorded before fire. A total of 30 species was involved. Of these, nine were doubtful identifications, mainly of geophytes, and the species may have been recorded subsequently under a different name. Two were seasonal ephemerals (Pterygodium catholicum (Orchidaceae) and an annual species in the Scrophulariaceae), whose presence is probably little affected by fire. If such species are excluded from the list, the mean number of species lost amounts to 2,67. The highest number lost was 6, from plot 84, the richest plot. Only five species disappeared entirely from the sample (Table 4.1). One of these was the exotic herb, Hypochoeris radicata, recorded as a single individual in one plot.

Eleven of the species which disappeared were sprouters which would normally be expected to survive fire and in every case they were recorded as regenerating on other plots. The remaining species were seeders of which all except Indigofera filicaulis and Protea repens were recorded as regenerating on other plots. The maximum cover-abundance rating assigned to these species which disappeared was +.

Table 4.1. Species lost after fire at Zachariashoek.

Species	Family	Comments
Cliffortia ruscifolia	Rosaceae	Seeding shrub
Hypochoeris radicata	Asteraceae	Sprouting herb, exotic
Indigofera filicaulis	Fabaceae	Seeding shrub
Protea repens	Proteaceae	Seeding shrub
Scrophulariaceae sp.		Annual

4.3.1.2. Species gained after fire At Jakkalsrivier, an average of 29 new taxa was added to the list for each quadrat after fire. At Zachariashoek the average was 47 (with a standard deviation of 16). The number recorded before fire at Zachariashoek and the number added were very weakly correlated (r = 0,248). Most species added were geophytes and fire ephemerals, although many newly recorded species were sprouters which normally persist through the succession, or longer-lived obligate seeders.

Of the 213 species appearing as new records on one or more plots at Zachariashoek, 59 were deciduous geophytes. Of these, 35 had not been identified to the level of species. A further 13 were species added to the list for some plots, but which had been recorded before fire in others. Of those entirely new to the recorded flora, some, such as Thereianthus spicatus (Iridaceae), grew and flowered in abundance after fire, declining thereafter. Even in such cases, however, the plants may have been present in vegetative but cryptic form before the fire, and therefore overlooked.

Thirty-six of the 213 new species at Zachariashoek were fire ephemerals. The most common are listed in Table 4.2. Of these 20 were new records for these plots. The balance were species which had been suppressed on plots where canopy cover before fire was relatively dense, and survived on other plots as much reduced individuals where canopy was sparser. Selago spuria, Ursinia crithmoides and Erepsia anceps are examples. Only five of the fire ephemerals were monocarpic annuals.

Table. 4.2. List of common fire ephemerals at Zachariashoek.

Species	Family	Frequency	Comments
Thesium virgatum	Santalaceae	7	Lax shrub, root parasite
Selago spuria	Scrophulariaceae	6	Soft, low shrub
Thesium euphrasioides	Santalaceae	5	As for T. virgatum
Crassula filiformis	Crassulaceae	5	Annual
Leontonyx spathulatus	Asteraceae	5	Polycarpic forb
Lightfootia subulata	Campanulaceae	5	Polycarpic forb
Thesium euphrasioides	Santalaceae	5	As for T. virgatum
Aspalathus arida	Fabaceae	4	Woody shrub
Crassula fascicularis	Crassulaceae	4	Succulent sub-shrub
Erepsia anceps	Mesembreanthe-maceae	4	Shrub, succulent leaves
Roella ciliata	Campanulaceae	4	Low shrub
Thesium capituliflorum	Santalaceae	4	As for T. virgatum
Thesium nigromontanum	Santalaceae	4	As for T. virgatum
Ursinia crithmoides	Asteraceae	4	Lax shrub
Ursinia scabiosa	Asteraceae	4	Polycarpic forb

The remaining 117 species were perennials normally to be found in unburnt vegetation. Of these, nine were of doubtful identity. Once more, many of those recorded for the first time after fire were species which were cryptic and difficult to detect in unburnt vegetation, and may have been overlooked before the burn. Some were evergreen geophytes which evidently become dormant between fires. Common examples were Aristea racemosa (Iridaceae), Argyrolobium filiforme (Fabaceae), Ehrharta longifolia (Poaceae), and Mairea burchellii (Asteraceae). Fifty-one of the species recorded for the first time after fire on one or more plots were recorded as survivors on other plots. Many of these would have been cryptic in the unburnt vegetation. Among both seeding and sprouting species, however, local on other plots. short-range migration was sometimes involved. Protea amplexicaulis, whose seeds are rolled by wind, Phaenocoma prolifera (Asteraceae; wind dispersed), and Serruria rosea (Proteaceae), whose seeds are dispersed by ants, were recorded before the fire within a 2-m belt surrounding one or more of the plots, whereas seedlings were found within the plots after fire. The same applied for sprouters

such as Brunia nodiflora (Bruniaceae) and Osteospermum junceum (Asteraceae). These seedlings were all found immediately after fire, and apparently arose from parent plants which occurred within a few metres of the quadrats. There were two cases of long-range dispersal, where seedlings appeared with the nearest possible parents being at least several hundred metres away. There were Rhus tomentosa (Anacardiaceae, bird dispersed) and Pinus pinaster, a wind-dispersal exotic. In both cases, single seedlings were found in only one plot.

4.3.1.3. Turnover in species from year to year The turnover in species recorded for each plot was calculated as the complement of Czechanowski's coefficient, which is the ratio of the number of species recorded in both years to the average number of species in both years. This was done for only six of the nine Zachariashoek plots for 1981/82 because records for 1981 in these were incomplete. Turnovers are shown in Figs 4.1. and 4.2.

The greatest turnover occurred from immediately before to immediately after fire, mainly because of species gained. Turnover at Jakkalsrivier for this interval averaged 21,8%, and at Zachariashoek, 29,6%. At Jakkalsrivier, turnovers between years after fire were very low, averaging 5,3% and 3,0% for the 1980/81 and 1981/82 intervals respectively. At Zachariashoek they were higher, averaging 14,5%, 14,1% and 10,1% for the 1978/79, 1979/81 and 1981/82 intervals respectively.

4.3.1.4. Changes in species richness The mean numbers of species per 5x10 m plot before fire at Jakkalsrivier and Zachariashoek were 55.7 and 53.2 respectively. In all plots, the numbers of species recorded increased markedly after fire (Figs. 4.3 an 4.4). Richness increased by a mean of 18 species at Jakkalsrivier, and 21,7 at Zachariashoek. Increases in richness, as well as the number of species recorded per plot before fire, were much more variable at Zachariashoek than at Jakkalsrivier. The F-ratios were 30.1 and 6.12 respectively, indicating differences significant at 1% and 5% levels of probability. At Zachariashoek the plot poorest in species before fire (28 species) showed an increase to a maximum of 64 after fire; those

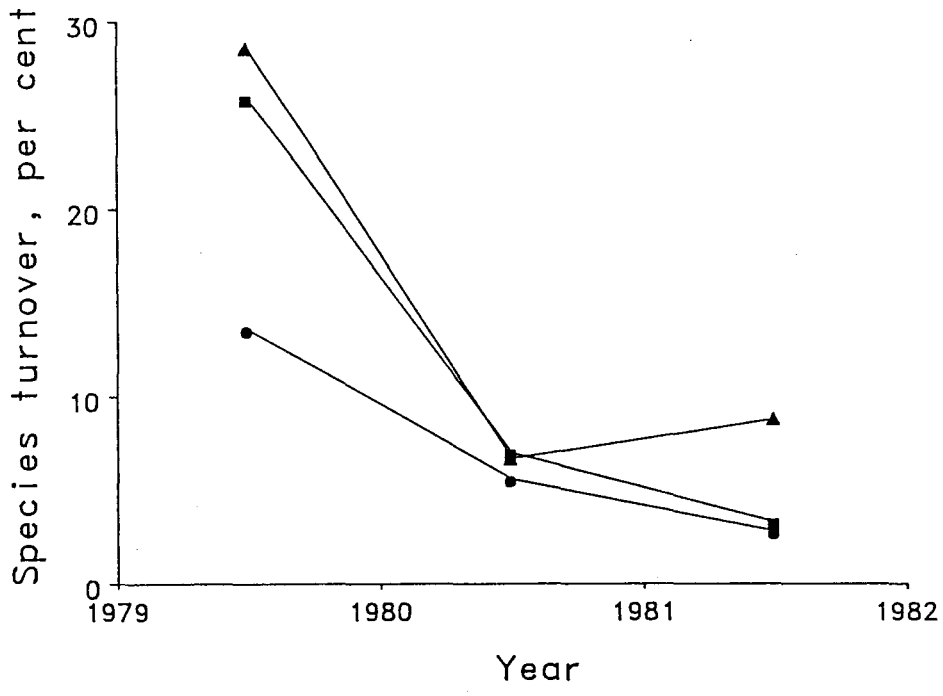


Fig. 4.1. Percentage turnover in species from one year to the next on the permanent quadrats at Jakkalsrivier. Dots: plot 1, squares: plot 2, triangles: plot 3.

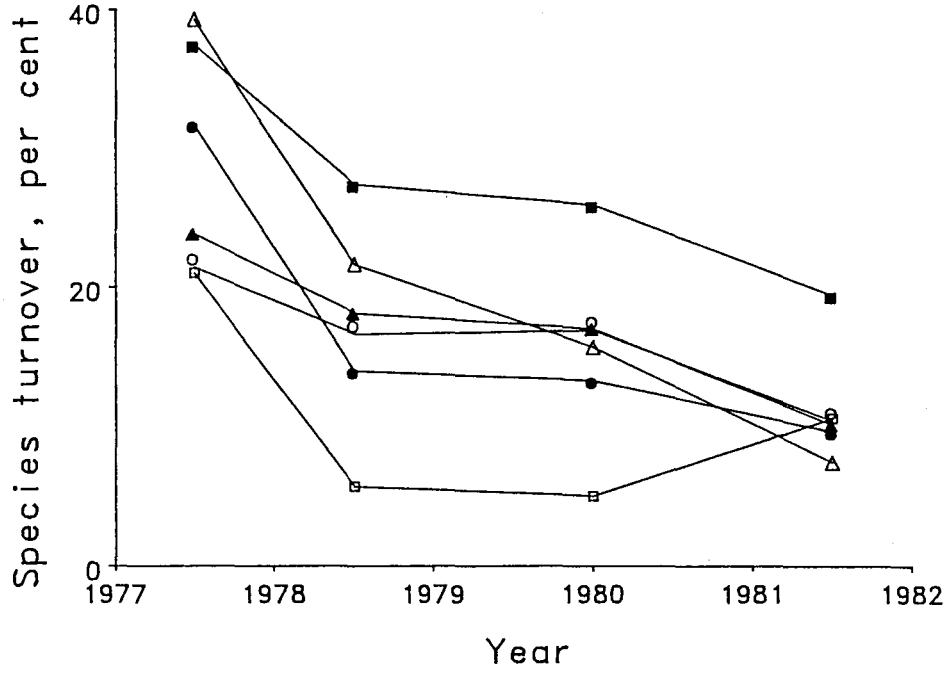


Figure 4.2. Percentage turnover in species from one year to the next at Zachariashoek. Triangles: plot 9, filled triangles: plot 15, squares: plot 16, filled squares: plot 17, circles: plot 82, dots: plot 84.

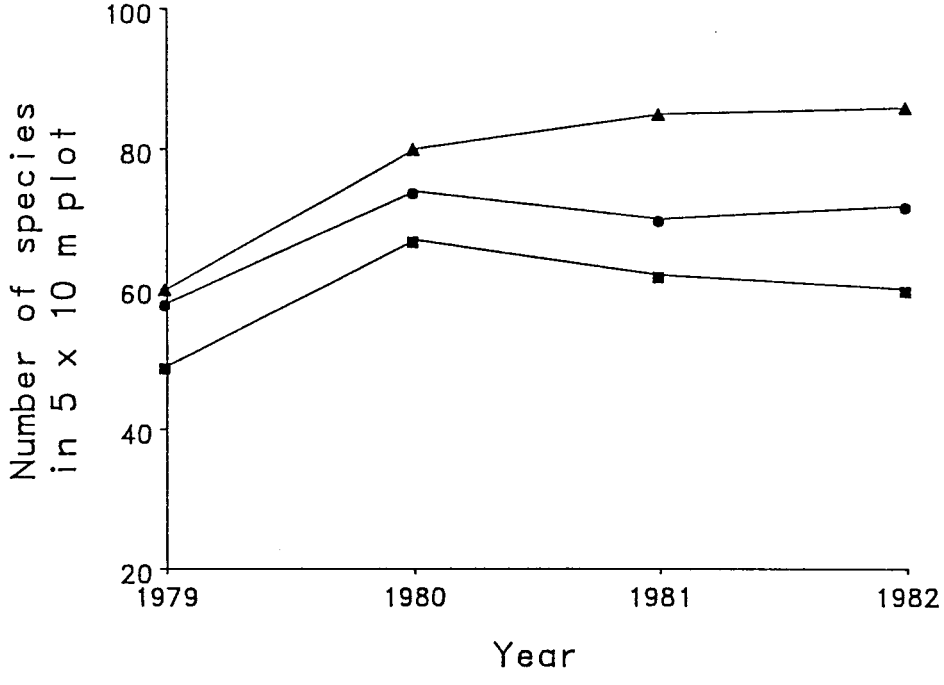


Figure 4.3 Changes in species richness after fire on 5 x 10 m quadrats at Jakkalsrivier. Dots: plot 1, squares: plot 2, triangles: plot 3.

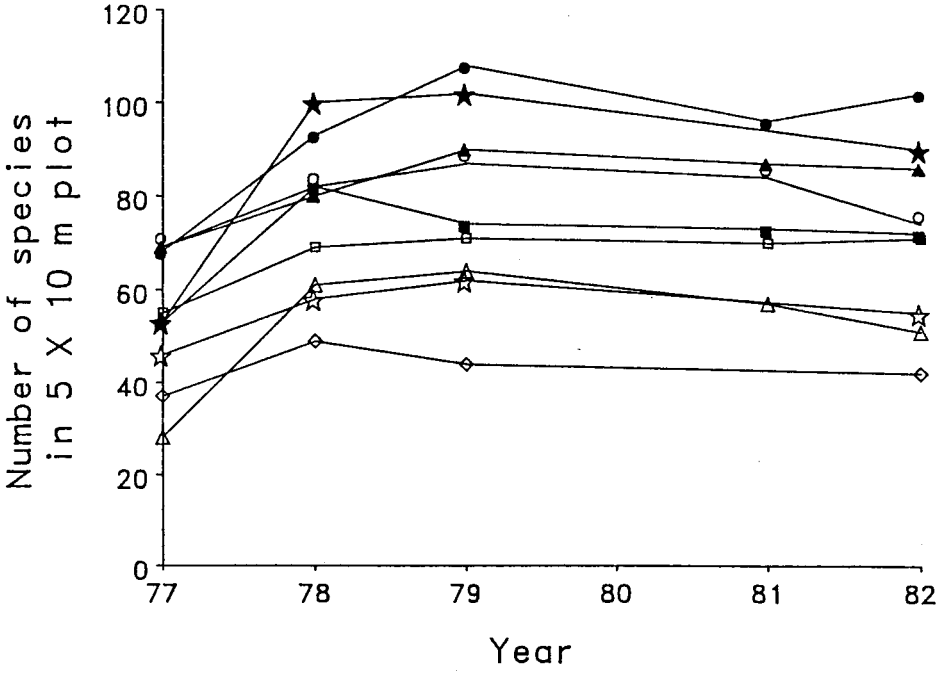


Figure 4.4 Changes in species richness on 5 x 10 m quadrats at Zachariashoek. Triangles: plot 9, filled triangles, plot 15, squares: plot 16, filled squares: plot 17, circles: plot 82, dots: plot 84, diamonds: plot 87, stars: plot 92, filled stars: plot 98.

richest in species (68 and 69) increased to maxima of 100 and 87.

Changes in species richness with time are shown in Figs. 4.3 and 4.4. The successional trends are variable. Although richness decreased after post-fire maxima in nine of the 12 quadrats, some showed no real change, and richness in plot 1g-3 at Jakkalsrivier was still increasing when observation ceased. Maximum richness was reached mostly in the second season after fire.

4.3.2. Gradient study at Jakkalsrivier Communities included in the sample varied widely in their structure. Height of the unburnt vegetation ranged from 0,45 m to 1,58 m, and mean projected canopy cover, from 57,5% to 89,5% (Table 4.3). Mean canopy volume of the unburnt stands ranged from 1,05 to 4,88 m^3 per quadrat. At the time of the survey, the values for mean height and cover of the burnt vegetation, then 2,5 years old, were 300 mm and 52,1%, respectively, as compared with 878 mm and 75,3% in the unburnt vegetation, then about 27 years old (Table 4.3). Mean canopy volume in the burnt vegetation was 24,7% of that in the burnt (Table 4.3).

The mean number of plant species in the unburnt quadrats was 25,6 per four-square-metre quadrat and 12,1 per 0,5 square-metre as opposed to 37,9 and 26,6 respectively for the burnt vegetation. Up to 34 species were recorded in unburnt quadrats, and 50 in the burnt. The difference in richness between unburnt and burnt members of quadrat pairs was very weakly correlated with pre-fire richness ($r = 0,559$, $P = 0,09$) but, on average, the difference was proportionately greater for poorer plots than for richer, with the slope of the regression equal to 0,346. In general, therefore, and despite the fact that this survey was conducted after some fire ephemerals had disappeared, fire is followed by a substantial increase in species richness.

The number of species in burnt quadrats varied quadratically with canopy volume of the unburnt quadrat, except that the quadrat with the greatest canopy volume departed significantly from this relationship. This relationship was marginally significant ($r^2 = 0,561$, $F = 3,84$, $P = 0,0844$). The relationship between the difference in richness between burnt and unburnt quadrats was also quadratic, and

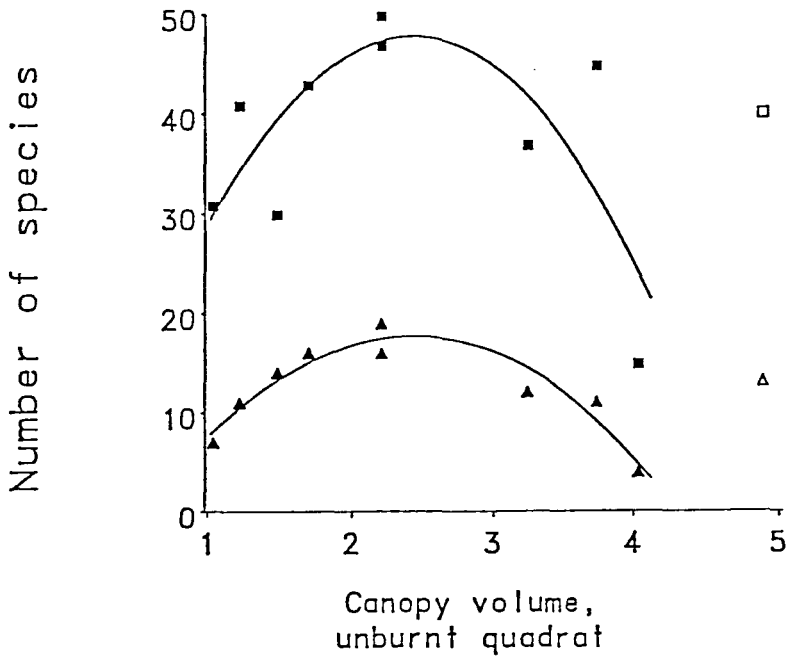


Figure 4.5. Relationships between number of species in quadrats and canopy volume (m^3 per 2x2 m quadrat) in unburnt quadrat of the same pair (squares), and increase in richness in burnt over unburnt quadrats against the same independent variable (triangles). Data from gradient survey of post-fire recovery patterns at Jakkalsrivier. Open symbols are outlier data points, not used in the regression (see text).

statistically significant (Fig. 4.5, Table 4.4). Species richness in burnt quadrats was similarly related to the relative degree of recovery in canopy of burnt vegetation (Fig. 4.5, Table 4.5). The number of species in the unburnt quadrats had no statistically significant relationships with canopy characteristics. Taking canopy volume, rather than cover (see also Chapter 5) to indicate biomass, and the ratio of post-fire canopy volume to pre-fire to indicate recovery rate, one may conclude that the relative increase in species richness after fire and hence the obverse, the number lost during succession, is related to biomass in the form of a hump-shaped curve. The increase in species after fire is thus related to pre-burn biomass and to post-fire recovery rate, with greatest gains in species being found at intermediate levels of biomass. However, the quadrat pair

Table 4.3. Statistics for paired sample of 2x2 m quadrats from burnt and unburnt vegetation at Jakkalsrivier. Standard deviations in brackets.

	Unburned quadrats (n=9)	Burnt quadrats (n=10)
Mean no. of plant species per 2x2 m quadrat	25,0 (7,31)	37,9 (10,3)
Mean no. of plant species per 0,5 square metre subdivision	11,6 (3,36)	20,4 (5,21)
Mean no. of plant species exclusive to member of quadrat pair	6,7 (1,77)	19,0 (4,69)
Total number of species encountered	94	153
Mean canopy height, mm	878 (47,8)	300 (108)
Mean canopy cover, %	75,3 (10,0)	52,1 (16,6)
Mean canopy volume, cubic metres	2,63 (1,39)	0,65 (0,31)

Table 4.4. Regression analysis of a quadratic model for difference in species between burnt and unburnt quadrats and unburnt canopy volume, without outlier quadrat pair no. 4. The model is $y = -11,73 + 24,27x - 5,01x^2$.

Source	Degrees of freedom	Sum of squares	Mean square	F	P	r^2
Model	2	158,0	79,0	27,03	0,001	0,90
Error	6	17,5	2,92			
Total	8	175,6				

Table 4.5. Regression analysis of a quadratic model for species richness in burnt quadrat on canopy recovery, i.e. the ratio of the canopy volume on the burnt quadrat to that of the unburnt. The model is $y = 17,8 + 1,67x - 0,0253x^2$, where y is the richness in the burnt quadrat and x is the ratio of canopy volumes.

Source	Degrees of freedom	Sum of squares	Mean square	F	P	r^2
Model	2	253,5	126,7	6,41	0,032	0,681
Error	6	118,7	19,8			
Total	8	372,2				

with exceptionally high biomass was an outlier in this relationship, being richer than would be predicted. Further sampling may therefore show that the relationships between diversity, productivity, and succession are more complex than this analysis has indicated.

Several unburnt quadrats had no distinguishable overstorey, being low heath formations with the shrub crowns intermingled with the restioid layer. The five quadrats which did have an overstorey did not differ significantly in their richness from those without an overstorey.

A total of 165 vascular plant species was recorded in the sample. A few species of mosses and lichen were recorded (though not identified) but these were nowhere important. The unburnt subsample contained 94 species, and the burnt, 153. There were proportionally more seeding than sprouting species in the burnt than the unburnt set (53 and 100 as opposed to 19 and 75, $\chi^2 = 5,19$, $P < 0,05$) mainly because no fire ephemerals were to be found in the unburnt vegetation (there were 19 in the burnt set) but also because these were proportionately fewer obligate seeders in the unburnt vegetation (19 vs 33). Sprouters were fewer mainly because fewer deciduous geophytes and grasses were detected in the unburnt vegetation. Most species recorded in the burnt vegetation but not in the unburnt had a low frequency; of 71 such cases, 86% occurred just once or twice in the burnt sub-sample.

The gain in species after fire, and hence the loss during pyric

succession, involves both fire ephemerals and longer-lived species. The attrition would appear to be progressive and gradual, rather rapid during the immediate post-fire period, as indicated also by the trends observed in the first few years at Jakkalsrivier and Zachariashoek (Figs 4.3 and 4.4). However, many of the species which disappear during the pyric succession are rare in any case.

4.3.3. Species' vital attributes and fire-response categories

Details for each positively identified species with regard to vital attributes and related features are given in Appendices 4.1 and 4.2. Sprouting species predominated in the floras sampled at Jakkalsrivier and Zachariashoek, comprising 67,8% and 69,4%, respectively, of the total numbers of species listed and classified by regeneration mode (Table 4.6). Of these, the auto-regenerating, long-lived sprouters predominated (97% and 98% of sprouting species, respectively). These included broad- and narrow-sclerophyllous shrubs, perennial herbs in the Restionaceae and Cyperaceae, and both evergreen and deciduous geophytes. A handful of facultative sprouter-seeders was recorded. These include, for example, Ehrharta ramosa, a weakly tufted aphyllous grass which sprouts after fire but multiplies profusely from seed if disturbance is severe. Few species were identified as obligate sprouters. Agathosma bifida at Jakkalsrivier sprouts from stems after fire but also multiplies readily by root-suckering, especially when soil is disturbed.

Of sprouters, most had effectively no secondary juvenile period and were classified as UI species in the Noble-Slatyer system (Table 4.6). Of the VI species at Jakkalsrivier, Bruniaceae were most prominent (Table 4.6).

At Jakkalsrivier, there was no significant difference between the three permanent succession quadrats in the proportion of seeders to sprouters (χ^2 = 2,43, P = 0,296). Seeding species constituted 28,7% of the flora on the mesic plot, and 35,6% on the other two.

In the gradient survey, the proportions of seeding to sprouting

Table 4.6. Analysis of floras in samples at Jakkalsrivier (J; permanent quadrat and gradient survey) and Zachariashoek (Z) in terms of Noble-Slatyer and fire response categories.

Fire response type	Generative regeneration (obligate seeders)						Vegetative regeneration (sprouters)				Total	
	seed widely dispersed		seed stored in the canopy		soil-stored seed		without juvenile period		with juvenile period			
	J	Z	J	Z	J	Z	J	Z	J	Z	J	Z
Seeders												
Fire ephemerals												
monocarpic	0	0	0	0	1	5	1	0	-	-	2	5
polycarpic	3	1	0	0	31	47	-	-	-	-	34	48
Obligate seeders	2	8	8	3	29	34	-	-	-	-	39	45
Neutral[a]	0	0	0	0	0	4	-	-	-	-	0	4
Sprouters												
Facultative sprouter-seeder	-	-	-	-	-	-	3	3	0	0	3	3
Auto-regenerating, long-lived	-	-	-	-	-	-	142	221	5	2	147	223
Obligate vegetative	-	-	-	-	-	-	1	1			1	1
Unclassified	-	0	0	0	1	0	0	0	0	0	5	54
Total	5	9	8	3	62	90	147	224	5	2	230	335

[a] Species whose germination is evidently not affected by fire.

species in the burnt quadrats varied significantly ($\chi^2 = 30,4$, $P = 0,0004$). The average proportion was 33%, varying mainly from 10% to 50%, with 65% in the species-poor phreatic plot. The numbers varied from 8 to 21 per 2x2 m quadrat. The numbers of seeders were not significantly linearly correlated with the number of sprouters ($r = -0,305$, $P = 0,391$), but the correlation was significant if the observation for quadrat pair no. 6, representing the phreatic site, was excluded ($r = -0,696$ $P = 0,037$). The phreatic site therefore had an unusually high proportion of seeders, unlike the heathlands of Australia (Specht 1981). Richness of seeders was not correlated with overall richness ($r = 0,09$) but richer plots contained more sprouters ($r = 0,92$, $P < 0,0001$, $b_o = 11,2$, $b_1 = 0,964$, $F = 45,2$). Neither the number of seeding species nor the number of sprouting species nor the proportion between the two was related in any statistically significant way to cover or canopy volume of unburnt vegetation, nor to relative recovery rate of canopy. This is also unlike the situation in Australian heathlands, where the denser the canopy the fewer seeder species are found. In the unburnt vegetation, seeders constituted an average of 17% of the species listed, varying from two to nine per quadrat with no significant relationships between sprouters and seeders evident.

At Zachariashoek, seeders averaged 33,9% of species listed in the nine quadrats, with numbers ranging from 10 to 31. The proportions did not vary significantly among quadrats, and the number of seeders per quadrat was linearly related to the number of sprouters ($r^2 = 0,747$, $F = 20,6$, $P = 0,0027$, $b_o = 18,24$, $b_1 = 0,695$), which was contrary to the pattern found in the gradient sample of small quadrats from Jakkalsrivier

The entire flora as sampled at Zachariashoek and Jakkalsrivier included 107 and 75 seeding species respectively. Of these, 54% and 48% respectively were fire ephemerals, the difference not being significant ($\chi^2 = 0,662$, ns). Most of the fire ephemerals were polycarpic, with only a handful of monocarpic species being recorded. One of the monocarpic species, Moraea ramosissima at Jakkalsrivier, was ambiguously recorded as a sprouter because it appeared to sprout

and flower after fire from a dormant corm from seedlings established after a previous fire, with the parent then dying.

Thirty-three species at Zachariashoek and 18 at Jakkalsrivier were classified as being highly dispersed (vital attribute D). These were mainly wind-dispersed, including species with dust and pappoid seeds. A few were bird-dispersed, i.e. one each at either site. Most were sprouters.

Species with soil-stored seed dominated the obligate-seeder category (Table 4.6). Serotinous species were surprisingly few, amounting to three at Zachariashoek and eight at Jakkalsrivier. A small minority of species at Zachariashoek was classified as tolerant. At Jakkalsrivier, Erica hispidula was classified as requiring some change to the site during succession for establishment (vital attribute R). All other species were classified as intolerant, since seedlings were not found from 12 to 24 months after fire.

The seeding floras of the three permanent succession plots at Jakkalsrivier were similar in composition. There was no significant difference in the proportions of fire-ephemerals to obligate seeders (χ^2= 0,052, ns). Fire ephemerals numbered 9, 13 and 15 in plots 1, 2 and 3 respectively. Among obligate seeders, serotinous species numbered 3, 7 and 2, respectively. In plot 3, these species occurred as singletons only and had very low biomass. Leucadendron xanthoconus and Erica sessiliflora were abundant in plot 1 before and after fire, and were prominent canopy species before fire (Chapter 5). In plot 2, three of the seven species were rare and peripheral. Nonetheless, the overstorey was dominated before fire by the serotinous species Berzelia lanuginosa (cover-abundance rating 4), Leucadendron salicifolium (2b), and Brunia alopecuroides (1).

Life-stage tables for species recorded in the three permanent quadrats at Jakkalsrivier are shown in Tables 4.8 and 4.9. There is little substantial variation within the Noble-Slatyer species-type categories and where species are identical in this regard they are not all shown.

Species with the "D" vital attribute are those whose seed disperses by wind or by animals (birds). Dust-seeded species of the Orchidaceae and Droseraceae apparently have this attribute. Despite their small seed, Ericaceae are presumed not to have this habit (see below), except in the case of Erica hispidula, a very widespread species with extremely small seed. Winged seed, or seed with other morphological features apparently favouring wind dispersal, may or may not be highly dispersed. Among Asteraceae, the pappoid fruits of Mairia crenata, some species of Senecio, and Stoebe spp., are readily shown to fly freely in light breezes. By contrast, species like Ursinia crithmoides, with limp pappi, do not. Only seventeen species other than Erica hispidula were classified as "D" species. Cassytha ciliolata was classified as a D species by virtue of its fleshy red fruits which are presumably carried about by birds.

Species with soil-stored seed were presumed all to belong to the S category, because exhaustion of seed banks by germination after fire is improbable (cf. Harper 1977). By contrast, all species with canopy-stored seed were presumed to have their seed banks exhausted by germination and other losses after fire, by analogy with other cases (Bond 1985), and were classified as C species.

All sprouting species were assumed to have the capacity to survive fire while in the juvenile state, i.e. there was none in the W class. This is reasonable because fire seldom recurs within 2-3 years in fynbos and young plants of sprouting species commonly acquire the sprouting mechanism within such a period (Frost 1984; Kruger and Bigalke 1984). Most sprouters flowered and set seed within the first season or two after fire, and were therefore classified as U species. A few had longer secondary juvenile periods, and were classified as V species. Two sprouting legumes were assumed to have soil-stored seed which survived the parent plants, and were classified as $\sum$ species (Table 4.8).

As noted above, species were classified tentatively according to the vital attribute group which relates a species to conditions determining establishment by observing germination behaviour. Thus, Erica hispidula was classified as an R species. Seedlings or young plants are frequent in mature and senescing fynbos (see chapter 5).

Table 4.7. Abstract list of species types at Jakkalsrivier classified according to the scheme of Noble and Slatyer (1981), with life stage parameters. Seeding species only. m = stage of maturity, l = death of population, e = local extinction i.e. that stage where all propagules as well as parent plants have been lost. Fire response types are according to Bell et al. (1984).

Species	Fire-response type	Life-stage at given time since fire in years											
		0	1	2	3	4	6	10	20	30	50	80	120	∞
Species type = DR														
Erica hispidula	OS						m			l				e
Species type = DI														
Senecio rigidus	PFE		m		l									e
Senecio pubigerus	PFE		m				l							e
Othonna quiquedentata	PFE		m					l						e
Stoebe incana	PFE					m			l					e
Cassytha ciliolata	OS					m					l			e
Species type = SI														
Heliophila crithmifolia	MFE	m	l								e			
Selago verbenacea	PFE	m			l					e				
Lebeckia carnosa	PFE		m		l								e	
Ehrharta rehmannii	PFE		m		l							e		
Hypocalyptus oxalidifolia	PFE		m		l								e	
Agathelpis dubia)	PFE													
Leontonyx spathulatus)	PFE		m					l			e			
Ursinia crithmoides)	PFE													
Roella incurva)	PFE													
Lightfootia subulata	PFE			m		l					e			
Aspalathus globosa	PFE			m		l							e	
Centella difformis	PFE			m					l		e			
Thesium euphorbioides	PFE			m					l			e		
Erica longifolia + 7 others	OS						m			l		e		
Cliffortia atrata	OS						m				l		e	
Species type = CI														
Berzelia lanuginosa	OS						m				l			e
Nebelia fragaroides	OS)						m			l				e
Erica sessiliflora	OS)													
Leucadendron xanthoconus)														
+ 2 others	OS)													
Protea neriifolia	OS							m			l			e

Table 4.8. Abstract list of sprouting species types at Jakkalsrivier classified according to the scheme of Noble and Slatyer (1981), with stage parameters. See Table 4.7 for further explanation.

Species	Fire-response type	Life-stage at given time since fire in years												
		0	1	2	3	4	6	10	20	30	50	80	120	200	∞
Species type = WI															
Disa cornuta, Mairia crenata + 10 others	ALS) ALS)	m					(m)						l		e
Species type = ΣI															
Argyrolobium filiforme	ALS	m					(m)					l		e	
Aspalathus millefolia	ALS	m					(m)					l		e	
Species type = UI															
Festuca scabra	FSS	m							le						
Lobelia linearis + 2 others	ALS	m									le				
Aristea racemosa) Penaea mucronata) Corymbium glabrum) Tetraria fimbriolata) + 43 others)	ALS	m								le			le		
Ehrharta ramosa	FSS		m						le						
Drosera ramentacea + 6 others	ALS		m								le				
Elegia juncea + 35 others	ALS		m										le		
Agathosma bifida	OVS		m										le		
Species type = VI															
Cliffortia eriocephalina + 1 other	ALS				m								le		
Nebelia paleacea + 1 other	ALS					m							le		
Brunia nodiflora	ALS						m						le		

But seedlings were found for the first time about two to three years after fire. Some condition of the habitat must therefore change in the period after fire to allow establishment. It may of course be that time is required for the seed to arrive on the burnt site but then one would expect to find seedlings along fire boundaries immediately after fire, and this was not the case. Species in the Ericaceae on plot 3 did not appear as seedlings in the first season after fire, but only in the second. However, at least some of these, such as Erica longifolia and E. sessiliflora, did germinate in the first year on plot 1 and it was therefore assumed that these species were not R-species.

Seedlings and young plants of the majority of the flora are seldom seen in mature fynbos. Twenty-three-year-old fynbos at Jakkalsrivier was surveyed for regeneration in November 1981. Twenty-five female Leucadendron xanthoconus shrubs were selected at random, and an area within a radius of 1 m around each was searched for young and subadult plants of the same species as well as of any Ericaceae. Density of female Leucadendron plants estimated from distance measures was about $2900.ha^{-1}$. Mean canopy cover of Ericaceae was about 50%. The sample yielded one young Leucadendron ($127.ha^{-1}$), and 12 young Ericaceae. Thus, some regeneration does occur, but it is sparse and plants established under such conditions probably seldom reach reproductive maturity (see also Chapter 6). Therefore, the assumption that all species were intolerant of conditions in the established stand and classified I, unless there was clear evidence to the contrary, was reasonable.

Except that plot 1g-3 had a very sparse complement of C species, the vegetation of the three burnt quadrats at Jakkalsrivier did not differ substantially in composition by species type. The sclerophyllous shrubland on the mesic site at plot 1g-1 was therefore analysed for replacement sequences using the species whose attributes are given in Table 4.9. Erica hispidula was added to the list despite its absence from plot 1g-1, because it occurs in the immediate vicinity and apparently has the potential to occur on this specific site. The analysis of the replacement sequences is depicted in Fig. 4.6.

Twenty-five states are possible for this community. In many cases, differences between states are small, arising from the transition from juvenility to maturity or vice versa of one or a few species. The major features of the analysis are outlined below.

(a) Where fire recurs at 20-30-yr intervals, a Protea-Leucadendron proteoid shrubland is maintained. This is represented by the first six states in the top row of the diagram.

(b) Where this sequence is interrupted by fire within 10 years, the vegetation loses Protea neriifolia and becomes a shrubland with Leucadendron xanthoconus representing the proteoid element (second and third states in second row).

(c) Interruption of the sequence at intervals of less than six years produces a mixed ericoid heathland, with Erica longifolia prominent.

These major sequences, the mixed proteoid shrubland, the Leucadendron xanthoconus proteoid shrubland, and the mixed ericoid shrubland, converge on a heathland dominated by Erica hispidula if fire is absent for more than 50 to 120 years, because the principal species are inhibited from recruitment in the presence of an established canopy and once seed stocks are lost are unable to re-enter the stand through long-range dispersal.

The herbland successional pathway is assumed to arise when ericaceous shrubland is repeatedly burnt while S- and V- species are in the juvenile stages. This is because the soil-stored seed stocks must eventually be exhausted, and V-species must eventually succumb to very frequent fire. For example, Bruniaceae have been seen to be eliminated from firebreaks at Jonkershoek (personal observation).

Neither Erica hispidula heathland nor the herbland can revert to the original formation, because the lost species are not vagile. In reality, the Proteaceae and ericoids may return in due time, since

short-range dispersal will allow some migration of plants with each generation (e.g. Manders 1986).

4.3.4. Succession on soil slips All soil slips examined occurred on quartzite substrata. Where mass wastage had removed A horizons, very pale, leached E horizons, saprolite, or bedrock were exposed. Very few and sometimes no plants were encountered on such exposures, those listed including Erica hispidula, Hypochoeris radicata (an introduced species), and Leucadendron xanthoconus. More species were encountered on exposed A_2 and B horizons, including those listed as colonisers in Table 4.11, with several others native to Jakkalsrivier. Among these were also species of Drosera, Restio and Tetraria, which normally regenerate vegetatively after fire. Just over two and a half years after the erosion, plants on these sites were still too sparse for populations to be sampled.

The quadrat samples included four units from undisturbed vegetation, four on denuded sites, and two on rubble. The cover of the regenerating vegetation was markedly lower on disturbed sites than on undisturbed ones, amounting to about 8% on rubble and 30% on denuded sites as opposed to an average of about 80% on undisturbed sites (Table 4.10). The canopy of the disturbed vegetation was also lower on average (Table 4.10). Many plants had survived the mass wastage and had regenerated by sprouting. Despite these effects, species richness was little affected, being the same on undisturbed and denuded sites (about 31 to 32 species each) and perhaps somewhat lower on the rubble, where 19 and 22 species were recorded in the sample (Table 4.10).

The patterns of dominance were markedly changed by the disturbance. The undisturbed quadrats were dominated by ericoid shrubs, although grasses, sedges and restios were also ranked high (Table 4.12). The shrubs were mainly seeders and as a result, the disturbed sites, were dominated by grasses and restios, with some forbs occasionally prominent, and the correlation between the ranked list of dominant species was poor (Table 4.11). Even so, 10 of 28 species listed as dominants on disturbed sites were included in the list of 16 for the undisturbed sites, and those which were not included had all been recorded at one or more stages of the pyric successions on the permanent quadrats. Very few of the species in the complete lists for

Table 4.10 Abstract life-stage table for the vegetation on the mesic plot at Jakkalsrivier. Species of the same type but differing in their life stages are distinguished by numerical superscripts. Erica hispidula was recorded on this plot but occurs close by and is potentially present.

	Species type	Life-stage at given time after fire, year.													
		0	1	2	3	4	6	10	20	30	50	80	120	200	∞
Erica hispidula	DR	----------	----------	----------	----------	----------	----------	m	----------	----------	----------	----------	----------	----------	le----
Stoebe incana	DI	----------	----------	----------	----------	m	----------	----------	l	----------	----------	----------	----------	----------	e-----
Protea neriifolia	CI^1	----------	----------	----------	----------	----------	----------	----------	m	----------	----------	le	----------	----------	----------
Leucadendron xanthoconus	CI^2	----------	----------	----------	----------	----------	----------	m	----------	----------	le	----------	----------	----------	----------
Heliophila crithmifolia	SI^1	ml	----------	----------	----------	----------	----------	----------	----------	----------	----------	e	----------	----------	----------
Roella incurva	SI^2	------	m	----------	----------	----------	----------	l	----------	----------	e	----------	----------	----------	----------
Erica longifolia	SI^3	----------	----------	----------	----------	----------	m	----------	----------	l	-----	e	----------	----------	----------
Festuca scabra	UI^1	m	----------	----------	----------	----------	----------	----------	le	----------	----------	----------	----------	----------	----------
Restio dispar	UI^2	m	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	le	----------	----------
Mairia crenata	ΔI	m	----------	----------	----------	----------	----------	----------	----------	----------	----------	l	----------	----------	e-----
Aspalathus millefolia	$\sum I$	m	----------	----------	----------	(m)	----------	----------	----------	----------	l	----------	----------	e	----------
Brunia nodiflora	VI	----------	----------	----------	----------	----------	m	----------	----------	----------	----------	----------	le	----------	----------

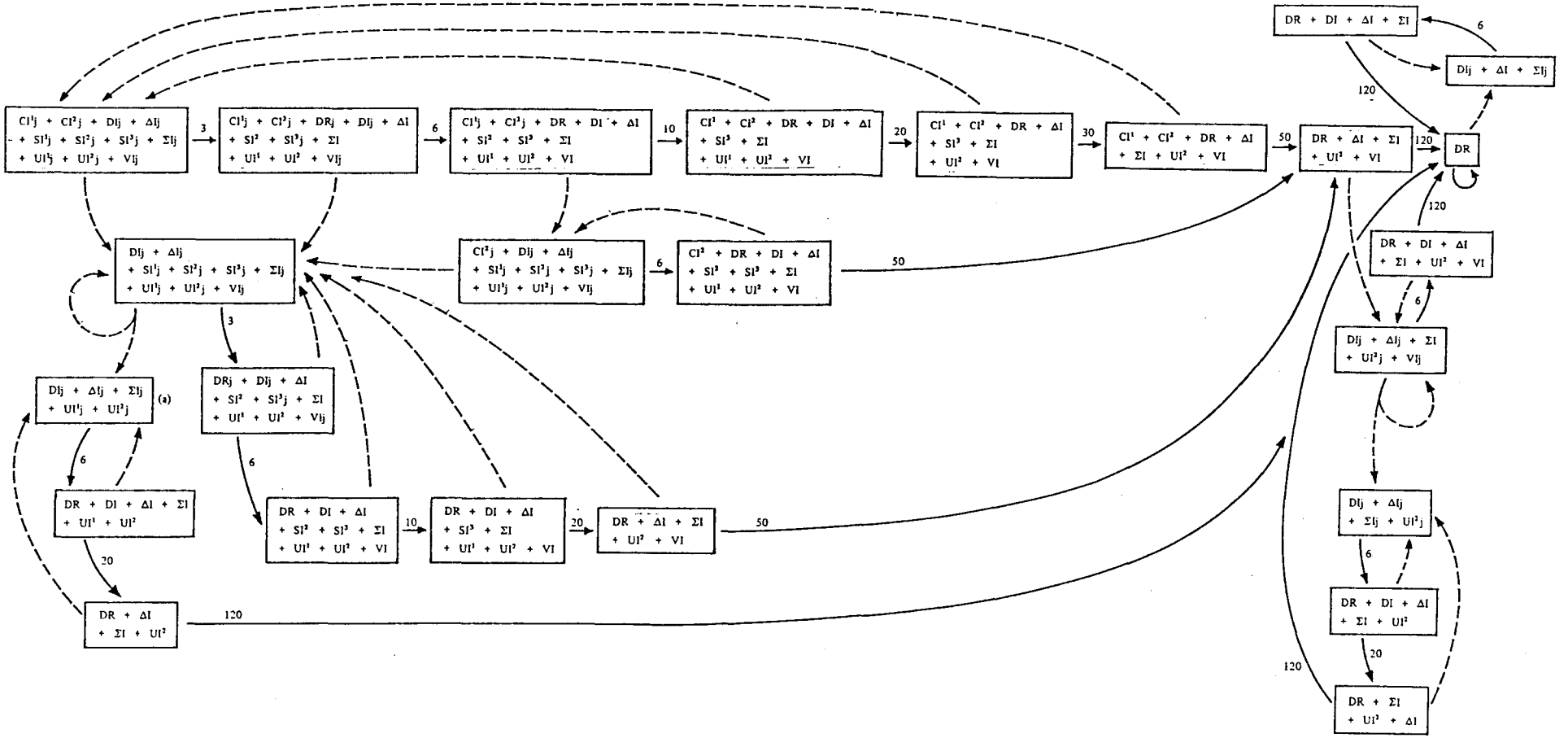


Figure 4.6 Analysis of different successional pathways under varying hypothetical fire regimes in broad-sclerophyllous fynbos at Jakkalsrivier, based on the system of vital attributes developed by Noble and Slatyer. The symbols refer to the species listed in Table 4.10. Arrows with solid lines indicate a transition without fire and those with dashed lines indicate transitions which occur when the vegetation is burnt. Figures above the solid arrows give the total time in years which has passed without fire from the time the base state arose.

Table 4.10. Species richness in samples of 2 x 2 m quadrats on soil slips at Jakkalsrivier, compared with richness in undisturbed vegetation. See text.

	Samples on soil slips		Undisturbed sample
	Sites disturbed by colluvial rubble	Sites denuded of vegetation	
n	2	4	4
Mean no. of species	23,0	31,8	31,3
Range, no. of species	19-27	26-40	29-36
Mean height, mm	160,0	291,0	657,0
Range in height, mm	143-176	157-444	494-1044
Mean cover, %	7,8	29,7	79,9
Range, %	7,6-8,0	19-43	65-86

Table 4.11. List of dominant species in the sample of 2 x 2 m quadrats from soil slips at Jakkalsrivier. (G = regeneration by germinative means, i.e. seeders, and V = regeneration vegetative, i.e. sprouters).

Species	Regene-ration mode	Growth form	Colonist or not	Average ranking by biomass	
				Undisturbed	Disturbed
Blaeria dumosa	G	shrub	yes	1	16
Erica hispidula	G	shrub	yes	2	26
Grubbia tomentosa	V	shrub	no	3	16
Pentaschistis colorata	V	grass	yes	4	1
Thamnochortus gracilis	V	restio	no	5	4
Restio dispar	V	restio	no	6	7
Leucadendron xanthoconus	G	shrub	yes	7	-
Tetraria thermalis	V	sedge	no	7	-
Penaea mucronata	V	shrub	no	9	-
Chondropetalum deustum	V	restio	no	10	9
Leptocarpus membranaceus	V	restio	no	10	5
Sympieza articulata	G	shrub	yes	10	-
Tetraria fasciata	V	sedge	no	10	-
Tetraria flexuosa	V	sedge	no	10	-
Anthospermum prostratum	G	forb	yes	15	12
Elegia racemosa	V	restio	no	16	3
Ehrharta ramosa	G/V	grass	yes	-	2
Centella eriantha	G	forb	yes	-	6
Pentaschistis steudelii	G/V	grass	no	-	8
Osmitopsis afra	V	forb	no	-	10
Merxmuellera rufa	V	grass	no	-	11
Mimetes cucullatus	V	shrub	no	-	13
Hypodiscus aristatus	V	restio	no	-	14
Drosera ramentacea	V	geophyte	no	-	15
Corymbium glabrum	V	geophyte	no	-	16
Metalasia muricata	G	shrub	yes	-	19
Stoebe incana	G	shrub	yes	-	19
Ficinia filiformis	V	sedge	yes	-	21
Tetraria fimbriolata	V	sedge	yes	-	21
Haplocarpha lanata	V	geophyte	no	-	23
Mairea crenata	V	geophyte	no	-	23
Pseudopentameris macrantha	V	grass	no	-	23
Cassytha ciliolata	G	vine	yes	-	26
Centella difformis	G	forb	yes	-	26

the quadrats on the soil slips had not been recorded in the post-fire succession, and all of such species had been collected several times previously at Jakkalsrivier in undisturbed vegetation. The fynbos at Jakkalsrivier, like the heathlands of Australia (Grubb and Hopkins 1986), has few weedy species.

Several species were identified as colonists of the soil slips, i.e. had germinated on bare patches from seed evidently dispersed from close by. These included seeding and sprouting species (Table 4.11). Among these were some grasses and forbs, such as Ehrharta ramosa and Centella eriantha, which dominated some quadrats and were also prominent in pyric successions elsewhere. However, dominants on the disturbed quadrats were also often species characteristically dominant in older vegetation (Table 4.11).

4.3.5. Changes in the vegetation on the transect at Jonkershoek

Twenty-six species were recorded by R.S. Adamson on the transect in 1948, with a sedge, Ficinia filiformis, having greatest cover, followed by a graminoid member of the Iridaceae, Bobartia indica, the seeding shrub Anthospermum aethiopicum, and the sprouting shrub Leucadendron salignum (Table 4.12). Thirty-three species were recorded in 1981. The dominant species in terms of cover was the seeding shrub, Erica sphaeroidea, the sprouting dwarf shrub Helichrysum teretifolium, Bobartia indica, and Anthospermum aethiopicum. Only eleven species were common to both lists. About three of the species recorded by Adamson were not fully identified or could have been misidentified (e.g. Tetraria capitata) and may therefore still have been present in 1981. Most of the change in the flora seems to have been real, however. Although the two samples were not taken in the same month of the year (September 1948, vs August 1981), the difference is small and ought not to have affected the results. One of the species recorded in 1981 but not in 1948, Helichrysum teretifolium, was recorded by Adamson's party on chart quadrats in the vicinity in 1948, but the others were not. H.C. Taylor listed species in Abdolskloof in January and April 1963, and recorded at least eight of the "new" species found in 1981. By the time that quantitative analyses of the vegetation in Abdolskloof

Table 4.12. List of species recorded on the transect at Abdolskloof, Jonkershoek. See text. "t" indicates cover less than 0,1%.

Species	Growth form	1948 Survey		1981 Survey	
		Frequency	Mean cover %	Frequency	Mean cover %
Ficinia filiformis	sedge	18	14,95	11	0,32
Bobartia indica	restio	19	10,10	20	7,40
Anthosperum aethiopicum	shrub	19	9,91	20	6,60
Leucadendron salignum	shrub	8	5,90	7	1,26
Corymbium africana	geophyte	14	5,26	0	0
Stoebe fusca	shrub	10	4,56	0	0
Psoralea bracteata	shrub	11	1,38	0	0
Stoebe plumosa	shrub	5	1,26	0	0
Tetraria capitata	sedge	3	0,80	0	0
Berkheya armata	geophyte	13	0,74	14	t
Montinia caryophyllacea	shrub	3	0,61	0	0
Corymbium villosum	geophyte	3	0,510	2	t
Chrysocoma tenuifolia	shrub	6	0,17	0	0
Helichrysum sp.	?	6	t	0	0
Anthericum hirsutum	geophyte	3	t	0	0
Pentaschistis curvifolia	grass	3	t	7	0,220
Protea acaulos	shrub	3	t	0	0
Oxalis spp.	geophyte	7	t	0	0
Sebaea exacoides	annual	5	t	0	0
Diosma vulgaris	shrub	4	t	4	t
Rhus rosmarinifolia	shrub	2	t	6	0,270
Adenandra uniflora	shrub	3	t	0	0
Mohria caffrorum	fern	2	t	1	t
Pelargonium tabulare	forb	2	t	0	0
Phylica spicata	shrub	1	t	0	0
Rhus tomentosa	shrub	1	t	1	t
Erica sphaeroidea	shrub	0	0	20	12,0
Helichrysum teretifolium	shrub	0	0	13	9,60
Cymbopogon marginatus	grass	0	0	12	2,80
Pentaschistis colorata	grass	0	0	11	1,91
Merxmuellera stricta	grass	10	0	10	0,830
Tetraria cuspidata	sedge	0	0	10	0,580
Erica hispidula	shrub	0	0	1	0,150
Helichrysum cymosum	forb	0	0	1	0,150
Oxalis purpurea	geophyte	0	0	7	0,130
Galium tomentosum	forb	0	0	3	0,105
Oxalis sp. cf. O. obtusa	geophyte	0	0	17	t
Oxalis tenuifolia	geophyte	0	0	17	t
Iridaceae sp.	geophyte	0	0	15	t
Caesia eckloniana	geophyte	0	0	9	t
Cyphia bulbosa	geophyte	0	0	3	t
Iridaceae spp. (Geissorhiza sp.?)	geophyte	0	0	3	t
Gnidia inconspicua	shrub	0	0	1	t
Pelargonium longifolium	geophyte	0	1	t	
Cyphia volubilis	geophyte	0	0	1	t
Pentaschistis steudelii	grass	0	0	1	t
Unknown geophyte	geophyte	0	0	1	t

began in 1963, the species dominant in the transect in 1981, such as Erica sphaeroidea, Helichrysum teretifolium, and Cymbopogon marginatus, were common (personal observation).

The analyses conducted by Adamson's party in 1948 were detailed, and herbarium specimens were collected for identifications. It must be concluded that the changes recorded in this case were real. Most of the dominants persisted but some, such as Corymbium africana and Stoebe fusca, did not, though they are still found elsewhere in the area. The Helichrysum sp. recorded in 1948 may have been H. teretifolium. The dominants added to the list, i.e. Erica sphaeroidea, and the grasses Cymbopogon marginatus and Pentaschistis colorata, are common at Jonkershoek. Their addition to the list at the Abdolskloof site represents a substantial change in the vegetation.

4.4. Discussion and conclusions

4.4.1. Primary versus secondary succession It was clear from the study of succession on the soil slips that the fynbos at Jakkalsrivier lacks plant species which are strictly pioneers of severely disturbed sites. Prolific colonizers of exposed soils, such as Anthospermum prostratum, Centella eriantha, Ehrharta ramosa, and Pentaschistis colorata were typical also of pyric successions. Soils thoroughly exposed by mass wastage were colonized by few plants, which were also members of the vegetation of stable sites. Therefore, in terms of the floras involved, there was no difference between primary and secondary successions here. Resilience, in terms of the rate of recovery of the vegetation to a given proportion of original structure and function (Westman 1986), is predominantly dependent on recovery in situ, and few species recovered by processes involving substantial migration (cf. Grubb and Hopkins 1986).

4.4.2. Stability of fynbos under the influence of fire The fynbos vegetation sampled in this study proved to be extremely stable in that most or all species in any given stand survived fire. The only ones recorded to have disappeared after fire were rare in the stand before the fire and were often seeders occupying marginal habitats. Most disappeared from one or a few plots, and survived elsewhere.

The large gains in species after fire are due to several factors. Many of the new species were fire ephemerals, temporary members of the community only in the sense that for most of the period between fires they were present as seed. About half of the flora of seeding species were fire ephemerals. Some species entered the quadrats as a result of small-scale, local migration. However, some longer-lived obligate seeders and sprouters were lost from the record for a given stand when fire was absent for a prolonged time (20 years or more) and reappeared after burning, as shown in the results of the gradient survey at Jakkalsrivier. With such species the apparent gain may or may not be real, because the shoots of these plants are often reduced to etiolated wisps in the unburnt vegetation and are difficult to see and identify. Even so, the gradient sampling, which involved small quadrats and close searches of 0,5 m^2 sections, would have given a reliable data set.

4.4.3. Models for pyric succession in fynbos The turnover of species within quadrats from one year to the next, greatest from the unburnt to the burnt stage, reflected the large gains in species. In subsequent years the turnovers are low, arising from the loss of fire ephemerals, gains in a few species such as Erica hispidula, and errors of observation. Thus, one may reject the facilitation or relay floristics model of succession. The general lack of recruitment in the established stand supports an inhibition model, rather than a tolerance model.

There was not a uniform decline in richness from a maximum immediately after fire but the overall pattern was of such a decline and this fits the general picture for shrublands of mediterranean-type ecosystems (Kruger 1983), rather than the more complex picture of a progressive increase up to the seventh year, as reported by Adamson (1935). Adamson's report showed substantial losses of species after fire (48 of 91 original species) as well as substantial gains. Of 167 native species recorded in total in his study, 76 were newly recorded after fire. His list of new species includes many fire ephemerals or other

appears to have been real. However, he recorded high turnovers in species composition from one period of observation to the next, from 44% after the fire, to 24% from the third to the seventh years after fire. These results contrast markedly in several repects from mine. However, the accuracy of his observations is doubtful. Adamson's information came from an ill-defined site of observation rather than from a set of permanent quadrats or from some other appropriately rigorous sample. Errors of observation were also evident in his data. For example, Protea lepidocarpodendron was listed as missing after fire, but reported in his text as having regenerated. Many of the sprouting species recorded as additions to the list, such as Elegia juncea, Myrsine africana, and Pterygodium catholicum, must have been overlooked prior to the fire. Some sprouting species recorded before the fire were not recorded again until three or seven years after the fire, yet were very likely to have been present in the interim period. Thus, the temporal trends in his data are difficult to evaluate.

Van Wilgen and Kruger (1981) reported a 50% turnover in species in permanent quadrats after a fire at Zachariashoek, although the entire flora in the sample of 33 quadrats did not change. The results from my study suggest that, aside from observer error, most of the turnover must have been from gains to the lists for individual quadrats.

There is no evidence from the gradient survey at Jakkalsrivier where the unburnt vegetation was 24 years old, of recruitment of species into a decaying stand, as reported for fynbos at Jonkershoek (Van Wilgen 1981) and coastal sage scrub California (Westman 1981). Also, a search of about 3 ha of senescent 24 year-old Protea lacticolor fynbos at Jakkalsrivier by a team of four persons in March 1982 for late-successional or forest-precursor species such as Maytenus oleoides, Hartogia schinoides, or Kiggelaria africana revealed none, nor were any such species to be found in senescing fynbos elsewhere at Jakkalsrivier. The former two species as well as other "forest" species such as Olea capensis subsp capensis and Myrsine africana are to be found occasionally on or near rock outcrops in the area. They produce fruit attractive to birds, and frugivores such as the red-winged starling Onycognathus morio are frequent visitors to the

area, so that dispersal may be assumed to occur. The lack of recruitment of such species is an intriguing problem.

Recruitment after fire to the flora of a stand of the size sampled here has interesting aspects. Some of the recruitment reflected apparent rather than real gains, because of problems of detecting and identifying vestigial vegetative material in old fynbos. Others involved regeneration of plants which survived in situ as seed or underground organs. In certain cases, the gains involved local small-scale migrations, as discussed earlier. In Protea, seed are dispersed after fire by being rolled about by wind (Bond 1980, 1985) and recruitment may occur up to about 30 m from the parent plant (Manders 1986). In these, and in Serruria rosea and other myrmecochorous species (Bond and Slingsby 1983), individuals are evidently dispersing on a scale sufficient to cause some flux through a plot of the size used in this study, and this could be seen essentially as a random local process.

Long-range dispersal is rarely implicated. At another plot at Zachariashoek, Rhus tomentosa appeared as a seedling three years after fire. Presumably, the seed was delivered to the site incidentally by a frugivorous bird but this was an entirely new addition to the flora sampled and if Rhus were to establish it could provide the focus for the process of succession by nucleation (Yarranton and Morrison 1974; Frost 1984). By coincidence, the introduced tree Pinus pinaster, appeared after fire in the same plot but from seed dispersed by wind from trees in the general vicinity (i.e. within 500 to 2000 m). A single individual was involved, but if this were to grow to maturity and be left to reproduce, profound changes to the community would follow.

The evidence from both Jakkalsrivier and Zachariashoek tends to support the conceptual model of pyric succession in fynbos outlined in Chapters 1 and 2. However, evidence from lowland fynbos tends to refute the model.

Hoffman, Moll and Boucher (unpublished) have followed succession for

five years after fire in Coastal Fynbos at Pella, 60 km north of Cape Town, having recorded vegetation composition before fire in permanent 5x10 m quadrats. They were also able to compare the composition of regenerating vegetation with that in other stands up to 19 years old, in a relatively uniform environment. Maximum species richness was found in stands five years old, and there was little difference between these and the older stands, i.e. there was a reduction in richness after fire and a rapid recovery thereafter. The flora at Pella is rich in annuals, which amounted to about 17% of the total number of species (as opposed to 2 and 9 species for Jakkalsrivier and Zachariashoek, respectively - Table 4.7). The greatest diversity of annuals, i.e. about 6-8 species per quadrat, was recorded in vegetation about 20 years old, and in these stands the richest geophyte floras were also recorded. These authors recorded substantial turnover in species composition between the pre-fire stands and the regenerating stands, with about 50% of species being lost in each stand after fire and only about 30% of species being in common to pre- and post-fire stands.

This is in marked contrast to the observations for my sites, where, for example, the average similarity in species composition between stands before and after fire was about 72% and most change was arose from the addition of species. Hoffman et al. suggest that the changes in composition associated with the fire at Pella were owing to the fact that the burn occurred in November, and that a fire in late summer or autumn may have produced different responses. However, the stands at Zachariashoek were also burnt in November, but their composition remained relatively stable. Hoffman et al. imply also that the drier environment at Pella, which receives an average rainfall of about 400 mm per annum, could influence the major patterns of pyric succession. It is possible that a sparser canopy of vegetation, allowing more space for recruitment, could result in fundamentally different successional processes than those found in more mesic environments. Their results emphasize the need to quantify the relationships between the trends in community properties during pyric succession and primary productivity, especially as reflected in canopy structure.

4.4.4. Changes due to factors other than fire Though fire is apparently the dominant factor affecting short-term successions in fynbos, the flux of species in the inter-fire period may be important in determining longer-term trends. Some of the species which disappeared from the quadrats were sprouters which would not normally be destroyed by fire. In one case this involved a sprouting Bruniaceae, Berzelia abrotanoides, which sprouted but died subsequently. An allied species, Nebelia paleacea, was present in some abundance in the vicinity before and after, having resprouted immediately after the fire. Of 25 plants censused in November 1981, 20 months after fire, one had apparently died in the fire, two were alive, and 22 had sprouted and then died. A year after, all remaining plants in the vicinity had died, and the species which had previously been a conspicuous member of the community had thus vanished. Symptoms suggested that mortality was due to root pathogens and if this were so, the disease may or may not have been associated with fire. Such processes will require attention if the longer-term dynamics of fynbos are to be understood.

The very marked changes in vegetation composition at Abdolskloof over 23 years seem unlikely to have been the result of some progressive influence of fire regime, since the treatments have varied randomly in terms of frequency and season. Since Jonkershoek became a State Forest only in 1933 and had been used for stock-farming before that, it is possible that the changes in the vegetation arose from withdrawal of grazing or some other extraneous factor. What is important is that changes of this magnitude are possible without a progressive change in fire regime, and that ecologists should design their long-term research accordingly.

4.4.5. Patterns in the distribution of species with different attributes of life history Fire, in concert with physical environmental factors which determine potential primary productivity in different habitats, may select for different plant forms in different places. Recruitment to existing populations in the case of seeders generally occurs in the first spring after fire. In many sprouters, however, flowering and fruiting are confined to the first

one or two seasons after fire. At Jakkalsrivier, about 12-16% of the flora had a maximum flowering age of six years or less. Seed would not be produced by the new shoots until after first flowering. If such species are not hard-seeded, recruitment must occur from seed released soon after fire. Since the post-fire environment becomes progressively more competitive, at least in terms of certain resources (Chapter 6), there would be strong selection for recruitment to occur soon after fire, for sprouters of this kind to be confined to habitats with sparse vegetation, or both. So, at Jakkalsrivier for example, seedlings of Corymbium africana and Senecio pinifolius, both with flowering confined to the first season after fire, were found in abundance in the spring of 1981, 20 months after fire. Although there was no significant difference in the richness of such precocious species between the different habitats at Jakkalsrivier, populations were substantially more abundant on the xeric and mesic sites at plots 1 and 3, than in plot 2 on the phreatic site (see Chapter 5).

The constitution of the different fynbos stands sampled here varied surprisingly little in terms of ratios between numbers of sprouting and seeding species and proportional frequency of species types and fire-response types. The relationships reported for Australian heathlands, where sprouting dominance increases with increasing canopy density (Specht 1981), was contradicted at Jakkalsrivier. The relative proportions of sprouting and seeding species varied in opposite fashions at Jakkalsrivier and Zachariashoek. There is little evidence from this study therefore, to support a general model which relates community composition in terms of sprouters and seeders to canopy dynamics.

The composition of vegetation of different habitats tended to differ in regard to the abundance of serotinous species. Serotinous species are few and rare at Zachariashoek, at least partly because of land-use history (Van Wilgen and Kruger 1981). At Jakkalsrivier differences in richness and abundance of serotinous species were related to habitat, such species increasing their prominence as productivity increased. This could be because the sharply cued germination of seed from serotinous species would be advantageous in the more strongly

competitive post-fire environment where regrowth is rapid (J.J. Midgley, personal communication). Polycarpic fire ephemerals also tended to be richer in species and more abundant (Chapter 5) on the phreatic site at Jakkalsrivier than any other, and this is likely to be owing to the fact that the higher growth rates possible on this site accommodate the short life-cycles of these species better than elsewhere (see also Chapter 6).

4.4.6. Relationships between fire, productivity, and species richness There is little evidence from Jakkalsrivier to support the Australian model, which predicts a progressive decline in species richness with productivity, and that the degree of decline in richness at a given stage of pyric succession would be related to the overstorey canopy cover. Rather, the data support the hump-shaped curves predicted by disequilibrium and resource-competition hypotheses.

4.4.7. Analytical models of pyric succession from vital attributes of species The attempt to deduce vegetation replacement sequences from the analysis of the fynbos stand in terms of vital attributes and life-stage information was satisfying in that plausible sequences were derived, which are at least partly corroborated by observation. The analysis showed that four principal states were feasible for the communities in question, with degraded or impoverished communities arising from fire regimes with too short or too long periods. In sum, the pyric successions at Jakkalsrivier and Zachariashoek fit the inhibition model of Connell and Slatyer (1977), except that facilitation may operate in one or more species (e.g. Erica hispidula) and, given the necessary dispersal, these latter species will dominate if fire does not recur. Fire is strongly implicated in maintenance of community richness and the nature of the effect is dependent on vegetation recovery rates and, by inference, fire frequency.

5. PYRIC SUCCESSIONAL CHANGES IN VEGETATION CANOPY STRUCTURE AND COMPOSITION

5.1 Introduction

There are many descriptions in the literature of the recovery of the canopy of fynbos vegetation following fire but there have been few quantitative studies (Kruger and Bigalke 1974). Quantitative description of such changes is important for several reasons. First, it would provide a more rigorous basis for development of certain aspects of succession theory. Second, a knowledge of structural changes in vegetation canopies is important for prediction of changes in water balance, fire probability and behaviour, and similar properties and processes which are important in the management of ecosystems. Finally, a quantitative understanding allows for analysis of changes which are important in determining interactions between species as well as for the modelling of processes within the canopy (e.g. Grace 1977).

This study was aimed at quantifying changes in vegetation cover, canopy structure, and composition in the communities sampled, and examining variation in these variables among communities. At Jakkalsrivier the aim was to explore the relationship between productivity and successional pathways. The purpose was to describe these changes, as a contribution toward knowledge of fynbos dynamics.

5.2. Methods

The catchment study at Jakkalsrivier involved experimental burning of the vegetation of a certain set of sub-catchments, and protection against fire in a second set. Measurements of vegetation properties were required to allow proper interpretation of results of hydrological studies intended to show the effects of veld burning on water yield from the catchment. Cover and biomass of vegetation canopies were selected as the most meaningful variables to measure. The vegetation was predominantly about 11 years old when the first treatments were applied in 1969. Measurements before these burns and

subsequent monitoring provided useful data to quantify vegetation succession. For canopy cover, the initial sampling plan was to establish 10 sample plots at random in every sub-catchment, and survey each by means of 250 point-quadrats (Fig. 3.2). When the first sample was completed this approach was found to be impractical in the steep terrain. As a result, two plots were selected to represent major vegetation types in each of the larger sub-catchments sampled subsequently. Each plot had relatively homogeneous vegetation and each was sampled by means of 1000 point-quadrats. Smaller sub-catchments were sampled by means of 1000 point-quadrats distributed over the major, representative portion of each catchment (Fig. 3.2). The surveyed portions were marked permanently for subsequent surveys. In addition, the two permanent succession quadrats lg-2 and lg-3 (see Chapter 3) were sampled annually after the burn of 1980, mostly by means of 500 points each. Plot lg-1 fell within a 1000-point subsample in the sub-catchment concerned. The permanent succession plots at Zachariashoek were all surveyed by means of 500-point samples.

The technique used for point-quadrat surveys was a modified version of the descending-point technique described by Roux (1962). The sampling apparatus consisted of a portable frame with a tubular guide through which a graduated staff tipped with a steel needle could be lowered. The needle was 4,7 mm in diameter and 110 mm long, and ground to a fine point. The observer held the frame vertically and allowed the shaft to descend steadily, noting when the tip of the needle struck any plant or standing dead material, the height of the strike, and also the basal strike (whether or not on plant parts, bare soil, etc). Only first strikes were recorded since in the relatively dense vegetation it was impossible to follow the needle through the canopy and record secondary strikes without disturbing the vegetation. Data for basal strikes were not used in this analysis since the primary interest is in canopy dynamics. Windy conditions were avoided during surveys. The technique could not be used in vegetation taller than about 1,5 m.

Point-quadrat sample data when obtained with a rod or needle of finite diameter are subject to considerable error. This has been shown by

Goodall (1952) and Winkworth (1955) by comparing survey data obtained using needles of different diameters with data obtained using a cross-hair sighting tube. Warren Wilson (1963) has analysed such error, and shown it to be more dependent on leaf size than leaf shape, doubling, more or less, for each halving of leaf breadth or doubling of needle diameter. For fine-leaved forms the error can easily exceed 100% with a needle of 2 mm diameter, and increases as the angle of leaf departs from normal to the trajectory of the needle, i.e. from horizontal where vertical point-quadrats are used. In this study errors of this kind were restricted by observing strikes on the sharpened point of the needle and by regularly training observers. The results must nevertheless be interpreted with caution.

Initially (before 1974), strikes on dead plants were not recorded, and if a strike occurred on dead leaf or shoot of a live plant, it was recorded for that species without discriminating between dead or alive. Later, strikes on standing dead were distinguished as were strikes on live and dead parts of the canopies of living plants. In the 10-year period following fire, dead canopy strikes amounted to a maximum of 8% of total canopy strikes in any one plot and such observations were included with live canopy strikes in analyses. Data from vegetation without fire for longer periods were analysed for trends in dead canopy cover.

A survey team consisted of an observer and a recorder, and roles were changed every 100 points to counteract bias. In every survey after the first, at least one of the team had been a member of the team in the prior survey. Each survey was preceded by a training session in technique and plant identification, and where identification was difficult a scrap specimen was collected for later naming in the herbarium. Even so, a certain number of strikes would not be identified, particularly soon after fire. Especially for Restionaceae and Cyperaceae, many strikes were simply recorded by family. Shrub seedlings could usually be classified to the level of species, except in families such as Bruniaceae and Ericaceae where the small seedlings are difficult to identify. In such cases these were recorded by family or simply as narrow-leaved shrub seedlings.

The first survey of the first sub-catchment was conducted immediately before the treatment burn, i.e. in early spring. Thereafter, surveys were conducted as much as possible in the summer, when vegetation was nearly dormant. In practice the survey season included the months of December to March, sometimes including the first half of April. After the 1980 burn, the permanent quadrats were surveyed once annually in late spring. Plots in unburnt vegetation, where changes were expected to be slow, were surveyed as and when resources permitted. Surveys were conducted on one plot at short internals in different seasons to test for seasonal changes.

On larger demarcated plots, points were located 1 m apart on lines 100 m long, with lines 7,6 m apart (conveniently, three survey staff lengths). Survey lines were established on fixed compass bearings and marked by ranging rods. Initially, points were located by pacing but later, steel or fibre surveyor's tapes were used. This sampling pattern was followed to overcome problems arising from bias due to systematic sampling of a contagious variable, while avoiding the cost of random sampling (Tidmarsh and Havenga 1955). On the 5x10 m plots, points were spaced at 1 m intervals on lines 1 m apart. On sub-catchments, points were spaced at 1 m intervals and lines were spaced so as to give a 1000-point sample.

The sub-catchments in the study area were burnt in 1969 (September to November) and 1970 (March) and again in October 1979 and March 1980. Plots were sampled at progressively longer intervals after fire. After 1980, only the fixed 5x10 m quadrats (see below) were sampled for cover changes, except that at the mesic site (plot 3) the point-quadrat sampling was done over a uniform area of 1 ha within which the 5x10 m quadrat was located. In these cases, surveys were conducted annually.

The data obtained from the point-quadrat samples were expressed as p, the mean number of first contacts per 100 quadrats, taken to be percentage canopy cover (cf. Warren Wilson 1965). When comparing the canopy cover of different layers of vegetation, cover was expressed as the proportion of contacts in the layer of interest to the number penetrating the overlying layers.

The mean number of first contacts per 100 mm layer of canopy was used to calculate the foliage-height profile, i.e. the distribution of proportions of total foliage area found in each defined height-interval (MacArthur and Horn 1969; Warren Wilson 1965; Aber 1979). The integral value of the foliage area in a given layer is calculated as:

$$F = \ln[(1-p_1)/(1-p_2)],$$

where p_1 is the proportion of points entering the layer and p_2 is the proportion penetrating through the layer.

Theoretically, the total LAI (leaf-area index) of the canopy can be estimated in the same way from the total number of point-quadrats in the sample and the proportion which penetrates through the canopy (Warren Wilson 1965; Aber 1979). The accuracy of this estimate is strongly affected by sample size and depends on random distribution and orientation of foliage, which seldom obtain. Aber (1979) has shown that LAI in deciduous forests is inaccurately estimated by this method. LAI values calculated for the fynbos sampled here are therefore used with caution. However, foliage-height profiles, which are independent of LAI estimates, can be accurately measured in this way if leaf inclination and clustering do not vary from layer to layer (Aber 1979). Aber (1979) showed that the foliage-height profile estimated by this method for a North American hardwood forest was indistinguishable from one estimated by direct sampling.

The form of a foliage profile was assessed by calculating the profile half-heights (cf. Cody 1975, 1983), nine-tenths heights, and indexes of foliage-height diversity. Half-height was taken to be that where half the leaf area of the canopy was above and half below, and was calculated by linear interpolation. Similarly, nine-tenths height was calculated as that below which 90% of canopy leaf area fell. Simpsons' diversity index, which is inversely related to the evenness of the canopy profile, was calculated as

$$S = \sum p_i^2$$

where p_i was the proportion of canopy leaf area in the ith layer. The Shannon-Wiener index was used as a measure of heterogeneity of the canopy profile, and calculated as follows:

$$H' = -\sum p_i . \ln(p_i)$$

5.3. Results

5.3.1. Vegetation structure before fire At Jakkalsrivier, the 11-year-old vegetation was predominantly a restioid or an ericaceous fynbos, with the broad-sclerophyllous proteoid shrubs seldom exceeding 10% of canopy cover. The canopies were relatively dense, having an average over all plots of 74% cover with a standard deviation of 18%. The lowest canopy cover, 30-60%, was recorded for low ericaceous fynbos on rocky north-facing sites.

Taller vegetation, with mature overstorey heights of 2 m or greater, is confined to phreatic sites and to more fertile soils derived from shales. In these situations, a distinct overstorey of narrow-leaved Bruniaceae, in the former case, and broad-sclerophyllous Proteaceae, in the latter, may be distinguished. On the phreatic sites, the overstorey canopy had a cover of 25 to 30% or more, but the proteoid fynbos sampled here had a maximum overstorey cover of only 20%. Proteoid shrubs, especially Leucadendron xanthoconus, are abundant but usually have sparse, slender crowns with little cover. Protea lacticolor formed dense thickets in small patches in the vicinity of shale outcrops where favourable soil moisture and fertility levels coincide, but these could not be sampled by the point-quadrat technique used here. The prevailing overstorey cover at Jakkalsrivier is less than the 30-40% or more predicted by Specht and Moll (1983).

The data from the 1969 surveys were used to analyse relationships between the over- and understorey layers of vegetation. Only the plots with an overstorey were used in the analysis. Overstorey species were classified by the rough rules applied by Specht and Morgan (1981). Leaf-area indices were calculated by the method of MacArthur and Horn (1969). Relationships between canopy cover and species nichness were

also examined with the data. Species richness was expressed as the number of species per 250 quadrats and only the data from large plots were used, i.e. not those from 5x10 m quadrats nor those from entire sub-catchments. Canopy cover of these overstorey species ranged from 0,4 to 28,8%, and included 1-12 species per sample. Leaf-area index of the overstorey ranged from 0,004 to 0,34; the total leaf-area index of the canopy varied from 1,15 to 3,12.

The understorey canopy cover in this sub-set of the plots was uniformly high, varying from 68 to 91%, with LAI from 0,92 to 2,15. Understorey cover was not related to overstorey cover, although understorey leaf-area index declined linearly with overstorey LAI (r^2 = 0,491, F = 12,5, P = 0,0036; b_o = 1,78, b_1 = 2,45; Fig. 5.1). The slope of this latter relationship departed significantly from unity (F = 24,9, P = 0,0002). This indicates that the leaf-area indices of the respective layers were together associated with physical environmental variables, rather than reflecting some competitive relationship. Plant species richness

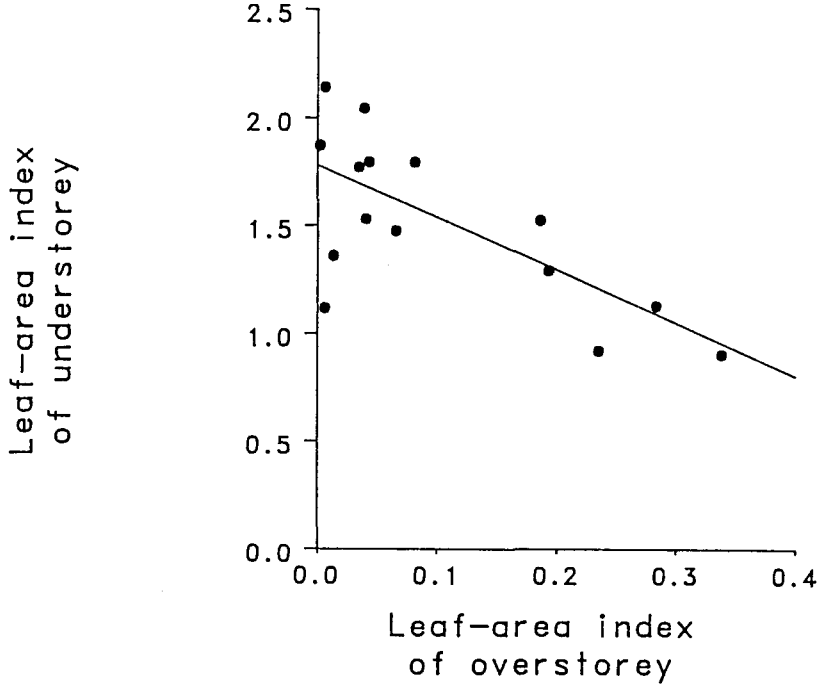


Figure 5.1. Relationship between understorey leaf-area index and overstorey leaf-area index in 11-year old vegetation at Jakkalsrivier. See text.

i.e. numbers of species per 250 point-quadrats, was not significantly related to overstorey canopy cover or LAI, or total LAI, neither linearly nor curvilinearly.

5.3.2 Local environmental effects on the patterns of pyric succession The essential features of the changes in cover and cover composition are shown in Fig. 5.2 and 5.3. The first is for a tall broad-sclerophyllous shrubland with heathy understorey, dominated mainly by Leucadendron xanthoconus and the second is for a low heath, dominated by Ericaceae. The communities regained their pre-fire growth-form composition within about ten years and this was the case for all plots. Cover is restored relatively rapidly, reaching nearly 80% of pre-fire levels on all plots within four years. This is principally because of the regrowth of herbs

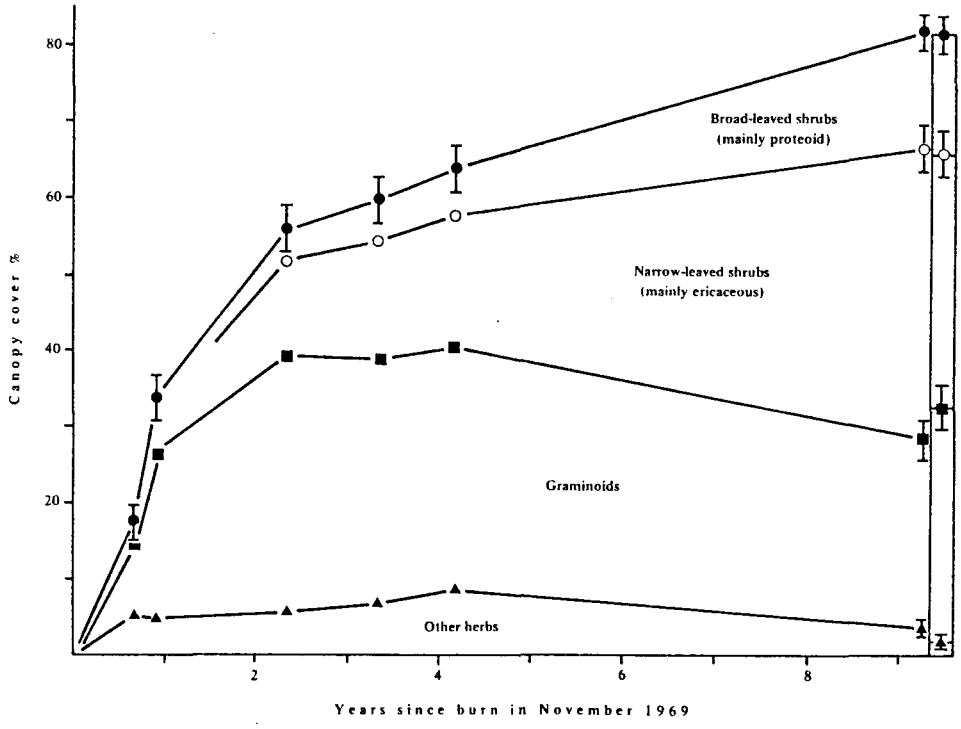


Figure 5.2. Trends in vegetation cover after fire in proteoid shrubland at Jakkalsrivier, 1969-1979. Broad-leaved shrubs are mainly proteoids, especially Leucadendron xanthoconus. Narrow-leaved shrubs are mainly Ericaceae. Graminoids include Cyperaceae, Proteaceae, and Restionaceae. Other herbs include geophytes. Cover estimates not corrected for layering. Ninety-five percent confidence intervals are shown. Bars at right represent preburn composition.

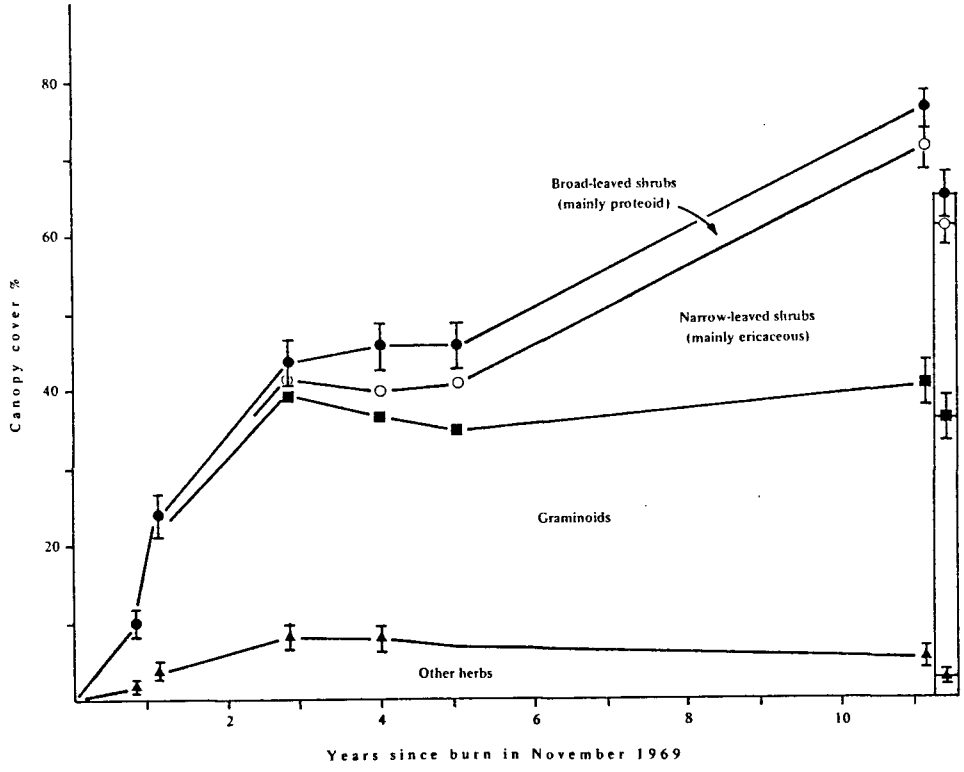


Figure 5.3. Trends in vegetation cover after fire in an ericaceous shrubland at Jakkalsrivier, 1969-1979. See Fig. 5.2 for explanation.

(graminoids, restioids and forbs - mostly sprouters) and sprouting shrubs, the combined cover of which is constant or tends to decline after the fourth year, while seeding shrubs, present from the first year, increase progressively (Fig. 5.4).

Despite considerable variation in height of the vegetation of different plots before fire, total canopy cover before fire in the treated plots varied little (mean 81%, standard deviation 9,5%, for 13 plots). Cover varied more between plots in early stages of succession than later. Coefficients of variation declined more or less uniformly from 33,8% at 7-8 months to about 9% at 110 months, as cover increased. Thus it was the rate of canopy growth which varied between sites. Patterns of variation were explored by analysing variation in canopy cover at about one year after fire. Recovery rates correlated negatively with relative insolation i.e. the potential annual solar radiation received by a site of given slope and aspect expressed as a percentage of that received on level ground, calculated from Frank and Lee (1966). The exception was a

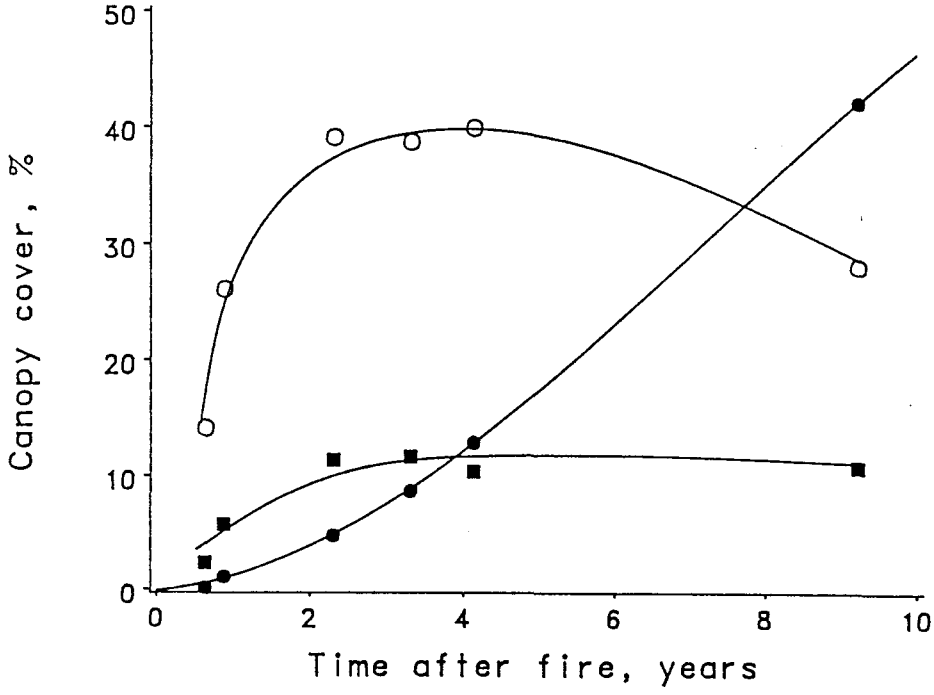


Figure 5.4. Changes in the relative composition of the canopy of a proteoid shrubland at Jakkalsrivier, 1969-1979. Circles represent the cover of herbaceous species, filled squares, sprouting shrubs, and dots, seeding shrubs. The herbs were mainly graminoids and sprouters. Lines are spline interpolations.

phreatic site that had by far the greatest rate of recovery (Fig. 5.5). It is commonplace for fynbos vegetation of moist to wet sites to regrow quicker than others. Cool southerly sites also usually recover quicker than warm northerly sites, and this presumably reflects a more favourable water balance on the former.

Although pyric successional change in community composition was broadly similar on the different plots sampled, some variation between sites was evident. This variation was described by principal components analysis, and the relationships between changes in vegetation composition and time since fire as well as habitat factors were examined by examining correlations between principal components, vegetation age, altitude, and relative insolation.

In the analysis of the principal components of variation in vegetation composition, each survey on each plot was treated as a sample unit, and the descriptor variables for vegetation composition were the cover values for species in seven growth form categories, i.e. broad-leaved

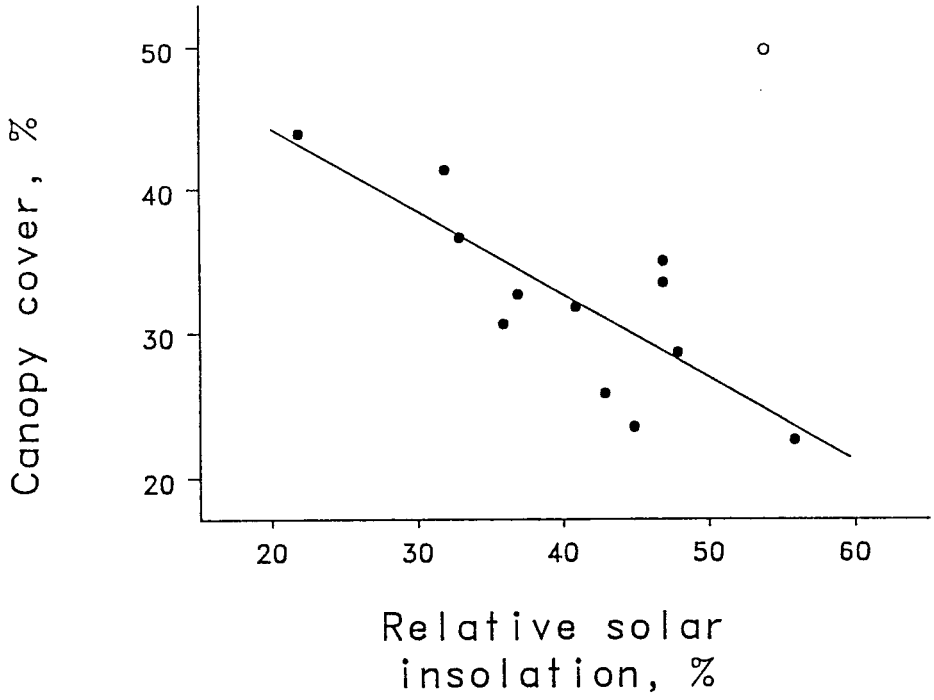


Figure 5.5. Relationship between total canopy cover at 11–13 months after fire and relative solar insolation at Jakkalsrivier. The regression was the form y = 55,7 – 0,575x, with y being the canopy cover and x relative solar insolation, per cent (r_2 = 0,640, F = 17,8, P = 0,0018, b_o = 55,7, b_1 = -0575). See text. The outlier value (circle) is from a plot on a seepage site, i.e. plot 1a-8.

shrubs (predominantly proteoids), narrow-leaved shrubs (mainly ericaceous, but Bruniaceae were sometimes prominent), grasses, sedges, restioids, geophytes (evergreen and deciduous) and other herbs (forbs). A minor category of succulent and semi-succulent plants was omitted. There were six or more sets of observations for most of the burnt plots, at about 0,5, 1,0, 2,6, 4,4 and 9,5 years after fire, and immediately before fire (11 years old). Fire to six sets of surveys were available for the unburnt plots.

The 21 plots yielded a set of 134 observations, to give a data matrix of 134 x 7 values. Principal components were calculated from the correlation matrix of the untransformed values of cover for each growth-form category in each observation (R-type principal components analysis; Pielou 1969; SAS Institute Inc. 1985). Summary descriptive statistics for the analyses are given in Table 5.1.

The eigenvalues of the first four principal components accounted for 84,9% of the variation in the data, with the first, second and third accounting for 29, 24 and 20% respectively. Shrubs, sedges, and restioids (the persistent components of canopy cover) were heavily weighted on the first principal component, in contrast with grasses and forbs (Table 5.2). Grasses and forbs were heavily weighted on the second principal component, geophytes in contrast with seeders and forbs, on the third, and broad-leaved shrubs on the fourth (Table 5.2).

The relationships between the courses of succession and altitude and relative insolation were examined for the data for plots in the burnt catchment alone, since observations for the immediate post-fire period were not available for the rest. The first principal component was strongly correlated with post-fire age ($r=0,875$, $p<0,0001$), but not significantly with altitude and relative insolation. The second principal component was not significantly correlated with any of the three independent variables. The third correlated fairly strongly with altitude ($r=0,503$, $p<0,0001$), and weakly though significantly with age ($r=0,224$) and relative insolation ($r=0,232$). The fourth was not correlated with age, negatively with altitude ($r=0,245$, $p<0,01$), and positively with relative insolation ($r=0,341$, $p<0,005$).

Not surprisingly, most of the variation in growth-form composition was therefore associated with post-fire age, the cover of most components increasing with age but that of grasses and forbs decreasing (Table 5.3). Overall variation in cover of narrow-sclerophyllous, restioids, and forbs was less affected by physical factors of the habitat. The variation in the third principal component, i.e. mainly the abundance of geophytes, was affected by altitude rather than age, while variation in the fourth, reflecting mainly the abundance of broad-scelrophyllous shrubs, was affected by the negetative association between altitude and relative insolation (Table 5.3). Figs. 5.6 and 5.7 show a selection of the data plotted on axes for the first and the second and second and third principal components respectively. These show the trajectories of change followed by the vegetation on the plots with respect to these principal components of composition. The coordinates of each point are the principal

Table 5.1 Statistics for the canopy cover data used in the analysis of principal components of canopy variation at Jakkalsrivier. Sample size was 134. See text for explanation.

	Canopy cover, per cent						
	Broad-leaved shrubs	Narrow-leaved shrubs	Grasses	Sedges	Restioids	Geophytes	Forbs (other herbs)
Mean	4,40	13,7	9,81	7,53	13,5	3,42	2,47
Std.deviation	4,23	13,0	5,32	5,01	6,84	3,02	2,89
	Correlations						
	Broad-leaved shrubs	Narrow-leaved shrubs	Grasses	Sedges	Restioids	Geophytes	Forbs (other herbs)
Broad-leaved shrubs	-						
Narrow-leaved shrubs	0,365	-					
Grasses	-0,032	-0,298	-				
Sedges	0,253	0,356	0,083	-			
Restioids	0,131	0,561	0,130	0,209			
Geophytes	0,014	-0,102	0,377	-0,244	0,298	-	
Forbs (other herbs)	0,095	-0,188	0,519	0,213	-0,072	-0,115	-

Table 5.2 Eigenvectors for the analysis of principal components of variation in canopy cover at Jakkalsrivier. Values are standardized loadings.

Canopy cover component	Eigenvectors of given principal components			
	1	2	3	4
Broad-leaved shrubs	0,390	0,159	-0,137	0,857
Narrow-leaved shrubs	0,641	-0,056	0,071	-0,094
Grasses	-0,216	0,672	0,060	-0,070
Sedges	0,400	0,244	-0,409	-0,283
Restioids	0,452	0,268	0,408	-0,348
Geophytes	-0,089	0,318	0,667	0,225
Forbs (other herbs)	-0,134	0,536	-0,440	0,009

Table 5.3 Coefficients of correlation between vegetation and environmental variables.

	Correlation coefficients		
	Altitude	Relative insolation	Post-fire age
Broad-leaved shrubs	0,104	-0,275	0,333
Narrow-leaved shrubs	-0,058	-0,034	0,903
Grasses	0,273	-0,122	-0,213
Sedges	-0,275	0,126	0,391
Restioids	0,168	-0,083	0,670
Geophytes	0,545	-0,324	0,105
Forbs (other herbs)	0,192	0,039	-0,209

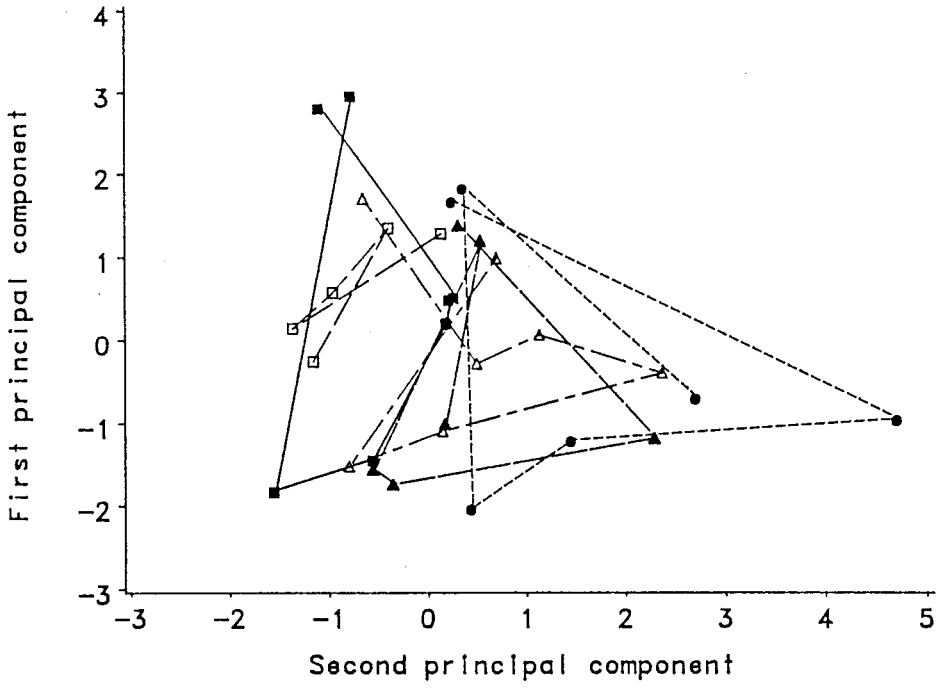


Figure 5.6. Plot of canopy samples on first two principal components of variation at Jakkalsrivier. The first component reflects increasing cover of shrubs, especially narrow-leaved shrubs, together with sedges and restioids. The second represents increasing cover of grasses and forbs. Filled triangles: plot 1a-4, a mesic heathland; dots: plot 1a-8, a phreatic site; triangles: plot 1b-2, a high-altitude heathland; filled squares: plot 1g-1; open squares: plot 2b-1, a dry heathland protected against fire. See text.

components scores for a given age, and points are connected in temporal order, from immediately before fire to about 10 years after.

The figures show how temporal changes in the canopy composition vary among the plots. The successional courses terminate close to the original pre-fire positions defined in terms of the principal components, indicating stability in terms of growth-form composition, as discussed earlier. However, the trajectories differ among plots. In the case of the proteoid shrubland at plot 1g-1, where growth-rates are moderate (see later), fire is followed simply by a general reduction in the absolute values for and relative importance of the shrubs and sedges and restioids, with some increase in terms of component 2 at intermediate stages. There is little change in respect

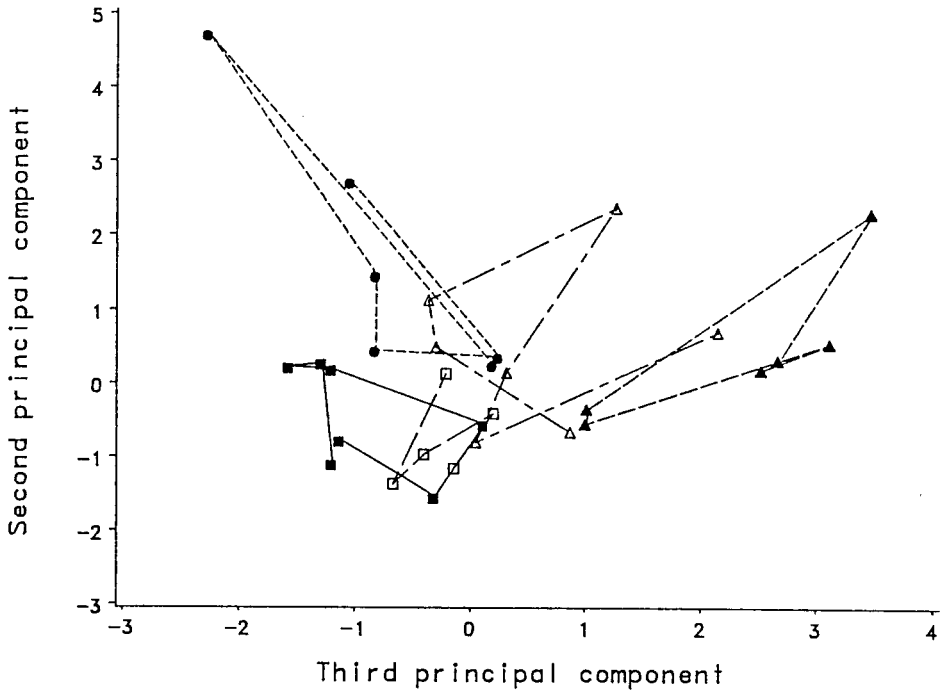


Figure 5.7. Plot of canopy samples on second and third principal components of canopy variation. The third component represents increasing geophyte cover. Filled triangles: plot 1a-4, a mesic heathland; dots: plot 1a-8, a phreatic site; triangles: plot 1b-2, a high-altitude heathland; filled squares: plot 1g-1; open squares: plot 2b-1, a dry heathland protected against fire. See text.

of component 3. By contrast, plot 1a-8, on a phreatic seepage and where growth is rapid (see later for an analogous community), also shows the temporary reduction in terms of component 1 but then a marked increase in terms of component 2. This reflects the dominance of grasses such as Merxmuellera cincta and of the shrubby herb Carpacoce spermacocea, at intermediate stages of succession. Interestingly, plot 1a-4, which rated high on principal component 3 because of the abundance of such species of evergreen geophyte as Corymbium latifolium, maintained high scores on this component at intermediate and later stages of succession; the perennially green geophytes evidently do not show marked growth responses to a single fire. The protected sites, such as at 2a-1, show little change in terms of these components.

Thus it is clear that though the courses of change after fire in the fynbos communities at Jakkalsrivier are relatively uniform, reflecting principally the recovery of the prior dominant forms. There is nevertheless a measure of variation in these courses that is related to physical environmental factors. The relative roles of grasses, forbs, and broad sclerophyllous shrubs, mainly Proteaceae, in the successions depended on the habitat. A more thorough analysis of habitat would be needed to identify the roles of individual factors, but those jointly governing productivity appear to be cardinal.

5.3.3. Pyric succession during the first 10 years after fire Cover surveys were conducted at about three and five years after fire at Zachariashoek and at 0,7, 1,7 and 2,8 years at Jakkalsrivier. Plot 1g-1 at Jakkalsrivier was also surveyed immediately before and five years after fire.

No plants on the study sites were resistant to fire, so that live canopy cover was reduced to zero. The patterns of vegetation recovery after the 1977 burn at Zachariashoek and the 1979 burn at Jakkalsrivier were essentially as depicted in Figs. 5.2 and 5.3. Rapid regrowth of sprouting species ensures that most of canopy cover is restored within about three years (Table 5.4). The quickest canopy recovery occurred on plot 1g-2 at Jakkalsrivier, a phreatic site.

Table 5.4 Statistics for canopy cover measurements about three years after fire at Zachariashoek and Jakkalsrivier. Data are for descending-point surveys on 5x10 m plots, except for Jakkalsrivier No. 1, where an area of about 0,5 ha was surveyed.

Plot no.	Post-fire age, yr.	Canopy cover, %	Leaf-area index	Half-height, mm	9/10 height, mm	Proportion of cover, %		Proportion of cover,%				
						Seeders	Sprouters	Shrubs		Restio-naceae	Cypera-ceae	Poacea
								B-S	N-S			
Jakkalsrivier												
1	2,8	66,9	1,11	198	378	8,5	91,5	7,8	34,2	20,5	22,3	9,6
2	2,8	92,8	2,63	379	708	41,2	58,8	5,9	10,8	24,6	9,7	13,4
3	2,8	60,0	0,916	177	316	20,8	79,3	1,0	19,7	20,1	16,7	23,1
Zachariashoek												
9	3,1	80,4	1,63	416	686	11,4	88,6	11,4		56,2	3,0	24,1
15	3,0	53,8	0,772	158	374	15,2	84,8	22,7		34,6	14,5	16,0
17	3,1	50,2	0,697	134	295	21,1	78,9	13,9		45,0	15,5	12,0
82	3,0	48,2	0,658	218	419	11,2	88,8	13,3		41,9	28,2	7,1
87	3,1	41,4	0,534	226	400	17,4	82,6	15,5		74,9	2,9	0,5
92	3,1	57,6	0,858	233	418	5,6	93,8	49,7		28,5	15,6	3,8
98	3,1	57,0	0,844	248	444	19,0	81,1	35,8		31,6	14,7	9,1
Mean		60,2	1,04	231,1	434,2	18,2	81,8	24,8		39,0	13,8	11,2
Standard deviation		14,2	0,574	85,9	131	9,58	9,55	12,5		16,1	7,25	7,20

However, the next quickest recovery was on plot 9 at Zachariashoek. This was not a phreatic site, but the vegetation was dominated by a clonal population of Cannomois virgata, a tall, rapidly growing member of the Restionaceae. Slowest recovery rates were in plots in mid-dense restioid fynbos at Zachariashoek. Recovery rate was related to height-growth of vegetation. For example, LAI at three years had a correlation coefficient of 0,854 with nine-tenths canopy height, but this was strongly affected by the observations from the two tall communities. Initial cover was dominated by sprouters. At three years, canopy cover of fire ephemerals averaged around 4,6% (standard deviation = 3,36). Highest cover at this age was on plot 1g-3 at Jakkalsrivier, with ephemerals having 9,6% cover. At Jakkalsrivier plot 1g-2, fire ephemerals initially constituted 19,0% cover, about one-third of the total. At two years, this had reduced to 8,4%, about one-tenth of the total, and at three years it amounted to one-twentieth. At plot 1g-1, these ephemerals never constituted more than 1%. At plot 1g-3, the cover increased in successive years.

Development of the foliage profile is illustrated for the three Jakkalsrivier plots in Figs. 5.8 - 5.10.

A plot of LAI against half-height in time sequence illustrates relative changes in canopy density with succession (Fig. 5.11). Each plot maintains rather constant canopy density initially as the relatively abundant regrowth gains height and leaf area. Canopy development on the phreatic site is markedly more rapid than on the other two sites. Recovery patterns at Zachariashoek may be compared with those from Jakkalsrivier by means of similar data for the surveys at about three years after fire (Table 5.4). Most Zachariashoek plots develop relatively sparse canopies in this time, and though there was some height growth from three to five years, there was little accumulation of leaf area beyond 1,0. The exception once more is plot 9, which continued to grow vigorously during the five-year observation period. Foliage-height diversity, measured by the Shannon-Wiener index, increases with age as the canopy grows in height, middle layers gain leaf area, and the lower layers are suppressed (Figs. 5.8 - 5.10, 5.12).

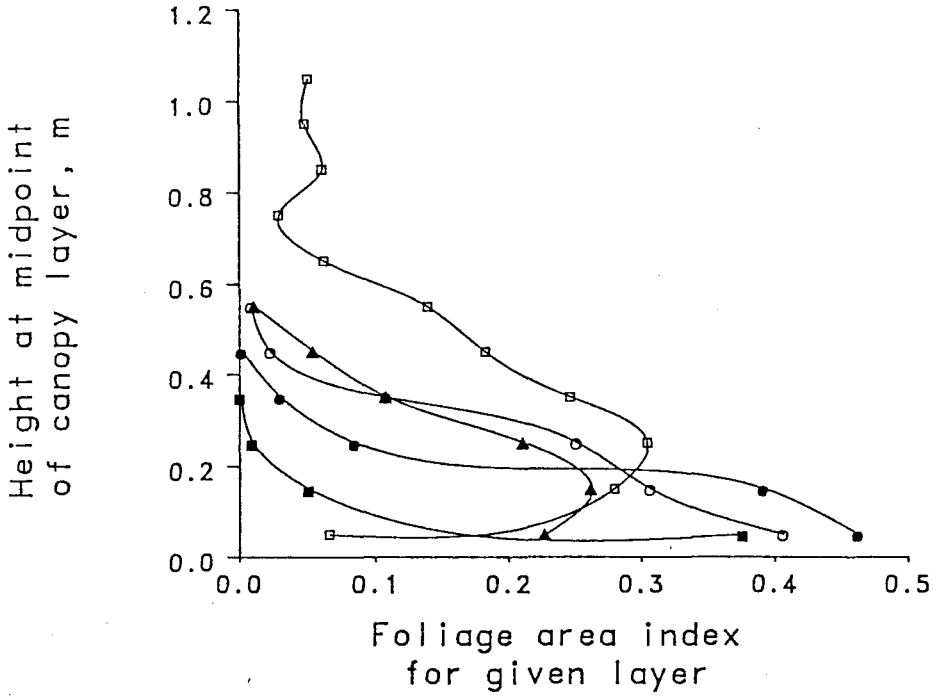


Figure 5.8. Foliage profiles for plot 1g-1 at Jakkalsrivier. Closed squares: 0,7 yr after fire, dots: 1,7 yr, circles: 2,8 yr, triangles: 5,0 yr, and open squares, 10 yr. Points are connected by parametric spline interpolation.

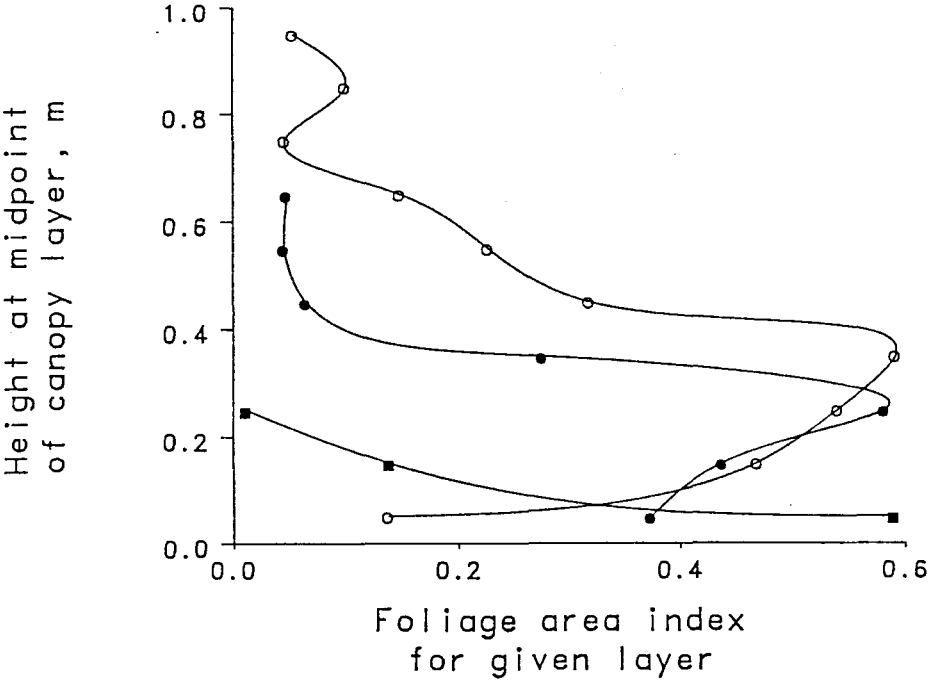


Figure 5.9. Foliage profile for plot 1g-2 at Jakkalsrivier. Closed squares: 0,7 yr after fire, dots: 1,7 yr. circles: 2,8 yr. Points are connected by parametric spline interpolation.

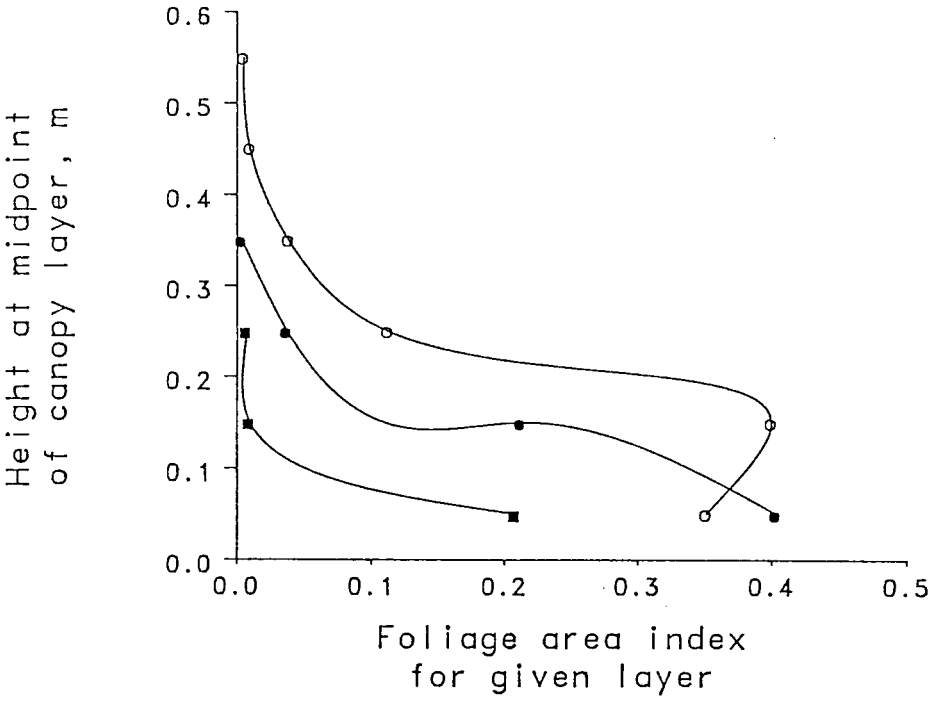


Figure 5.10 Foliage profile for plot 1g-3 at Jakkalsrivier. Closed squares: 0,7 yr after fire, dots: 1,7 yr, circles: 2,8 yr. Points are connected by parametric spline interpolation.

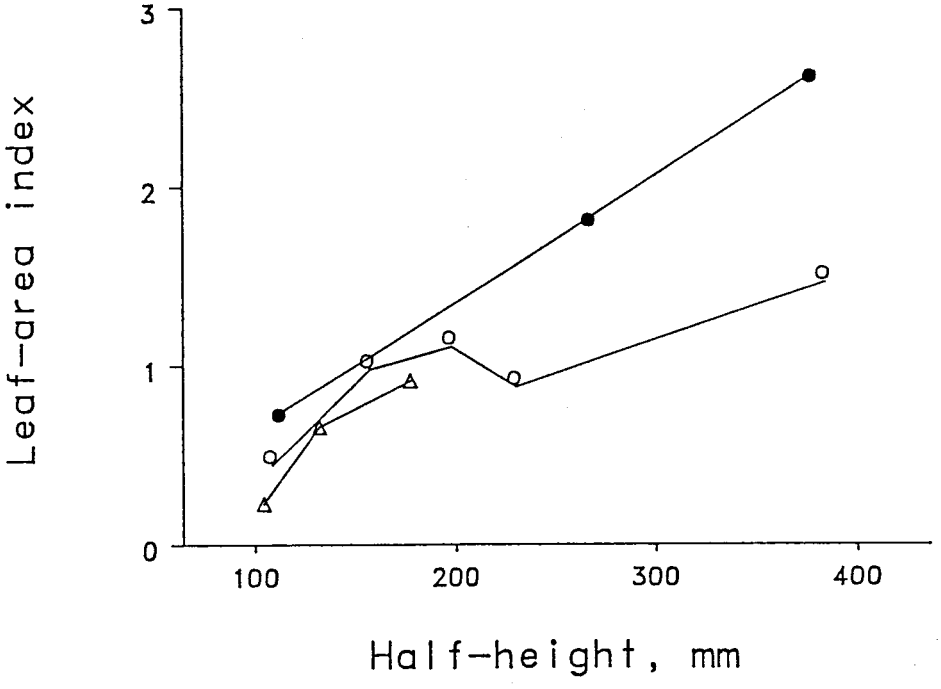


Figure 5.11. Trends in leaf-area index and canopy height in the three plots at Jakkalsrivier. The points are connected in sequence, from 0,6 - 0,7 yr after fire, to 1,6 - 1,7, and 2,8 yr. Points for 5 and 10 yr are given for plot 1g-1. Circles show plot 1g-1, dots plot 1g-2, and triangles, plot 1g-3.

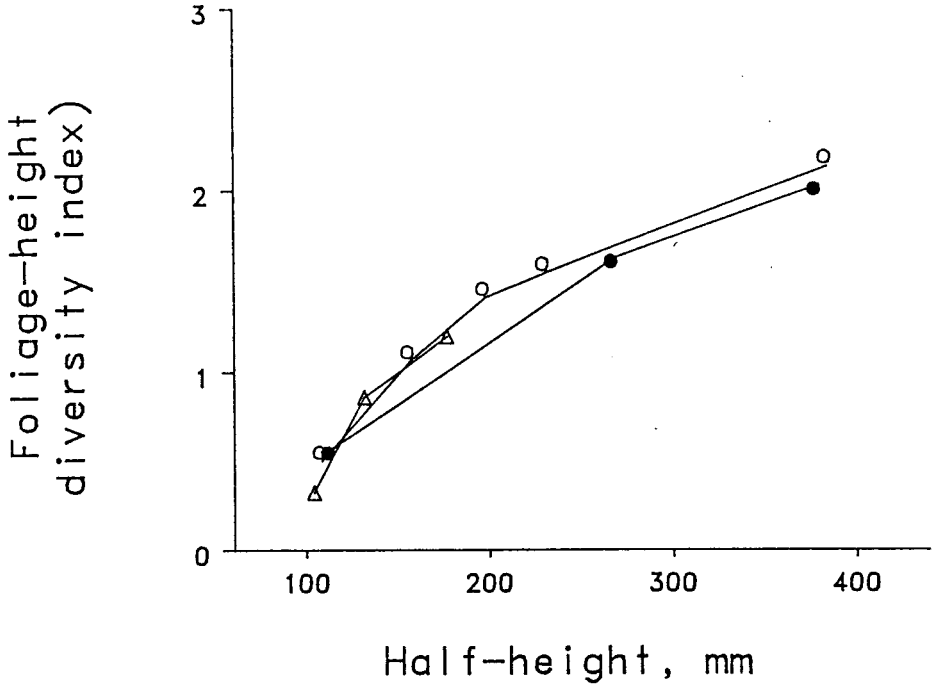


Figure 5.12. Changes in foliage-height diversity, measured by Shannon-Wiener index H', in relation to canopy height at Jakkalsrivier. Circles are for plot 1g-1, dots for plot 1g-2, and triangles for plot 1g-3. Data points are connected in successional sequence, as for Fig. 5.11.

The rate of canopy recovery was not strongly related to the growth-form composition of the vegetation. The highest correlation with LAI at three years was in grasses, with a coefficient of 0,404.The proportion of canopy cover constituted by seeding species had a correlation coefficient of 0,559 with LAI at three years, reflecting principally the rapid recovery in plot 1g-2 at Jakkalsrivier, where seeding species were abundant in the canopy at this age.

The additional data for plot 1g-1 at Jakkalsrivier illustrate longer-term trends. Height growth continues from about two to five years, but there is little increase in canopy density (Fig. 5.11). This corroborates the data from earlier monitoring (Fig. 5.2 and 5.3). This may reflect height-growth in seeding shrubs, without expansion of crowns. Young plants of most taller species of Proteaceae and Ericaceae are slender and often without branches.

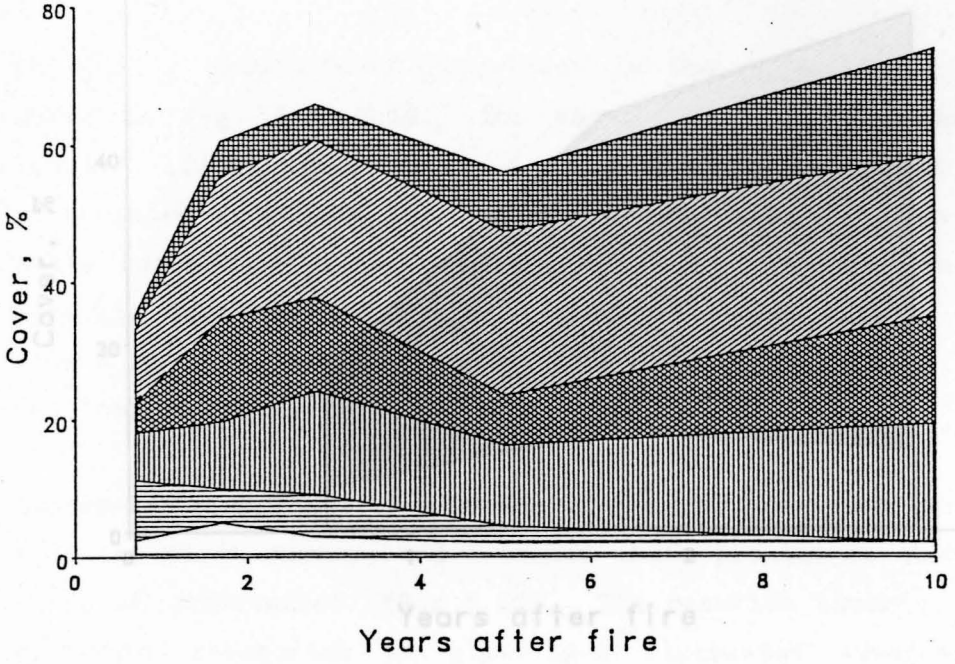


Figure 5.13. Changes in the cover of plants of different growth-form categories at Jakkalsrivier 1g-1. The cover for the different growth-form categories is shown from bottom to top for geophytes and other non-graminoid herbs, grasses, sedges, restioids, narrow-sclerophyllous shrubs, and broad-sclerophyllous shrubs.

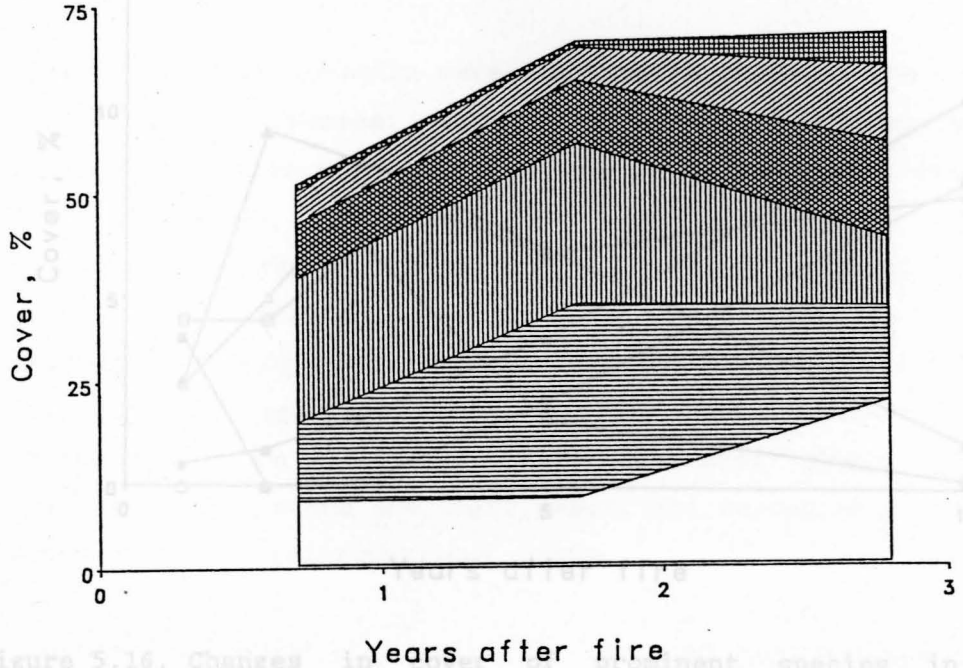


Figure 5.14. Changes in the cover of plants of the different growth-form categories at Jakkalsrivier plot 1g-2. The sequence from bottom to top as in Fig 5.13.

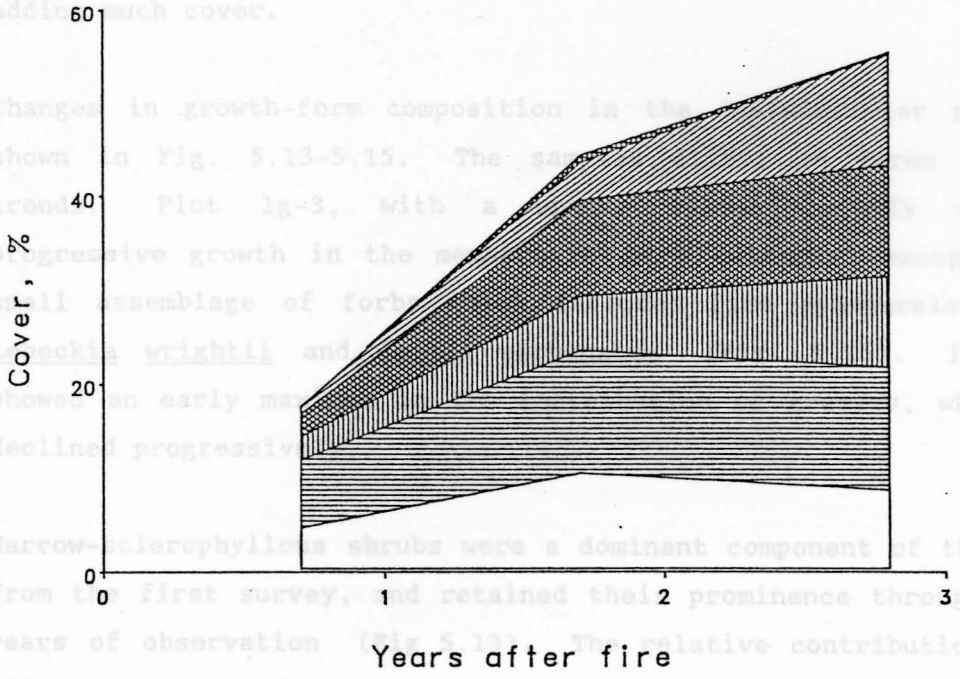


Figure 5.15. Changes in the cover of plants in different growth-form categories at Jakkalsrivier plot 1g-3. The sequence from bottom to top is as in (Fig 5.13).

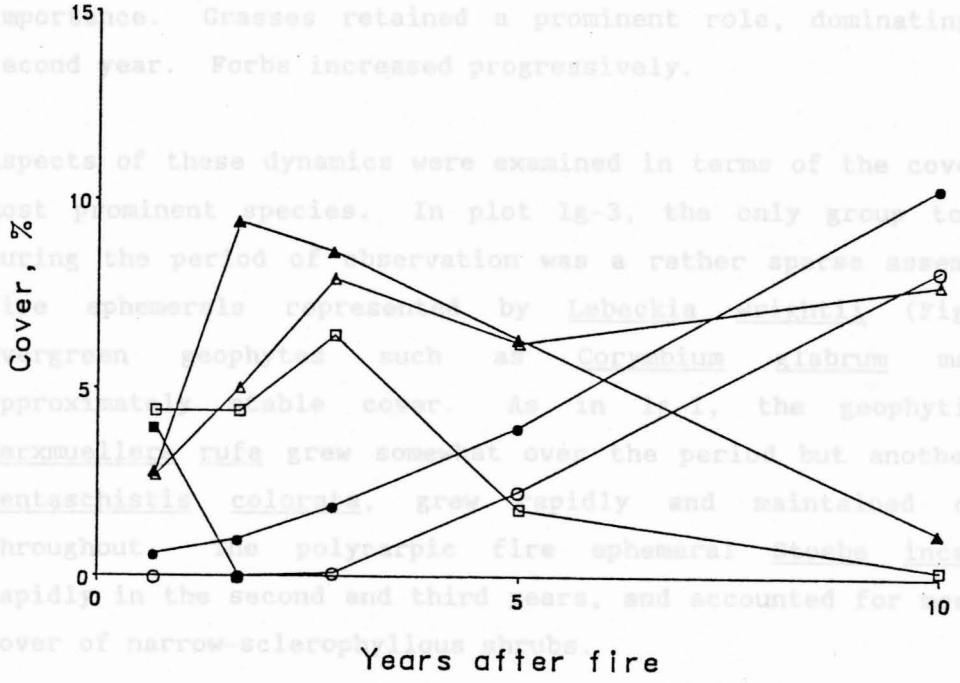


Figure 5.16. Changes in cover of prominent species in 1g-1 at Jakkalsrivier. Filled triangles: Aspalathus millefolia; open triangles: Tetraria fimbriolata; squares: Mernmuellera rufa; filled squares: Pentaschistis viscidula; dots: Leucadendron xanthoconus; and circles, Erica sessiliflora.

Also, flowering shoots add to the height of graminoids without adding much cover.

Changes in growth-form composition in the Jakkalsrivier plots are shown in Fig. 5.13-5.15. The samples differ in terms of these trends. Plot 1g-3, with a sparse canopy, simply showed a progressive growth in the members of each category, except in the small assemblage of forbs which includes fire ephemerals such as Lebeckia wrightii and Selago verbenacea (Fig. 5.15). Plot 1g-1 showed an early maximum in the contribution of grasses, which then declined progressively.

Narrow-sclerophyllous shrubs were a dominant component of the canopy from the first survey, and retained their prominence through the 10 years of observation (Fig 5.13). The relative contribution of the different categories in plot 1g-2 fluctuated considerably (Fig 5.14). Sedges dominated initially, and then declined markedly in absolute and relative terms. Geophytes were fairly prominent initially, but were no longer recorded by the third year. This contrasted with the other two plots, where they persisted or grew in importance. Grasses retained a prominent role, dominating in the second year. Forbs increased progressively.

Aspects of these dynamics were examined in terms of the cover of the most prominent species. In plot 1g-3, the only group to decline during the period of observation was a rather sparse assemblage of fire ephemerals represented by Lebeckia wrightii (Fig 5.18). Evergreen geophytes such as Corymbium glabrum maintained approximately stable cover. As in 1g-1, the geophytic grass Merxmuellera rufa grew somewhat over the period but another grass, Pentaschistis colorata, grew rapidly and maintained dominance throughout. The polycarpic fire ephemeral Stoebe incana grew rapidly in the second and third years, and accounted for most of the cover of narrow-sclerophyllous shrubs.

Grasses dominating 1g-1 initially included Merxmuellera rufa and a Pentachistis sp., probably P. viscidula (Fig 5.16). The former increased its contribution to cover initially, declining thereafter,

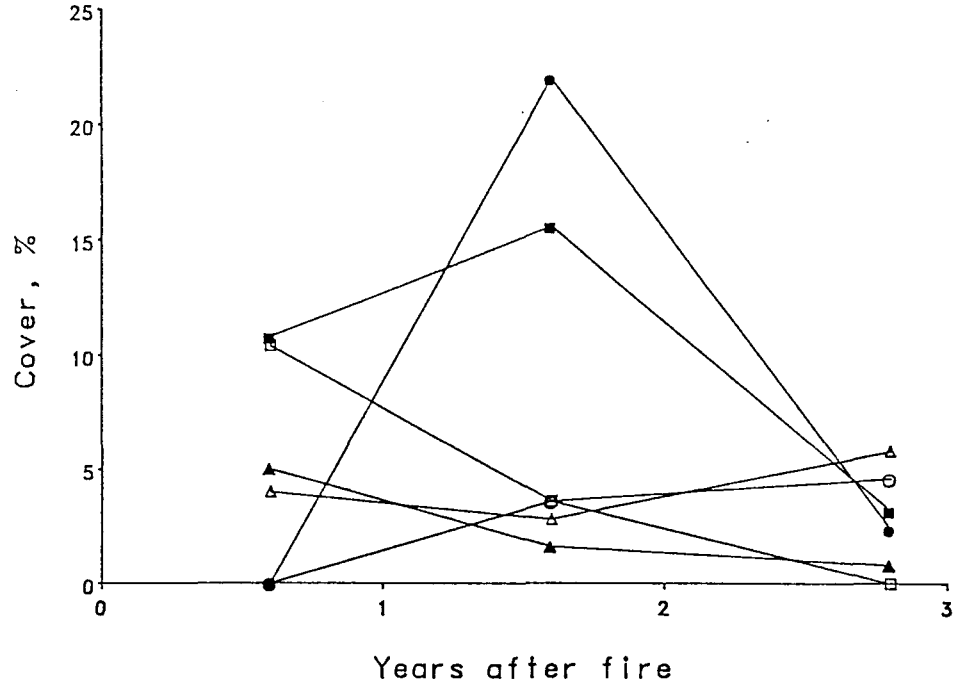


Figure 5.17. Changes in cover of prominent species in plot 1g-2 at Jakkalsrivier. Squares, Ehrharta rehmannii, filled squares, Ficinia capillifolia, dots, Ehrharta ramosa, circles, Carpacoce spermacocea, filled triangles, Selago verbenacea, and open triangles, Brunia alopecuroides and Bezelia lanuginosa.

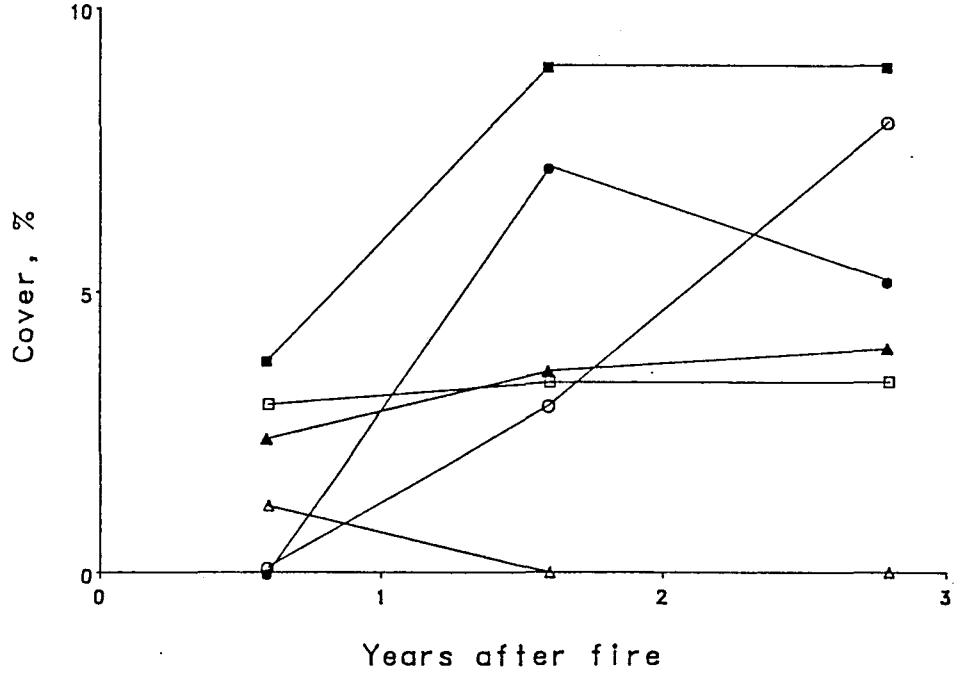


Figure 5.18. Changes in the cover of prominent species at plot 1g-3, Jakkalsrivier. Filled squares: Pentaschistis colorata; open squares: Merxmuellera rufa; closed triangles: Corymbium glabrum; open triangles: Lebeckia wrightii; dots: Restio dispar; and circles: Stoebe incana.

but the latter had disappeared from the record by the second year. The early prominence of narrow-sclerophyllous shrubs was mainly due to the rapid resprouting of Aspalathus millefolia (Fabaceae), which reached a maximum cover value in the second year and then declined progressively. Seeding Ericaceae, such as Erica sessiliflora, were recorded from about the third year onward, and their cover increased progressively. Seeding broad-sclerophylls such as Leucadendron xanthoconus were recorded from the initial survey and their cover increased progressively.The most pronounced changes in canopy composition in the first three years after fire were recorded in plot 1g-2 (Fig. 5.17). Ficinia capillifolia, a sedge of moist habitats, shared dominance initially with the grass Ehrharta rehmannii. The latter declined subsequently and disappeared from the record by the third year. The fire-ephemeral forb Selago verbenacea declined similarly from initial prominence. Also abundant in the first year was Moraea ramosissima, a tall geophyte in the Iridaceae, which had effectively disappeared by the second year. In the second year, Ehrharta ramosa dominated the canopy with the Ficinia, and both declined sharply thereafter. The third year saw the rise to prominence of soft forbs such as Carpacoce spermacocea (Rubiaceae) and Centella eriantha (Apiaceae) and the growth of shrubs, especially narrow sclerophylls in the Bruniaceae and Ericaceae, and to a lesser extent the broad-sclerophyllous Leucadendron salicifolium (Proteaceae). In each of these three successions, the sequence closely resembles the series generally typical of the initial floristic composition model of Egler (1954: see Gomez-Pompa and Vasquez-Yanes 1981; Finegan 1984).

5.3.4. Succession from 10 to 25 years after fire The permanent plots in vegetation protected against fire were dominated by ericaceous fynbos (Table 5.6). At the time of the last survey in 1982, LAI in these plots ranged from 0,744 to 0,858, half-heights from 306 to 450 mm, and nine-tenths heights from 610 to 1000 mm (Table 5.5). At this stage these communities therefore were not much taller than successional stands in the burnt vegetation, had sparse canopies, and relatively simple foliage profiles. This was mainly owing to the sparseness or absence of broad-sclerophyllous shrubs in these habitats.

Table 5.5 Canopy characteristics for vegetation on plots at Jakkalsrivier protected against fire, at a post-fire age of about 23 years, in 1982.

Plot no.	Canopy cover, %	LAI	Half-height, mm	Nine-tenths height, mm	Foliage-height diversity indices	
					Simpson	Shannon-Wiener
2a-1	51,6	0,744	306	611	0,170	1,962
2b-1	52,8	0,777	320	623	0,173	1,931
2b-2	57,2	0,853	449	1000	0,118	2,288

Highest values for all plots were recorded in 1979, lowest values in 1970 (Table 5.6). From February 1974 onward an increasing proportion of dead plants was recorded in the canopy, amounting to a cover of about 16 to 23% in 1982 (Table 5.6). Despite this, there was no substantial difference apparent in the canopy cover of live plants between 1974 and 1982.

The proportion of the canopy constituted by shrubs was at a maximum between 1972 and 1979 in plots 2a-1 and 2b-2, where shrubs were abundant. This proportion declined markedly from 1979 to 1982. Species of seeding narrow-sclerophyllous shrubs were most abundant. In every case, observed cover fluctuated considerably. In the cases of Blaeria dumosa (in plot 2a-1, taken together with Erica pulchella with which it was frequently confused), Erica longifolia, and Sympieza articulata (all Ericaceae), populations declined markedly over the period of observation. This was not the case with Cliffortia atrata (Rosaceae) and Erica hispidula (Table 5.6). Inspection in the field showed that shrubs in the population of Cliffortia atrata were relatively uniform in size, while Erica hispidula plants were variable, including many juvenile and intermediate individuals. A spot survey in the vicinity of plot 2b-1 in November 1982 was conducted to evaluate patterns of senescence and recruitment. Populations of E. hispidula and E. longifolia were sampled separately by means of 25 1-m^2 quadrats spaced at 5 m intervals. The presence

Table 5.6 Changes in composition of the canopy in three plots protected against fire at Jakkalsrivier.

Survey date	Veld age yr	Broad sclero-phylls	Canopy cover, %									
			Narrow sclerophylls				Grasses	Sedges	Restios	Other	Total live	Standing dead
			Erica hispidula	Blaeria dumosa +Erica pulchella	Clifortia atrata	Other narrow sclerophylls						
Plot 2a-1												
Jun. 1970	11,5	0,6	3,1	2,8	2,3	3,8	3,4	3,8	8,2	0,0	28,0	-
Nov. 1972	13,9	1,2	9,7	3,7	5,6	3,9	5,0	12,2	19,6	0,0	60,9	-
Jan. 1973	14,1	0,7	9,0	2,5	5,3	3,6	3,4	12,0	19,9	0,0	56,4	-
Jul. 1973	14,6	0,8	8,0	1,9	4,1	2,8	2,9	10,0	19,8	0,7	51,0	-
Feb. 1974	15,6	0,7	7,5	2,5	5,8	3,7	2,9	10,2	19,4	0,2	52,9	1,2
Mar. 1979	20,3	2,1	11,2	0,1	8,6	3,4	5,4	11,2	28,2	1,0	71,2	7,2
Mar. 1982	23,3	2,6	7,1	0,3	3,1	0,9	6,2	11,8	16,4	0,6	49,0	6,7
Plot 2b-1			Erica hispidula	Erica longifolia	Sympieza articulata	Other narrow sclerophylls						
May. 1970	11,4	3,1	0,6	1,9	0,7	2,9	5,4	8,3	11,3	2,5	36,7	-
Nov. 1972	13,9	5,6	1,1	5,6	2,3	4,3	5,6	12,5	22,0	2,9	61,9	-
Jul. 1973	14,6	4,0	0,9	1,7	1,7	3,0	5,0	14,0	20,5	1,3	52,1	-
Feb. 1974	15,2	3,5	2,2	4,2	0,8	2,0	5,2	12,4	17,8	4,1	52,2	0,0
Mar. 1979	20,3	10,1	1,7	0,0	0,0	5,0	10,0	13,5	29,8	2,1	72,2	2,8
Jun. 1982	23,5	5,9	4,0	0,2	0,2	4,1	5,9	14,6	18,2	0,8	53,9	15,7
Plot 2b-2			Erica hispidula	Blaeria dumosa	Sympieza articulata	Other narrow sclerophylls						
Jun. 1970	11,5	2,4	1,2	3,3	14,8	2,6	2,9	7,9	7,9	1,9	44,9	-
Nov. 1972	13,9	6,0	4,4	7,5	25,9	3,0	2,3	9,1	15,4	3,0	76,6	-
Jul. 1973	14,6	5,3	4,5	6,2	21,9	2,0	4,7	10,6	14,1	2,1	71,4	-
Jan. 1974	15,1	4,2	4,7	7,0	14,5	1,9	3,6	8,3	14,8	2,2	61,2	0,8
Mar. 1979	20,3	7,1	20,5	14,2	3,7	3,9	3,5	8,8	21,7	0,9	84,3	3,9
Mar. 1982	23,3	6,1	4,8	7,8	7,0	5,6	3,3	8,1	14,3	0,4	57,4	23,4

Table 5.7. Patterns of mortality and recruitment in Erica hispidula at plot 2b-1, Jakkalsrivier. See text.

	Parent present		Parent	Total absent
	Dead	Alive		
Daughters present	16	1	2	19
Daughters absent	3	1	2	6
Total	19	2	4	25

Table 5.8 Patterns of mortality and recruitment in Erica longifolia at plot 2b-1, Jakkalsrivier. See text.

	Parent present		Parent	Total absent
	Dead	Alive		
Daughters present	6	0	0	6
Daughters absent	15	0	4	19
Total	21	0	4	25

of live or dead adult plants and of any recruits was recorded for each quadrat. Results are summarised in Table 5.7 and 5.8.

Evidently, Cliffortia atrata was long-lived, not yet showing senescence. Populations of the first four Ericaceae had entered senescence between 15 and 20 years after fire, and there was little or no recruitment, as exemplified by E. longifolia (see also Chapter 4). Erica hispidula individuals senesce and die, but there was canopy strikes were on dead shoots in the 1982 survey, with about the same continual recruitment so that the population was approximately stable. The graminoids did not show real signs of decline during the period of observation although among restioids about 15-25% of proportions in the surveys from 1973 to 1979. The trend therefore was of an increasingly sparse canopy of shrubs over a more or less stable layer of graminoids, and a progressively accumulating amount of dead material in the canopy. Plot 2b-1 had up to about 10% of overstorey broad sclerophyllous shrubs (Table 5.6) but there was no trend in this component. There is no evidence in the observed trends of a competitive interaction between the principal components of the fynbos in these plots. Thus, despite the onset of senescence in dominant shrub populations, there was no increase in the cover of the graminoid component.

5.4. Discussion and conclusions

The plant communities sampled in this study lacked species resistant to fire. Fire reduced live canopy cover to zero, and recovery depended on the resilience of constituent species. In terms of the rate of recovery of prior canopy cover and growth-form composition, all communities sampled are similar despite the fact that growth rates are obviously higher on more mesic and phreatic sites. From the detailed comparison of the three plots at Jakkalsrivier, it is clear that environmental stress plays a role in the mechanisms of resilience, i.e. in the relative abundances of plants differing in their life-histories. Ephemeral plants were relatively abundant in the early stage on the phreatic site, and declined rapidly thereafter. Though present on the other two plots, their cover was sparse and where important (as in Stoebe incana on plot 1g-3), their

growth was slow. This pattern is much as predicted by Grime (1979) with respect to variations in successional pathways in relation to productivity.

The fire-ephemeral flora was relatively sparse overall. In California chaparral, for example, ephemeral herbs, mainly fire-ephemerals, would constitute a cover of around 30 to 80% in the first year after fire, depending on habitat and rainfall (Keeley et al. 1981; Sampson 1944). Thereafter, abundance declines markedly but third-year cover would amount to 5-30%, and ephemeral subshrubs would constitute 10-60% or more. In this respect, the results place the fynbos among mediterranean-type vegetations in the same category with regard to pyric succession as Australian heathland (Specht et al. 1958; Kruger 1983).

The recovery of canopy cover, relative to pre-burn cover, was quite rapid and was restored to about 80% of prior values by about three years. The rate of canopy development for the broad-sclerophyllous shrubland (plot 1g-1 at Jakkalsrivier) was about the same as that for dry sand-heath in Australia, as reported by Specht et al. (1958), whereas growth in total cover of chaparral of Southern California is apparently more rapid (Keeley et al. 1981), though direct comparison with their data is not possible. The phreatic fynbos sites had rates of canopy development similar to those of wet-heaths in Australia (cf. Russell and Parsons 1978). Initial recovery in fynbos was principally from the growth of sprouters except in the case of phreatic sites where seeding forbs may become prominent from the first year onward. Again, this was in marked contrast with chaparral where seeding herbaceous and subshrub species dominate early cover (Keeley et al. 1981). This also contrasted with wet-heath in Australia, where sprouters dominate the regenerating stand (see Chapter 2). Because the sprouters in fynbos are either tufted graminoids or shrubs, rather than creeping plants, height growth and development of foliage-profile diversity was also quite rapid.

Composition of the recovering canopy in terms of plant growth-forms is highly variable, with regard to broad-sclerophyllous shrubs, different categories of graminoids, geophytes, and forbs. This recovery

reflected the pre-fire abundance of species of different forms and hence, largely, environmental controls on species composition. This appears to be the prevailing pattern.

Community resilience, in terms of the rate of recovery of the growth-form composition that obtained prior to fire (Westman 1986), was similar among all the communities sampled at Jakkalsrivier, despite different growth rates. On the 10-year experimental burning cycle, these communities are evidently highly stable. Further development of the canopies did occur in stands from which fire was excluded, but this development was limited, marked by some increase in shrub cover followed after about 20 yr by a decline. This was accompanied by an accumulation of dead material in the canopies, a static layer of graminoids, and some cyclic recruitment in Erica hipidula but not in other shrubs.

There was no evidence that pyric succession at Jakkalsrivier was driven by the competitive effects of overstorey shrub layers on the understorey. Overstorey shrubs, mainly broad-sclerophyllous members of the Proteaceae, were very abundant in some communities (see Chapter 7) but their canopy densities are apparently limited by the potential productivity of the site so that canopies thin by senescence before any marked effects on the understoreys become apparent. This is in contrast with Australian heathland (Specht et al. 1958) and fynbos at other sites (Specht et al. 1983).

The relationships between the patterns of recovery of fynbos vegetation and the post-fire trends in stream discharge from mountain catchments is of considerable practical concern (Bosch et al. 1984). Assuming a 10-year fire cycle, one would predict for Jakkalsrivier that the increase in streamflow following fire would be relatively small because the vegetation does not attain high leaf-area indices. Cover, and hence leaf-area index, is restored to 80% of prior levels by about four years after fire, so that any enhanced level of stream discharge is not likely to be discernible beyond such an age. Canopies continue to grow slowly in height after this, but probably without any marked effect on the water balance. Denser canopies occur

on cool moist sites, and the stream-discharge responses to fire would be greater on catchments dominated by such sites, compared with those having warmer aspects.

An imponderable is the effects of canopy density on precipitation by fog interception. At Jakkalsrivier, fog interception is common, especially in summer (Chapter 3). Such precipitation would be negligible just after fire, increasing progressively thereafter.

Specht and colleagues in Australia found that the relationship between understorey and overstorey cover was direct, i.e. had a slope of -1,0, and deduced that the relationship reflected a competitive displacement of the latter. Westman (1983) has reported a similar relationship in chaparral (Chapter 2). In the fynbos at Jakkalsrivier, constraints of the physical environment, together with plant life-histories, rather than competition, seem to govern canopy dynamics (Specht et al. 1983). Where ericoid shrubs predominate, senescence in dominant canopy species sets in at about 15-20 years, and a sparse canopy is maintained thereafter by cyclic replacement in the population of tolerant Erica hispidula.

In conclusion one may emphasize the fact that the patterns of pyric succession in fynbos, though predictable in broad terms, and clearly distinct from patterns in Europe, California, and Chile, vary markedly in terms of the forms of plants involved and in the dynamics of canopy development. This variation is related to habitat and its prediction requires a better understanding of habitat controls on the structure of fynbos communities.

6. EFFECTS OF FIRE ON MICROCLIMATE, WATER AND NUTRIENTS AT JAKKALSRIVIER

6.1. Introduction

Shrublands of mediterranean-type ecosystems are characterised by relatively short cycles of regeneration after fire, with growth of the canopy to maturity and often a decline thereafter (Chapter 2). The development of the canopy in the shrublands is often accompanied by increased competition among plants for water in the dry summers and for light. Sequestration of nutrients in biomass, litter and standing dead shoots may contribute to nutrient stress. Many studies of the effects of fire on these shrublands emphasize the role of competition and of its moderation by fire. For example, Specht et al. (1958) concluded from studies in heathland in South Australia that "the stress on vegetation from insufficient water was relieved immediately after a fire". Gray and Schlesinger (1981) emphasized the dominant role that fire played both as a catalytic agent initiating succession and as a nutrient-recycling mechanism. These effects of fire on availability of resources are confounded by changes in the microclimate, when regenerating plants potentially face extremes of temperature, saturation deficit, radiant energy loads, and wind.

The possible role of competition in pyric succession was tested for the fynbos at Jakkalsrivier by addressing the following hypotheses:

(a) Regenerating plants on the burnt site would reflect the more freely available water and nutrients in the soils in their more favourable water and mineral nutrient status than the adult plant on the unburnt site.

(b) Pioneer plants (fire ephemerals) would have higher nutrient demands than climax plants (obligate seeders and long-lived sprouters), as reflected in foliar nutrient concentrations.

Vegetation canopies modify microclimates in ways of substantial importance to plants. Light is attenuated so that the energy penetrating the canopy is reduced in exponential relation to foliage area (Monteith 1973). Wind velocity beneath the canopy is altered in the same way (Monsi et al. 1973; Grace 1977). The effects of the canopy on microclimatic factors, especially light, temperature, vapour pressure deficit, and wind, may also play a role in affecting resprouting, recruitment, and mortality. Exposure of the site after a burn to heightened extremes in these factors may affect the success of regeneration and limit the range of life-forms that may endure the fynbos environment. This study was aimed at exploring possible changes of this kind at Jakkalsrivier.

The roles of these factors in pyric succession were analysed by comparing the habitat in the recent burn with the "control" on the site which had been burnt 24 years before (see Chapter 3).

6.2. Methods

6.2.1. Plant water potentials The water status of different plant species was compared by periodic measurement of plant xylem pressure potentials (ψ). At Jakkalsrivier, four "climax" species were selected for measurement of ψ, one being the tall broad-sclerophyllous shrub (Leucadendron xanthoconus), another the mid-height ericoid shrub (Erica hispidula), a third the low sprouting nanophyllous shrub (Penaea mucronata), and a fourth the restioid herb (Elegia juncea). Each was to be sampled as adults in the unburnt vegetation and seedlings or sprouts in the burnt vegetation, but since no Erica hispidula seedlings had appeared by April 1982, comparisons for this form were not possible. Spot measurements on Erica sessiliflora seedlings, sufficiently large for sampling by March 1982, were used instead. Xylem pressure potentials were measured before dawn and around midday, in order to assess plant water status in relation to soil ψ and diurnal evaporative stress, respectively. Diurnal curves were obtained for Leucadendron xanthoconus on most occasions, as well as for Erica hispidula on a few days. These curves indicated that pre-dawn

ψ did reflect overnight equilibrium, and that ψ was at a minimum for about three hours around solar noon. First measurements were made in March 1981.

After initial trials the following procedures were adopted for measurements from June 1981 onward, following Ritchie and Hinckley (1975). Shoots were collected arbitrarily from five or more healthy plants of a given species. Current shoots 100-150 mm long were cut from the upper half of the canopy of the plants, from a fully exposed location, and brought immediately to the pressure chamber. Stems were not recut. They were inserted into the rubber gland of the chamber top so that 5-10 mm protruded. In the chamber, pressure was increased at a rate of 0,05 to 0,07 $MPa.s^{-1}$. A 10x hand lens was used to observe end-points. The end-point was noted as the stage when xylem sap was expressed to the extent of fully wetting the cut surface. This was clear-cut with all species except Elegia, where sap appeared gradually and the face wetted progressively during a change in potential of about 0,5 MPa; it is not clear in this species (and in other Restionaceae - Miller et al. 1983) what end-point marks the actual balancing pressure. The point at which sap was first noted at the cut surface was recorded as the end-point for Elegia, but it was difficult to apply a consistent rule. Measurements were made initially with a pressure chambers according the design in Ritchie and Hinckley (1975) but from August 1981 onward a pressure chamber manufactured by PMS Instruments was used. The design of this latter apparatus allowed more rapid and efficient measurement than the former.

Because of the change in soil texture across the boundary between the burnt and unburnt vegetation at the intensive site, xylem pressure potentials were measured on two occasions on a site with more uniform soil. This was situated about 200 m to the north-east and about 80 m higher in altitude (Fig. 3.3). Soils there were fine sandy loams, similar to those on plot 1.

6.2.2. Soil moisture regime At the intensive study site the gravimetric surface soil moisture contents were determined on every day that plant xylem pressure potentials were measured. A sample of three units was taken from both the burnt and the unburnt sites, by

trowelling the upper 150 mm in several spots around three representative locations, and bulking the soil from the spots at each location. These samples were weighed, oven-dried at 105°C for 24 hours, and moisture content was expressed as percentage mass loss on an oven-dry basis.

6.2.3. Mineral nutrients The relative uptake of mineral nutrients by plants was assayed by sampling for foliar nutrient concentrations. The species chosen for studies of water relations and the soils on which they occurred were sampled on two occasions, in February 1982 and again in November 1982, to measure foliar nutrient concentrations and soil nutrient availability. A site with visibly more uniform soils was chosen about 200 m to the north-east of the intensive site (Fig. 3.3). Here, plants from burnt and unburnt sites were sampled by clipping current shoots from the upper half of the canopy of three or more arbitrarily chosen, healthy plants in such a way that all canopy sectors were equally represented. Foliage and stem material were not separated, the latter constituting only about 10% of total mass. These samples were placed in brown-paper bags and air-dried before analysis.

Soils were sampled at the same times and on the same sites by coring the upper 100 mm. A sample of three units from both the burnt and unburnt sites was obtained by coring spots at three representative locations and bulking the cores for each unit. Soils were air-dried and sieved through a 2 mm sieve. For soil nitrogen the procedure described by Stock (1983) was followed, to detect nitrogen in different forms and avoid changes which occur in stored samples. Fresh soil samples of standard mass from which stones and roots had been removed were shaken in a standard volume of 1N KCl in the field and returned rapidly to the laboratory (within three to five hours) where they were stored at about 2°C until they could be filtered. Each was filtered through a Whatman's No. 4 filter and again stored cold until despatch for analysis by the National Research Institute for Oceanography where they were analysed for nitrate, nitrite, ammonia and total nitrogen. Additional soil samples were oven-dried for 24 hours at 105°C to determine moisture content and allow N concentrations to be expressed in terms of soil dry mass. Samples were

taken in February 1982. All analyses except for those of nitrogen in different forms were undertaken by the Citrus Exchange Leaf Analysis Service. Details of analytic procedures are given in Appendix 1.7.

Plants of different successional status were compared in terms of their nutritional status by analysis of foliar nutrient concentrations. Nine species were selected for an investigation of possible patterns. These included both shrubs (all seeders) and graminoid herbs in each of two categories, pioneer and climax species. In each case, current shoots were sampled from representative plants on the burnt site during February 1983 in the same way as for earlier samples. In the case of shrubs, foliage and stem were separated. The samples were air-dried in brown-paper bags and then despatched to the Citrus Exchange Leaf Analysis Service for determination of concentrations of the major nutrients (excluding sulphur). Leaf samples were duplicated for chemical analysis; graminoid material (leaves in Tetraria, green stems in the aphyllous Elegia and Ehrharta) were replicated 3-4 times. Mean values were used in analysis of the data.

6.2.4. Microclimate The light environment was investigated by measuring total incoming solar radiation and photosynthetically active radiation (PAR) in the canopy of vegetation at different stages of development. This was done by mounting a metre rule horizontally at a given elevation and reading PAR at 100 mm intervals along the rule by means of a Licor PAR meter. Measurements were made through the day at one site per stand.

The radiation balance of the site was investigated by measuring total incoming solar radiation (Moll-Gorczinski solarimeter mounted at 1,2 m), reflected solar radiation (inverted Moll-Gorczinski solarimeter at 1,0 m on the burnt site and 1,4 m on the unburnt), and net radiation (Fritschen and Middleton net radiometers at 1,0 m on burnt site and 1,6 m on unburnt site, respectively) over time periods of 24 hours or more during clear or nearly clear days. Not enough instruments were available to allow full measurement runs on every occasion.

On selected clear days in November (late spring) and again in January (mid-summer) temperatures and relative humidities were measured for the following:

(a) ambient air at 2,0 m

(b) ambient air at canopy levels (1,2 m on the unburnt site and 150 mm on the burnt site)

(c) at 150 mm on the unburnt site

(d) on both the burnt and unburnt sites, temperatures at the soil surface, and at -50 and -150 mm.

Temperatures of leaves of Leucadendron xanthoconus were also measured on burnt and the unburnt sites.

Temperatures were measured by copper-constantan thermocouples (0,4 mm diameter for leaf and soil surface temperatures, 0,8 mm for air temperatures, and 1,2 mm, with three sensing thermocouples connected in parallel, for subsurface soil temperatures), switched through an Ancom Cucon thermocouple switchbox, and read by means of a Bailey digital thermocouple thermometer which gave readings to 0,1°C. Leaf thermometers were placed by passing the thermocouple through the leaf, reflexing it and inserting the fine thermocouple bead into the epidermis. Mature leaves were selected for measurement on vigorous shoots in the upper half of the canopy, on the northern side of the plant. For soil surface temperatures a spot was chosen about halfway between adjacent tufts of understorey graminoids. Thermocouple leads were staked for stability and the thermocouple beads were gently inserted between soil grains at the soil surface. Subsurface soil temperatures were measured nearby (within about 250 mm), but not so close that the excavation was judged likely to affect surface measurements. Wet-bulb temperatures were obtained by sheathing one of a pair of screened thermocouples in standard Lambrecht Assmann psychrometer wicks which led to small glass reservoirs of distilled

water. These psychrometer thermocouple pairs were shielded in 75 mm diameter PVC pipes, cut so that the half-cylinder of the pipe formed a roof over the thermocouples, and sprayed with white paint. Wicks were wetted or checked for wetness two minutes before each reading. Laboratory tests showed good correspondence between temperatures and wet-bulb depressions obtained in this way and those measured with an Assmann psychrometer, even with ventilation varying from nearly zero to average ambient wind-speed. Vapour pressures were calculated according to standard procedures of the South African Weather Bureau, using the derivative of the Goff-Gratch formula (SA Weather Bureau, unpublished).

The wind profile was monitored by means of cup anemometers mounted at 3,0 m at one representative site, and at 1,5 m and 300 mm at both the burnt and the unburnt sites.

6.2.5 Effects of shading on germination and early growth in Leucadendron xanthoconus Leucadendron xanthoconus was a useful species with which to test the effects of shading on seedling growth and establishment, it being the dominant broad-sclerophyllous shrubs on the site, and having seed that were easy to collect and germinate. The experiment to test the effects of shading on germination and early growth in Leucadendron xanthoconus was conducted under nursery conditions at the Jonkershoek Forestry Research Centre. Seed was collected from mature cones of L. xanthoconus at Jakkalsrivier in February 1983. The cones were air-dried until seed were released. Plump seed were sorted out and twenty seed were sown per tray for the germination trial. These were placed out on 4 April 1984, and shading treatments commenced immediately. For the trial to determine effects of shading on growth, three seeds were sown in sifted soil collected from Jakkalsrivier and placed in black polythene nursery bags, 300 mm deep and 300 mm in diameter. The containers were placed in the open air on 4 April 1984, and irrigated as needed. Germination was allowed to proceed until the start of shading treatments on 6 July 1984. All seedlings other than the first to establish were removed from each of the pots.

Shade was provided by frames 600 mm high and 1000 mm square, covered in black polythene shadecloth. One set of plants was grown in full sun, as a control. Treatments were 30% shade, 60% shade, and 90% shade. Measurements by means of a Delta-T bar pyranometer during full sun around solar noon in June 1985 indicated light reduction of 80,5, 74,7, and 41,8 per cent for the 90, 60 and 30 per cent treatments respectively.

Nineteen pots were assigned at random to each treatment and the control. Plants were harvested on 16 November 1984, 7 January 1985, 15 April 1985, and 11 June 1985. The main harvest was on 15 April; two or three plants were harvested on other dates. Pots were inspected about twice weekly and were irrigated with tap water whenever the surface layers of soil were seen to be dry.

Although irrigation was regular, it may have been that the soils in the controls dried quicker than the others and that this affected plant water status and hence growth. This was investigated by measuring leaf stomatal conductances immediately before the final harvest. Measurements were made under the prevailing experimental conditions, using a Beardsell porometer (Beardsell et al. 1972), between 3 and 7 June 1985, around solar noon. Two plants were chosen at random from each treatment for these purposes. Days were sunny.

At harvesting, plants were removed carefully from the loose sand and roots were washed thoroughly but gently in tap water until clean. Heights were measured as the distances between root collar and growing tip. Rooting depths were measured as the distance between root collar and furthermost root tips. Each plant was then subdivided into foliage, stem, and roots. Leaves were counted and leaf specific masses determined. At the major harvest, roots were subdivided into categories of coarse roots, i.e. greater than 2 mm in diameter, medium roots, between 0,5 and 2 mm, fine roots, up to 0,5 mm, and proteoid roots. Each component was oven-dried at 70oC until constant mass was reached.

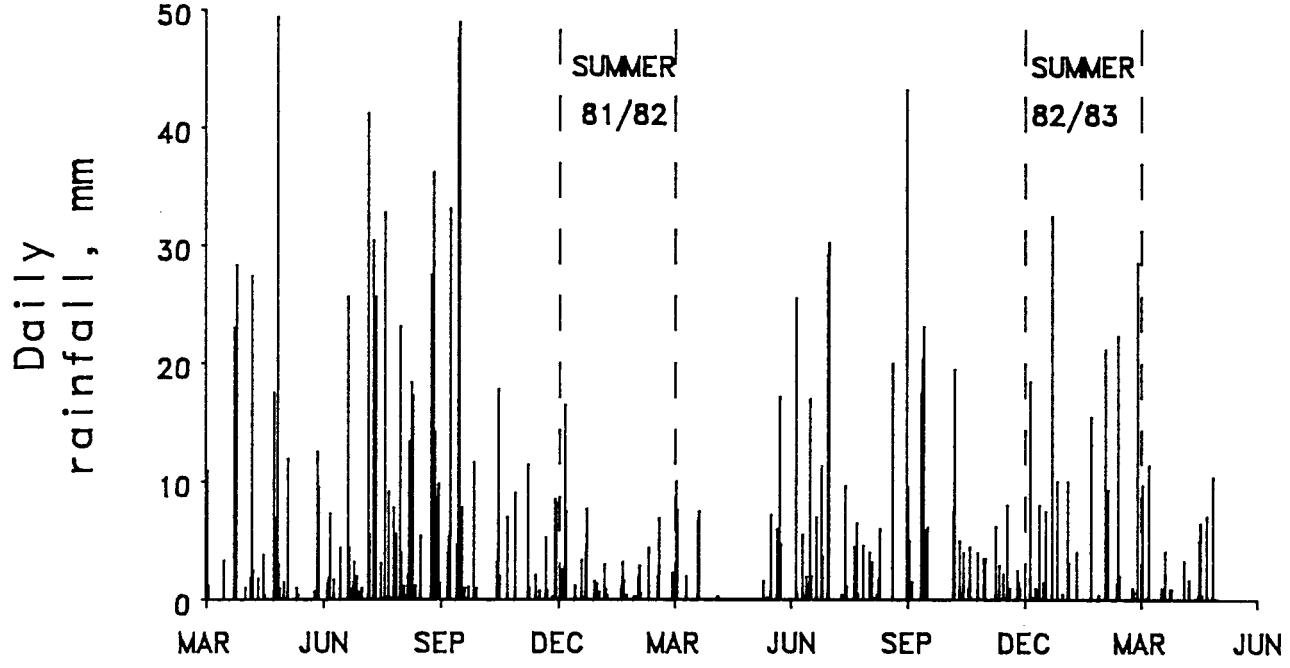


Figure 6.1. Daily totals of rainfall recorded at the main weather station during the period of water stress studies at Jakkalsrivier.

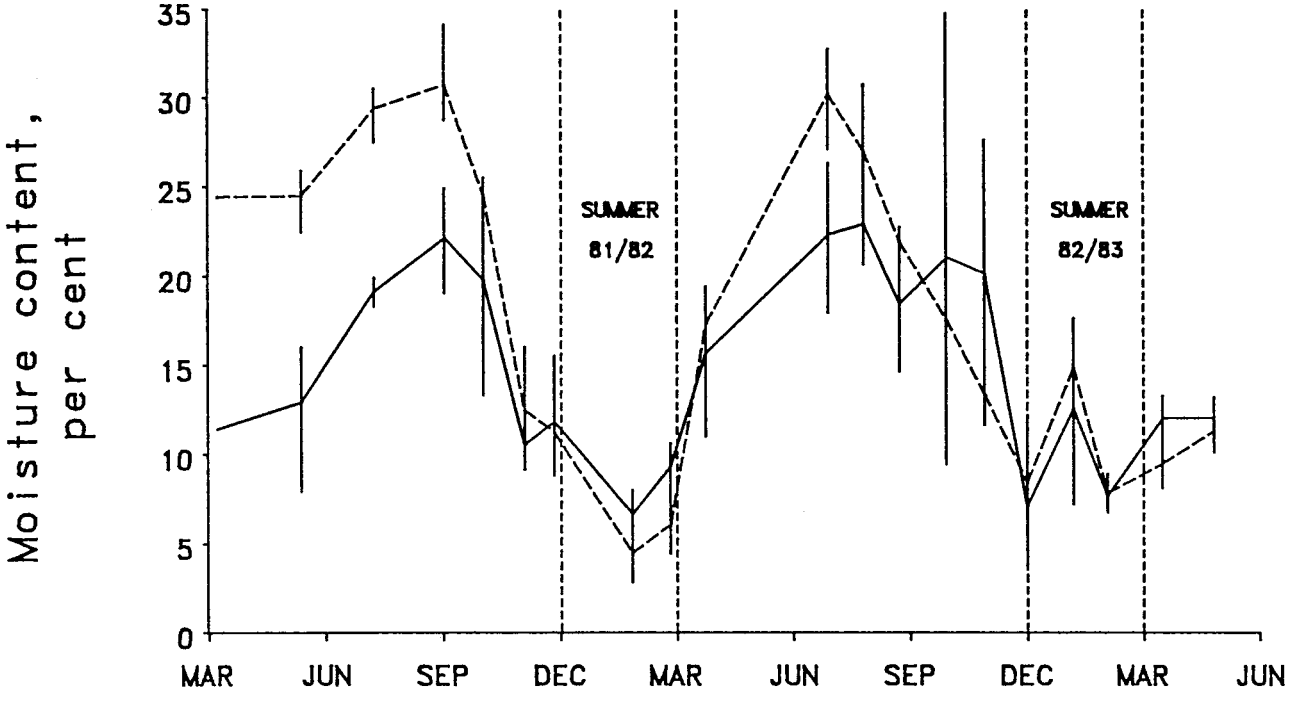


Figure 6.2. Variation in surface soil moisture contents during plant water stress studies at Jakkalsrivier. The continuous line represents values for the unburnt site, and the dashed line, the burnt site. Bars are ranges for three values.

6.3. Results

6.3.1. Plant water relations Rain fell fairly frequently during the period of observation, even in summer (Fig. 6.1). Consequently, surface soil-moisture contents were relatively high most of the time (Fig. 6.2). Soil moisture content samples were highly variable, making it difficult to compare the burnt with the unburnt site precisely without much larger samples. However, average soil moisture contents were significantly higher on the burnt site than on the unburnt site during the first winter and early spring, and again on one occasion during the following winter. Otherwise, moisture contents were essentially the same, and overall means nearly identical (15,2% vs 15,5%). The lowest moisture contents were observed in January and February 1982, when levels reached 4-6% on the burnt site and 7-10% on the unburnt (Fig. 6.2). The next summer, moisture contents fell to 8-9% and 7-8%, respectively. The moisture contents at permanent wilting point and at field capacity, respectively, of the A horizons are around 2,4% and 7,8% for the control and 10,4% and 16,8% for the unburnt site. Thus, surface soil moisture fell below permanent wilting point briefly on the burnt site, and not at all on the unburnt site (Fig. 6.2). The soil was saturated or nearly so on 18 occasions on the unburnt site, and on ten occasions on the burnt site. Potentials evidently fell below field capacity on three occasions on the burnt site, but did so on eleven occasions on the burnt site. Thus, though water contents on the burnt site were often higher, the finer texture of the soil resulted in lower (more negative) water potentials more often than on the unburnt site. Nevertheless, soil moisture was freely available to plants for most or all of the time on both sites despite occasional dryness in the surface soil on the burn.

Clear days were chosen for measurements of plant water potential. Days scheduled for field work often turned out overcast or wet so that measurements in some months could not be done if no alternative suitable days could be found. Twenty-two successful measurement runs were completed, on clear or nearly clear days. Correlations between dawn plant water potentials and soil moisture content were weak with the highest $r = 0,42$ ($P = 0,07$) for Penaea on the burnt site. On the

unburnt site, pre-dawn potentials in Erica were negatively correlated with soil moisture content ($r = -0,43$, $P = 0,06$). Given the high soil water potentials, high pre-dawn plant ψ could be expected. These poor correlations are not readily explained. For midday potentials somewhat higher correlations were obtained but only those for Penaea on the burnt site ($r = 0,54$, $P = 0,014$) and the unburnt site ($r = 0,40$, $P = 0,08$) were significant. Maximum daily vapour pressure deficits, calculated from psychrometer data for the Stevenson screen at the main weather station, varied between 0,02 and 4,1 kPa. Midday xylem pressure potentials were significantly correlated with daily maximum vapour pressure deficits in all cases except Leucadendron and Erica on the unburnt site (Table 6.1). Pre-dawn pressure potentials were not significantly correlated with maximum vapour pressure deficit on the previous day except in Penaea ($r = 0,53$, $P = 0,014$), which may be expected since plants would tend to equilibrate with soil water potential overnight. Maximum diurnal ranges in xylem pressure potential were small, varying from 1,8 to 1,9 MPa in Elegia and Erica to 1,1 to 1,5 Mpa in Leucadendron and Penaea. Thus plants responded to the level of evaporative demand of the atmosphere, but were not stressed.

There was little seasonal variation in the pre-dawn water potentials of plants measured here (Figs. 6.5 and 6.6). The most variable species were Erica and Elegia, whose pre-dawn potentials fell to -1,45 and -1,31 MPa respectively (Table 6.2), but with neither minima being recorded in summer. These are much higher values than those observed for shallow-rooted shrubs by Miller et al. (1983) and for Staberoha by Moll and Sommerville (1985). Seasonal variation in midday potentials was evident but weak (e.g. Fig. 6.5). Lowest midday potentials, -1,84 MPa and -2,39 MPa respectively, were also measured in Erica and Elegia (Table 6.2). The minimum observed in Leucadendron and Penaea were -1,34 and 1,55 MPa respectively.

Species were ranked in descending order of mean pre-dawn potentials as follows: Leucadendron > Erica > Penaea > Elegia. For midday potentials, the ranking was Leucadendron > Penaea > Erica > Elegia. Thus seeding shrubs, Leucadendron xanthoconus and Erica hispidula, showed less moisture stress overall than the two sprouting species.

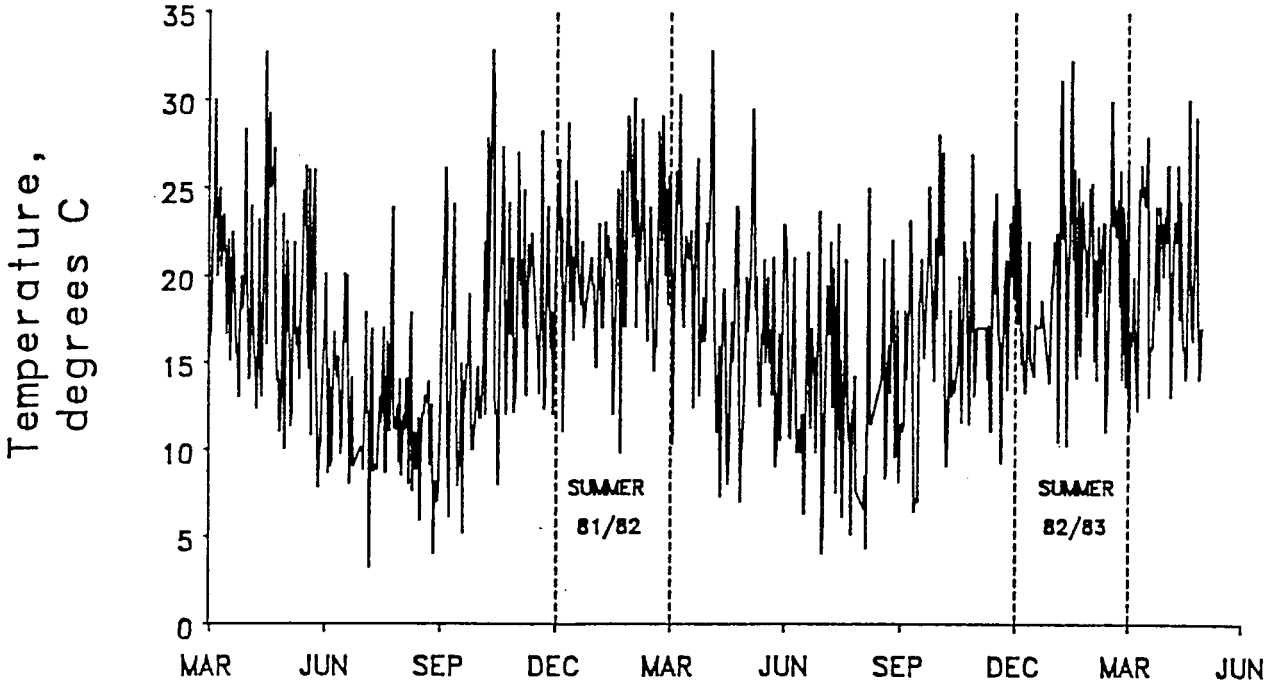


Figure 6.3. Daily maximum screen temperatures during the period of plant water stress studies at Jakkalsrivier.

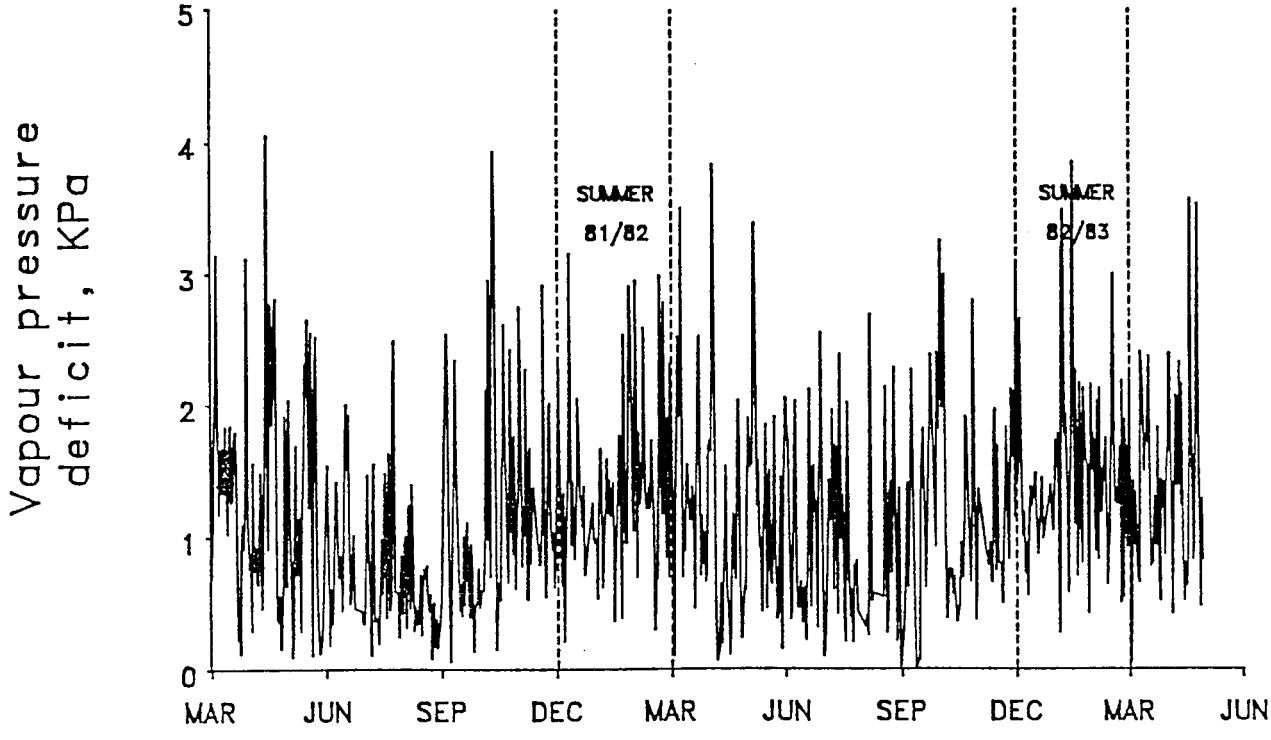


Figure 6.4. Daily maximum vapour pressure deficits during the period of plant water stress studies at Jakkalsrivier.

Table 6.1. Correlation between maximum daily vapour pressure deficits (measured by psychrometers in the Stevenson screen of the main weather station) and plant water potentials at Jakkalsrivier. Values in brackets are for significant values of P (n = 22). Pre-dawn potentials were correlated with maximum vapour pressure deficits for the previous day.

	Pre-dawn		Midday	
	Burnt	Unburnt	Burnt	Unburnt
Leucadendron	-0,047	0,096	-0,479 (0,024)	-0,409 (0,059)
Penaea	-0,403	-0,337	-0,587 (0,004)	-0,852 (0,0001)
Erica	-	-0,103	-	-0,401 (0,065)
Elegia	-0,076	-0,010	-0,599 (-0,004)	-0,596 (0,003)

Plant water potentials at the intensive study site and the uniform site upslope were compared by measuring midday potentials at both sites on 24 February 1982, between 12h00 and 15h00 SAST. Pre-dawn measurements for 24 February at the lower site were compared with dawn measurements for 25 February at the upper site. Pre-dawn measurements were similarly compared for 24 and 25 March 1982. Analysis of variance with data classified in species x site x treatment groups showed the means of the plant water potentials not to be homogeneous, at a highly significant level (Table 6.3).

Pairwise comparison of means using the Tukey-Kramer method appropriate to unbalanced data (SAS Institute Inc. 1985) showed that the inhomogeneity was mainly owing to differences between species. There were some differences within species between treatments. No

Table 6.2. Mean minimum plant xylem pressure potentials measured at Jakkalsrivier, March 1981 - April 1983, on given dates. Standard deviations are given for Erica sessiliflora.

Species	Pre-dawn potential, MPa		Midday potential, MPa	
	Burnt	Unburnt	Burnt	Unburnt
Elegia juncea	-1,45 (29 Jan 82)	1,31 (29 Jan 82)	-2,23 (24 Mar 82)	-2,39 (24 Mar 82)
Erica hispidula	-	-1,5	- (02 Sep 81)	1,84 (08 Mar 81)
Erica sessiliflora	0,62 ± 0,84 (n = 5) (14 Mar 82)	-0,61 ± 0,11 (n = 4) (14 Mar 82)	-1,72 ± 0,07 (n = 4) (14 Mar 82)	-1,63 ± 0,08 (n = 3) (14 Mar 82)
Leucadendron xanthoconus	-0,55 (09 Jul 81)	-0,51 (09 Jul 81)	-1,34 (08 Mar 81)	1,19 (08 Mar 81)
Penaea mucronata	-0,73 (01 Dec 82)	-0,89 (29 Jun 82)	-1,55 (08 Mar 81)	-1,48 (26 Apr 83)

Table 6.3. Significantly different dawn water potentials within species at two sites at Jakkalsrivier on 24 and 25 February 1982. See text for details. P = 0,95, alpha = 0,05, MSE = 0,0479, and the critical value of the studentised range = 0,488. With n_1 = 6 and n_2 = 8, for example, the least significant difference is 0,0892 MPa.

Species	Treatment	Mean water potentials, MPa (with n)	
		Lower site	Upper site
Erica hispidula	Unburnt	-0,29 (8)	-0,57 (7)
Penaea mucronata	Unburnt	-0,51 (7)	-0,37 (7)
	Burnt	-0,61 (8)	-0,46 (6)

significant differences were found within species between sites (upper and lower) and treatments (burnt vs unburnt), except in the pre-dawn measurements in March. In this case, significant differences were found between sites for Penaea (both burnt and unburnt), and Erica (Table 6.3). The February measurements were markedly more variable than those for March (MSE 0,180 vs 0,0479). Midday potentials measured at the two sites in February were very similar within species and treatments: for example, the mean ψ for Penaea in unburnt vegetation was -1,32 for the lower site and -1,31 for the upper site. The real differences at dawn in February were small and unlikely to have affected the relative condition of plants substantially (Table 6.3). One may assume therefore that comparisons between the burnt and the unburnt vegetation at the main study site will allow valid conclusions about the differences between the burnt and the unburnt vegetation despite the differences in soil physical properties of the respective sites.

Differences between plants on burnt and those on unburnt sites were not significantly correlated with maximum air temperature, minimum humidity, or vapour pressure deficit, neither linearly nor quadratically. In Leucadendron (Fig. 6.5) pre-dawn potentials on the burnt site were significantly lower on three occasions, and higher on two, but the differences were never greater than 0,2 MPa. Midday potentials on the burnt site were significantly lower on 10 occasions, and higher on one. The largest difference was 0,35 MPa. In Penaea, pre-dawn as well as midday potentials differed significantly on eight days (Fig. 6.6). Dawn potentials were sometimes higher on the burnt site. Regenerating plants had potentials at most 0,18 MPa lower than unburnt plants. When significantly different, midday potentials in regenerating plants were usually lower (more negative) than in unburnt plants; the largest difference measured was 0,52 MPa. In Elegia, burnt and unburnt plants differed significantly in their water potentials on just five occasions at dawn and four at midday. Comparisons between burnt and unburnt populations of Erica sessiliflora on 14 March 1982 showed no significant differences (Table 6.2). In balance, therefore, there were no consistent and substantial differences to be found in the water stress of plants in the burnt and unburnt environments.

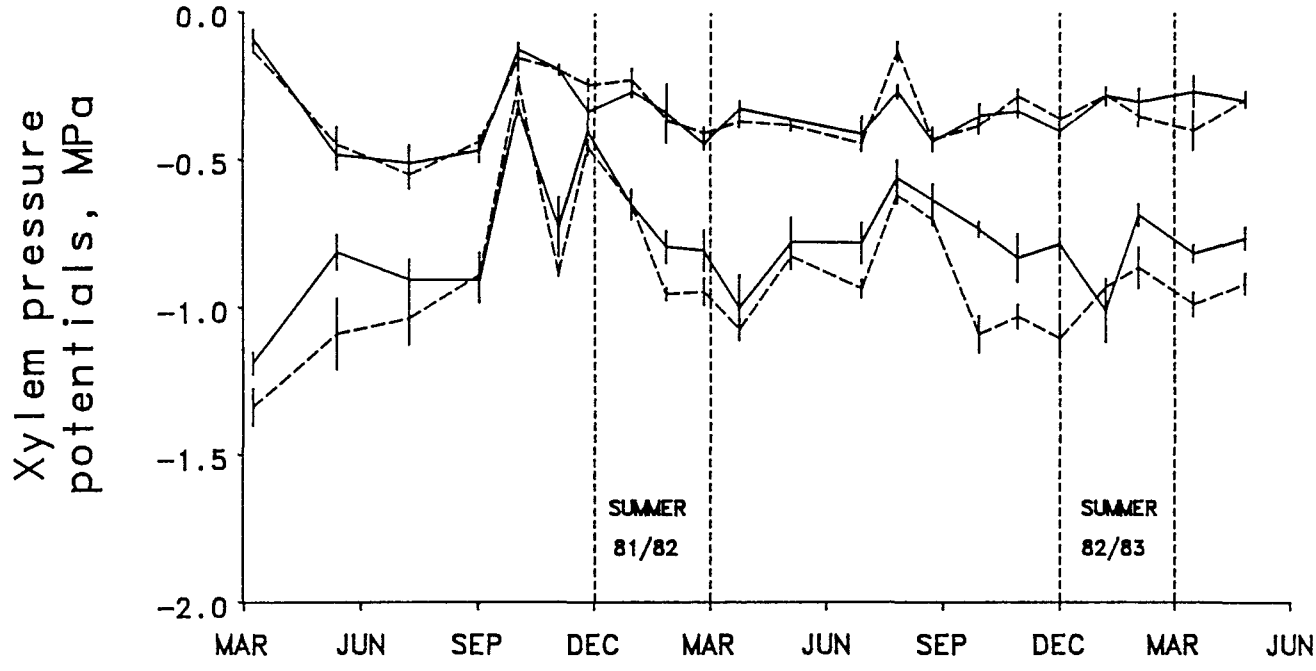


Figure 6.5. Variations in xylem pressure potentials in Leucadendron xanthoconus at Jakkalsrivier. Continuous lines represent values for plants from the unburnt site and dashed lines, those for the burnt site. Higher values are for pre-dawn measurements and lower values for midday. Bars represent double standard deviations.

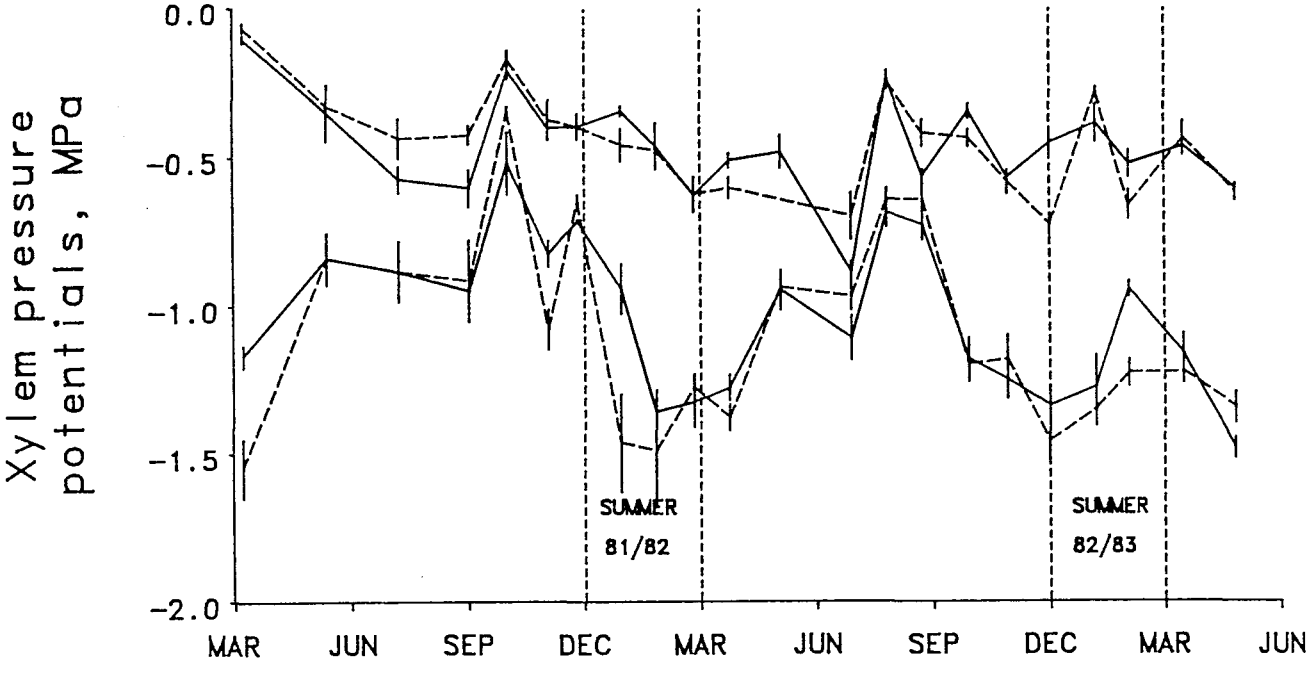


Figure 6.6. Variations in xylem pressure potentials in Penaea mucronata at Jakkalsriver. See Fig. 6.5. for explanation.

6.3.2. Mineral nutrients There were no significant differences between mineral nutrient concentrations in the soil of burnt and unburnt sites in the samples taken in November 1981 (Table 6.4). In those taken in February 1982, total and "available" (Bray No. 2 extract) soil phosphorus concentrations were significantly higher on the burnt than on the unburnt site ($t = 3,08$, $0,02 < \alpha < 0,05$ and $t = 4,16$, $0,01 < \alpha < 0,02$ respectively). Concentrations were 256,7 and 163,0 $mg.g^{-1}$ respectively for total and 6,67 and 3,0 for "available" P. This difference in summer could be owing to enhanced mineralization on the burnt site (Brown and Mitchell 1985). Sample variability in soil nutrient concentrations was high so that much larger samples would be required to detect differences for the other nutrients.

Foliar samples could not be tested for statistical significance except in the February samples for L. xanthoconus. In this case, only magnesium showed significant differences, with concentrations of 3,20 $mg.g^{-1}$ in the foliage of seedlings and, 1,80 $mg.g^{-1}$ in mature plants ($t = 6,17$, $0,001 < \alpha < 0,01$). Overall, however, foliar nutrients also tended to have higher concentrations in seedlings, though not in every case. Nitrogen and phosphorus differences observed between plants on the two sites, if any, were small (Table 6.5). For potassium, calcium and magnesium, ratios of concentrations in burnt to unburnt sites varied between 0,75 (magnesium in Elegia juncea) and 2,45 (calcium in Elegia juncea). Foliar concentrations of calcium were higher on the burnt site than on the unburnt site in all three species, as were concentrations of magnesium for Leucadendron xanthoconus and Penaea mucronata (Table 6.5). Potassium concentrations were higher in Leucadendron on the burnt site (4,25 - 6,5 $mg.g^{-1}$ vs 4,2-5,0), but lower for Penaea mucronata (6,7-6,75 vs 7,8-7,9) and Elegia juncea (12,25-14,9 vs 16,3-16,5). P. mucronata tended to have lower concentrations of nitrogen, phosphorus and potassium on the burnt site, and higher values for calcium and magnesium. There were no or small differences in nitrogen and phosphorus in Elegia, but potassium was lower on the burnt site, calcium was higher, and the differences in magnesium were inconsistent. It is clear that the plants from the two habitats, burnt and unburnt, hardly differed in foliar concentrations of

Table 6.4. Results of soil nutrient analyses for burnt and unburnt sites at Jakkalsrivier. (Units are $\mu g.g^{-1}$, n = 3, means and standard deviations given).

	Unburnt	Burnt
November 1981		
Total phosphorus (strong acid extract)	162 ± 25,1	192 ± 31,1
"Available" phosphorous (Bray No. 2 extract)	4,67 ± 0,58	5,67 ± 2,3
Potassium	111,7 ± 27,3	103,7 ± 27,5
Calcium	433 ± 95,4	339 ± 133,8
Magnesium	11,3 ± 15,6	89,7 ± 2,52
February 1982		
Nitrite	<2,03	<3,53
Nitrate	≈0	≈0
Ammonia	242,8 ± 61,0	231,4 ± 93,3
Total phosphorus	163,0 ± 50,0	256,7 ± 16,4
"Available" phosphorus	3,0 ± 0,0	6,67 ± 1,53
Potassium	133,0 ± 27,4	169,3 ± 27,20
Calcium	473,7 ± 119,6	628,0 ± 173,0
Magnesium	178,0 ± 28,5	124,0 ± 28,5
pH (H_2O)	5,17 ± 0,322	5,4 ± 0

Table 6.5 Foliar nutrient concentrations of plants in unburnt and recently burnt vegetation at Jakkalsrivier. (Units are $mg.g^{-1}$)

	Leucadendron xanthoconus		Penaea mucronata		Elegia juncea		Erica-hispi-dula
	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
November 1981[a]							
Nitrogen	4,6	4,6	4,7	4,4	4,0	4,0	-
Phosphorus	0,6	0,6	0,6	0,5	0,4	0,4	-
Potassium	4,5	5,9	7,9	6,7	16,5	14,9	-
Calcium	6,2	7,6	19,7	22,8	1,1	2,7	-
Magnesium	5,0	6,5	2,1	3,2	3,8	2,8	-
February 1982[b]							
Nitrogen	5,2 ±0,35	5,4	7,0	6,0	5,2	4,3	6,8
Phosporous	,33±0,115	0,445	0,4	0,3	0,2	0,2	0,3
Potassium	4,2 ±0,44	4,25	7,8	6,75	16,3	12,25	4,1
Calcium	4,47±0,81	3,75	19,0	20,9	1,85	2,20	2,2
Magnesium	1,80±0,20	3,10**	1,7	1,75	1,55	1,7	1,2

[a] n = 1 in every case.

[b] Mean of two values, except for Leucadendron on the unburnt site, where n = 3, and Erica hispidula, where n = 1.

nitrogen and phosphorus. The results, though tentative, suggest that differences among species in their response to availability of the different mineral nutrients would be worth investigation.

Substantial differences were found in nutrient concentrations of the foliage and stems between pioneer and climax species (Table 6.6). Climax species ranked lowest in foliar nitrogen concentrations. In the case of phosphorus, pioneer species were ranked highest except that the grass Ehrharta ramosa had the lowest concentration but one. For the other elements, the rankings were not consistent in

Table 6.6. Nutrient concentrations in "pioneer" and "climax" species from the burnt site at Jakkalsrivier.

Species	Family	Growth form	Successional status	Nutrient concentrations, $mg.g^{-1}$						
				N	P	K	Ca	Mg	Na	n
Foliage[a]										
Aspalathus globosa	Fabaceae	Shrub	Pioneer	25,0	0,75	7,1	6,4	1,30	5,15	2
Ehrharta ramosa	Poaceae	Graminoid herb	Pioneer	9,1	0,63	7,4	9,7	0,77	0,97	3
Hypocalyptus oxalidifolius	Fabaceae	Dwarf shrub	Pioneer	29,0	1,35	11,6	7,4	4,90	1,55	2
Othonna quinquedentata	Asteraceae	Shrub	Pioneer	13,2	0,95	22,1	27,9	14,35	4,65	2
Ursinia crithmoides	Asteraceae	Shrub	Pioneer	12,3	0,50	14,4	8,1	3,60	13,50	2
Elegia juncea	Restionaceae	Graminoid herb	Climax	8,4	0,38	13,0	2,4	1,83	13,70	4
Erica sessiliflora	Ericaceae	Shrub	Climax	8,4	0,70	4,6	4,8	1,95	1,10	2
Leucadendron xanthoconus	Proteaceae	Shrub	Climax	6,0	0,60	3,8	11,5	2,80	2,15	2
Tetraria bromoides	Cyperaceae	Graminoid herb	Climax	5,9	0,58	3,6	1,6	0,50	1,50	4
Stems										
Aspalathus				12,4	0,80	9,8	3,6	1,2	11,9	1
Hypocalyptus				11,2	0,50	8,6	5,3	2,5	1,6	1
Othonna				5,6	0,50	26,1	9,4	3,9	6,7	1
Ursinia				7,0	0,60	17,5	8,0	2,6	5,5	1
Erica				4,8	0,50	5,8	3,6	2,2	1,5	1
Leucadendron				3,0	0,50	5,5	2,9	2,6	3,9	1

[a] Green shoots in the cases of Ehrharta ramosa and Elegia juncea, which are effectively without leaves.

discriminating between pioneer and climax species. Nutrient concentration ratios were also analysed but the results did not discriminate between pioneer and climax species.

The correlation matrix for foliar nutrient concentrations is given in Table 6.7. Because the concentrations of different mineral nutrients were correlated, patterns of variation were examined for overall trends by analysis of the principal components of the variation. The results showed that 97% of the variability could be accounted for by the first three principal components (Table 6.8). The first principal component reflected overall concentration of nutrients (Table 6.8). The second represented a contrast between nitrogen and phosphorus (negative) and other elements, especially potassium and sodium. The third contrasted nitrogen and sodium with calcium and magnesium. Pioneer species were ranked highest on the first principal component, except for E. ramosa (Table 6.9).

Cluster analysis was used to illustrate relations among species, successional status, and foliar nutrient concentrations. Ward's method of partitioning groups into clusters and determining the distances between two individuals or clusters was used. The method finds the set of clusters such that the within-cluster sum of squares for each variable is minimized. The distance is determined as the sum of squares between the two individuals, added up over all the variables (SAS Institute Inc 1985). The method gave identical results to those obtained with an average linkage method.

The classification grouped species with low overall concentrations together, including Ehrharta ramosa (Fig 6.7). E ramosa is a pioneer grass with low foliar nutrient concentrations similar to those of a climax species. Elegia juncea had high concentrations of potassium and sodium, and in this respect resembled Ursinia crithmoides, a pioneer species. The pioneer species were a diverse group in terms of tissue nutrient status. Othonna quinquedentata was uniquely distinguished by generally high concentrations of nutrients, but by very high concentrations of bases other than sodium (Table 6.6). Aspalathus globosa and Hypocalyptus oxalidifolius, being legumes, were

distinguished by high nitrogen concentrations. H. crithmoides has high concentrations of nutrients overall, but was distinguished by high sodium.

Table 6.7. Correlation matrix for mineral nutrient concentrations in foliage of plant species sampled at Jakkalsrivier. See Table 9.5 for details. Values of α given in brackets.

Nitrogen					
0,757 (0,018)	Phosphorus				
0,246 (0,523)	0,263 (0,494)	Potassium			
0,117 (0,765)	0,381 (0,311)	0,699 (0,036)	Calcium		
0,174 (0,654)	0,473 (0,199)	0,830 (0,006)	0,953 (0,0001)	Magnesium	
-0,063 (0,873)	-0,494 (0,176)	0,494 (0,177)	0,001 (0,998)	0,039 (0,920)	Sodium

Table 6.8. Eigenvectors of the first three components of the nutrient concentrations in pioneer and climax plant species at Jakkalsrivier.

Nutrients	Coefficients for component		
	1	2	3
Nitrogen	0,272	-0,427	0,651
Phosphorus	0,377	-0,545	0,096
Potassium	0,482	0,337	0,197
Calcium	0,505	0,138	-0,361
Magnesium	0,543	0,134	-0,262
Sodium	0,028	0,608	0,574

Table 6.9. Ranks of pioneer (P) and climax (C) species by the first principal component of the foliage nutrient concentrations.

Species	Principal component		
	1	2	3
Tetraria bromoides (C)	-1,69	-1,311	-0,717
Ehrharta ramosa (P)	-1,21	-0,443	-0,374
Erica sessiliflora (C)	-0,993	-0,573	-0,723
Elegia juncea (C)	-0,851	1,96	0,953
Leucadendron xanthoconus (C)	-0,742	-0,042	-1,20
Aspalathus globosa (P)	-0,144	-0,890	1,09
Ursinia crithmoides (P)	0,127	1,72	0,965
Hypocalyptus oxalidifolius (P)	1,62	-2,28	1,083
Othonna quinquedentata (P)	3,88	0,866	-1,08
Proportion of variability accounted for by component.	0,51	0,30	0,17

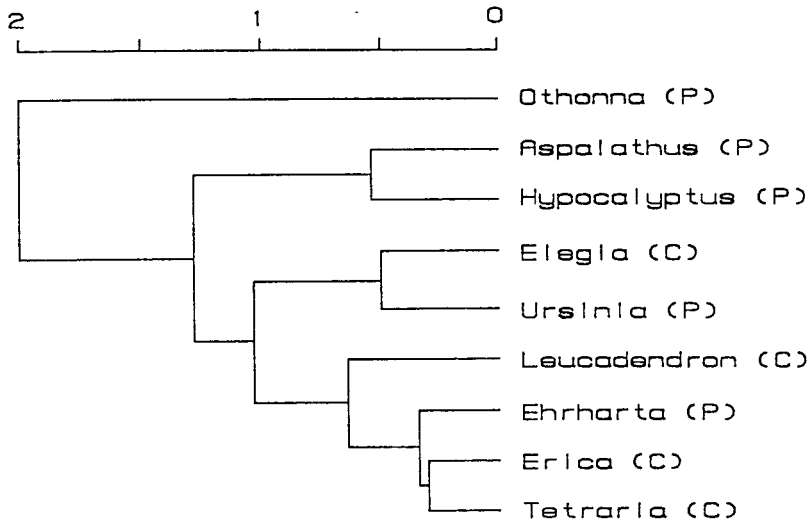


Figure 6.7. Dendrogram to depict cluster analysis of pioneer (P) and climax (C) plant species at Jakkalsrivier on the basis of their foliar nutrient concentrations. The classification was obtained by means of Ward's minimum variance hierarchical cluster analysis. Units on the axis are distances between centroids of groups. See text for explanation.

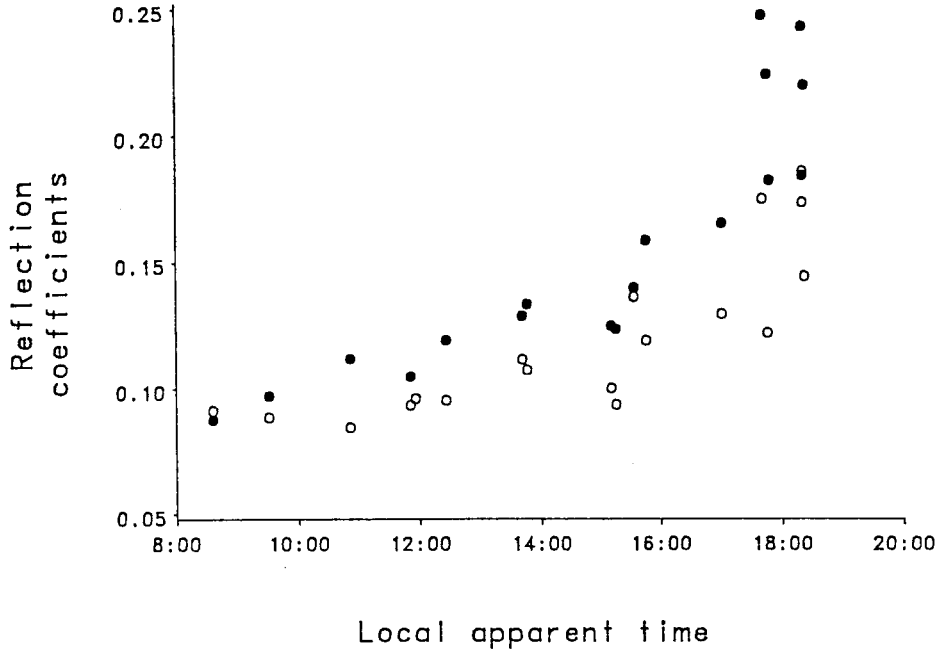


Figure 6.8. Diurnal courses of reflected radiation on the burnt (dots) and unburnt (circles) sites at Jakkalsrivier on 14 and 15 March 1982.

6.3.3. Microclimate

3.3.1. Radiant energy Records of radiant energy, mostly incomplete, were obtained on 4-6 November 1981, 26-27 January 1982 and March 1982. The data obtained are summarised in Table 6.10.

Records are average hourly or half-hourly values for cloudless or nearly cloudless days only and the data serve for comparisons between burnt and unburnt vegetation on an instantaneous or a daily basis, rather than to characterise the radiation climate of the site. The highest hourly average solar irradiance value recorded was 1,148 $W.m^{-2}$ on 6 November 1981, corresponding to a daily total of about 30,5 MJ (from Monteith 1973). This is the expected maximum for a clear day at this latitude. Instantaneous maxima recorded in January and March were 1,103 $W.m^{-2}$ and 1,024 $W.m^{-2}$ respectively. Integrated 24-hour values for insolation are given in Table 6.10.

Comparative measurements of net radiation were not obtained in November 1981. Net radiation on the unburnt site was 65% on 26-27 January and 57% of total solar irradiance on 14-15 March 1982. Net radiation on the burnt site tended to be consistently lower but though the difference in net radiation over 24 hours was relatively large on 26-27 January, it was small on 15 March, very likely because the difference decreased with cloudiness during the March days, whereas the January days were nearly clear.

Table 6.10. Daily radiation data for the intensive site at Jakkalsrivier (values in MJ). Reflected radiation corrected for slope.

	Total solar irradiance	Net irradiance		Reflected radiation	
		Unburnt	Burnt	Unburnt	Burnt
November 1981	29,55	-	-	-	-
26-27 January 1982	31,30	20,18	18,68	-	3,48
14 March 1982	20,92	-	-	-	2,38
15 March 1982	20,18	-	-	1,85	-
14-15 March 1982	20,25	11,46	11,28	-	-

Because sufficient sensors were not available, no simultaneous continuous measurements of the reflection coefficients of burnt and unburnt vegetation were possible during the early part of the study. The reflection coefficients in the visible spectrum were consistently lower on the unburnt than the burnt site (e.g. Fig. 6.8). During the morning the reflection coefficient of the unburnt vegetation varied between about 7,0% and 9,5%, the variation being due at least partly to the angle of the sun and the degree of cloudiness. On 15 March, for example, the integrated reflection coefficient for 07h00-16h30 was 9,2%. At solar noon, it was around 9,7%. There reflection coefficients are low for sclerophyllous shrublands, which may reflect on average as much as 21% (Monteith 1973). Morris (1981) recorded a reflection coefficients of 8-13% for fynbos, which are of the same order as the value for Jakkalsrivier. This has been corroborated by Johnston (1983).

On the burnt site, on a cloudless day, the reflection coefficient (corrected for the slope of the site) increased in the morning from 7,9% at 08h00 to 10,7% at 13h00, and then to 15,2% at 17h00; the coefficient at solar noon was around 11,2% and for the day, 11,4%.

Spot measurement on 4-6 November 1981, between about 08h00 and 17h00, gave reflection coefficients that averaged 10,1% and 12,5% respectively for unburnt and burnt vegetation. Coefficients increased strongly after 17h00, to 25%, and with these values averages are 11,6% and 15,5% respectively. Present data indicate therefore that the reflection coefficient for the unburnt vegetation is about 10% as opposed to 12% for the burnt site. This difference would be owing to the trapping of reflected radiation within the canopy of the unburnt vegetation (Monteith 1973). The data therefore show important differences in the radiation climates of the burnt and unburnt sites, as may be expected. However, the change in reflection coefficient was relatively small. Johnston (1983) recorded increases in reflection coefficients from about 10-15% before burning to about 23-26% after burning. This contrast is most likely owing to the fact that the Jakkalsrivier soils are relatively dark, especially compared to the coastal fynbos sites where Johnston made his study.

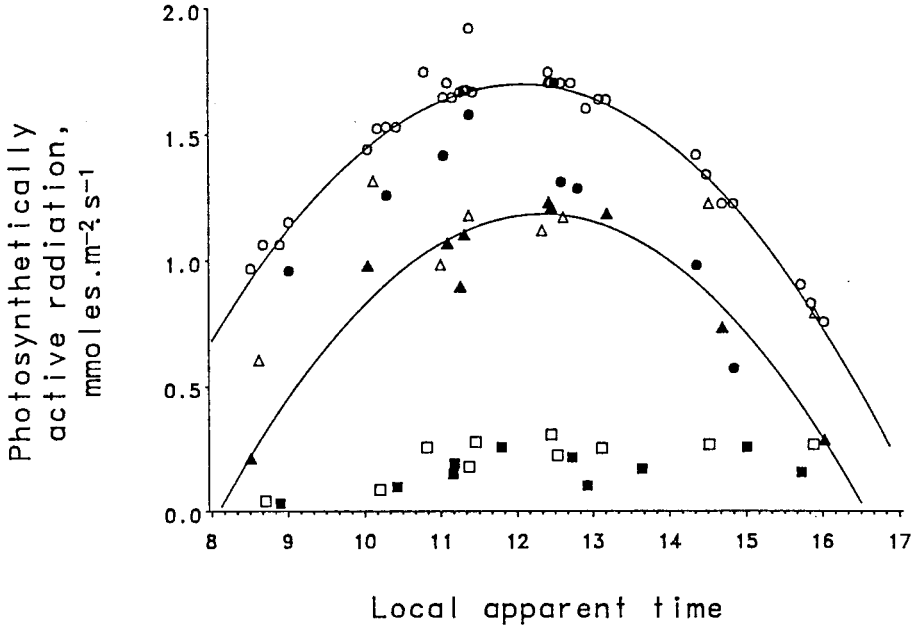


Figure 6.9. Diurnal course of photosynthetically active radiation measured under different canopies at Jakkalsrivier on 13-15 March 1982. Circles signify full-sun values, dots, values under unburnt Leucadendron canopy, filled squares, at 100 mm under unburnt vegetation, triangles, filled triangles and squares indicate values at 100 mm at plots 1-3 respectively on the burnt site.

6.3.3.2. Light under the canopy The results of the measurements of photosynthetically active radiation (PAR) under different canopies are shown on Fig. 6.9. The tall but sparse Leucadendron canopy reduces PAR by only about 25%, but an average of 15% of PAR reaches the 100 mm level beneath the understorey. In adjacent burnt vegetation, 60% of PAR was measured at 100 mm. In the sparse vegetation at plot 3 nearly 80% of PAR was measured at 100mm. By contrast, at the phreatic site (plot 1g-2) only about 12% penetrated, reflecting the very rapid regeneration of herbaceous vegetation there after fire.

Because of sunflecking, light is much more variable under the unburnt than the burnt canopies. Coefficients of variation for samples of 10 spot measurements on the racks in the unburnt vegetation at 100 mm averaged 53,3%, as contrasted with 28,1% on the adjacent burnt site. Under the unburnt canopy, some spots would receive 30 to 80% of full

sunlight at the same time that others received only 1-2%. Variation decreased with increasing solar elevation.

Under unburnt vegetation, PAR barely exceeds 300 $\mu mol.m^{-2}.s^{-1}$ and is usually much less. These light levels are too low to sustain net photosynthesis in most sclerophyllous plants (Oechel and Lawrence 1979). Thus, light is probably implicated in processes governing regeneration in fynbos. Furthermore, the rapid development of a dense cover on the phreatic site suggests that light extinction here can play a role in successional processes, which is not evident for less vigorous fynbos.

6.3.3.3. Wind Wind data for the intensive study site are summarised in Table 6.11. Wind-speeds are greatly reduced near the ground. Speeds at 1,5 m were reduced by 11-15% in the burnt vegetation and 29-36% in the unburnt. Near the ground in burnt vegetation there was considerable further reduction (55-60% less), but the canopy was still well ventilated, with average wind velocity of 0,6 to 1,5 $m.s^{-1}$. In unburnt vegetation, however, the layers near the ground were poorly ventilated (74-75% reduction, 0,03 to 0,93 $m.s^{-1}$). In both cases, wind speed at 0,3 m was linearly related to that at 1,5 m (r^2 = 0,98 and 0,91 for the burnt and unburnt sites, respectively) but wind-speeds at 0,3 m on the burnt site were about 40% of speeds at 1,5 m, while on the unburnt site speeds were about 25% of those at 1,5 m. In unburnt vegetation wind-speeds at 0,3 m ranged from 5 to 60% of those at the same height in the burnt vegetation.

Table 6.11. Mean wind speeds at different levels on burnt and unburnt sites at Jakkalsrivier. Units are $m.s^{-1}$.

		Burnt		Unburnt	
	3,0 m	1,5 m	0,3 m	1,5 m	0,3 m
2-3 November 1981	-	1,63	0,62	1,26	0,03
26 January 1982	3,72	3,16	1,50	2,45	0,93
14-15 March 1982	3,31	3,00	1,48	2,36	0,79

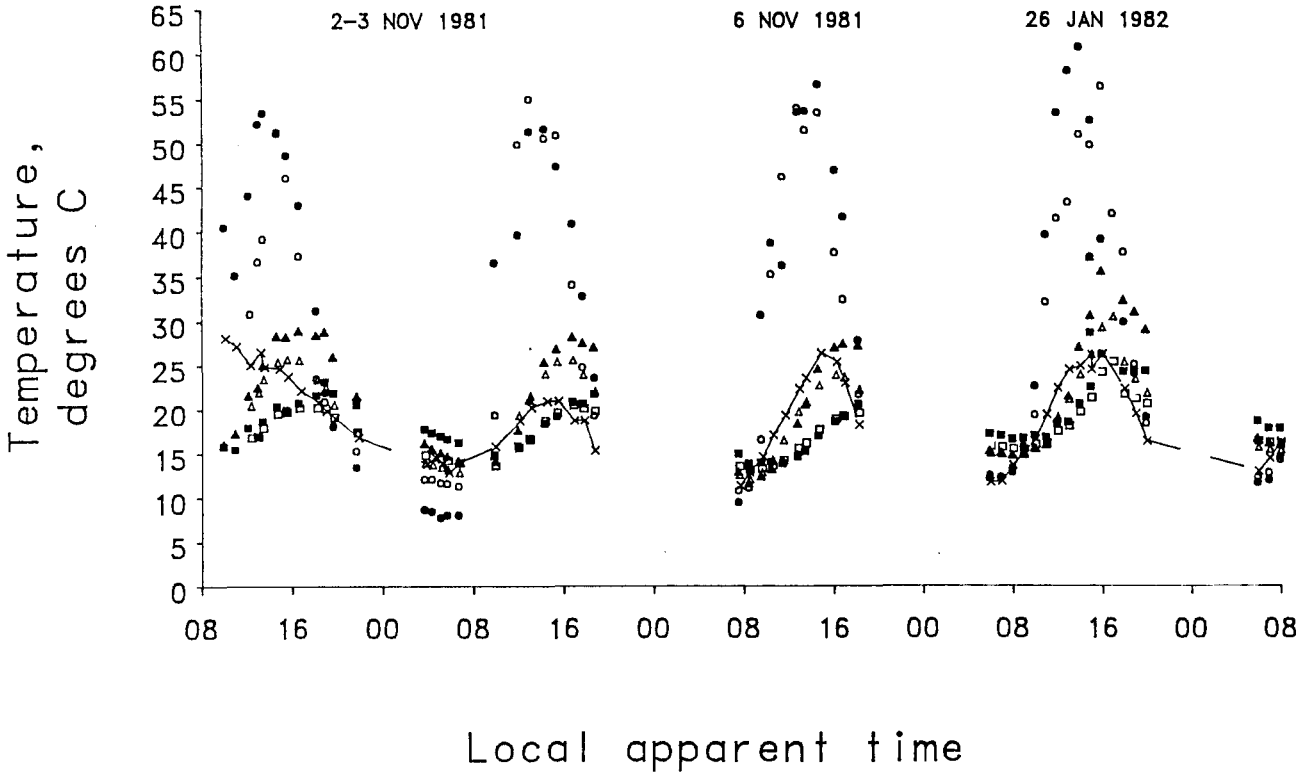


Figure 6.10. Diurnal variation in soil and near-surface temperatures during three periods of observation at Jakkalsrivier. The symbols signify the following: dots, soil surface temperatures on the burnt site; circles, soil surface temperatures on the unburnt site; filled and open triangles, temperatures at 50 mm below soil surface on the burnt and unburnt sites respectively; filled and unfilled squares, temperatures at 150 mm below the soil surface on the burnt and unburnt sites respectively; crosses represent air temperatures at 2,0 m on the burnt site; these points are joined by lines to show the diurnal change in ambient air temperatures.

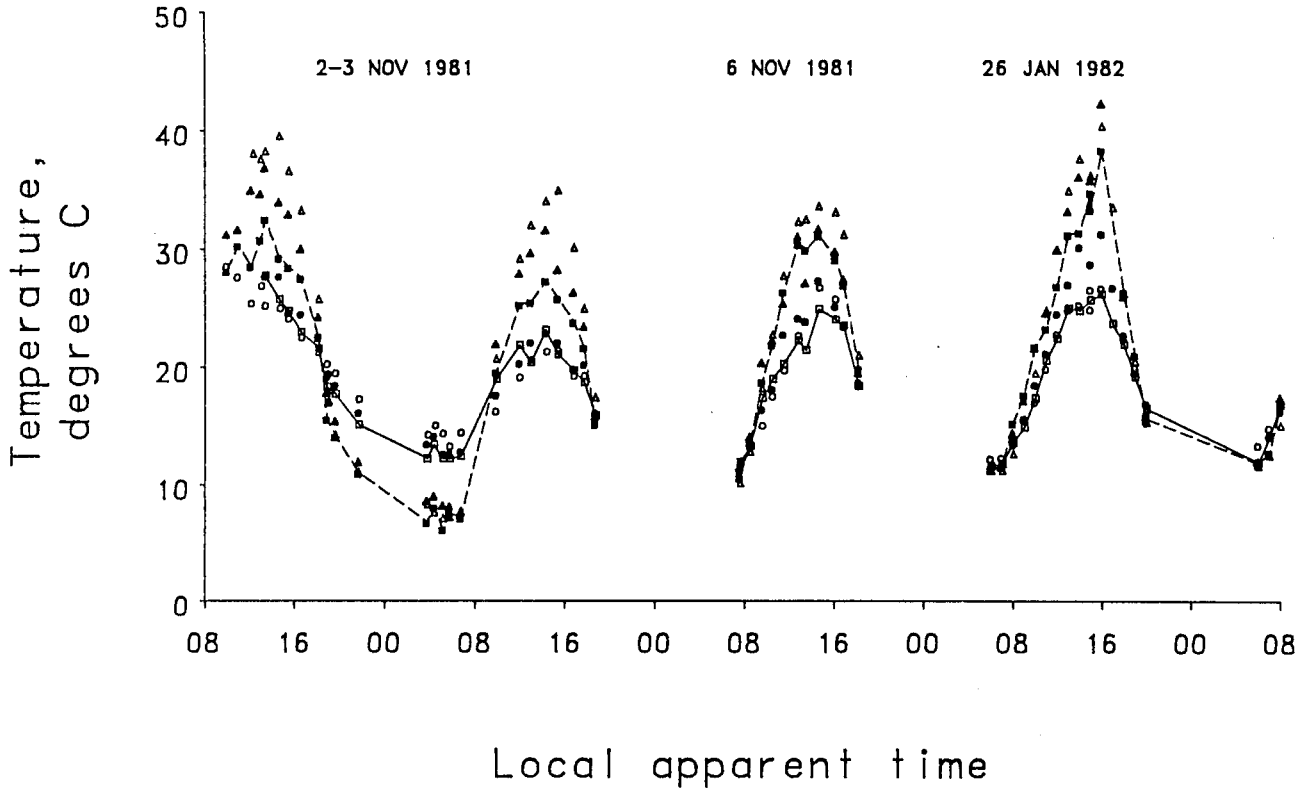


Figure 6.11. Diurnal variation in leaf and air temperatures during three periods of observation at Jakkalsrivier. Open triangles are temperatures measured at 150 mm above the ground on the unburnt site; filled triangles, temperatures at 150 mm above ground on the burnt site; filled squares, temperatures of Leucadendron xanthoconus leaves at 150 mm on the burnt site; open squares, leaf temperatures at 1,2 m for L. xanthoconus on the unburnt site; circles, air temperatures at 2,0 m on the burnt site; and dots, air temperatures at 1,2 m on the unburnt site.

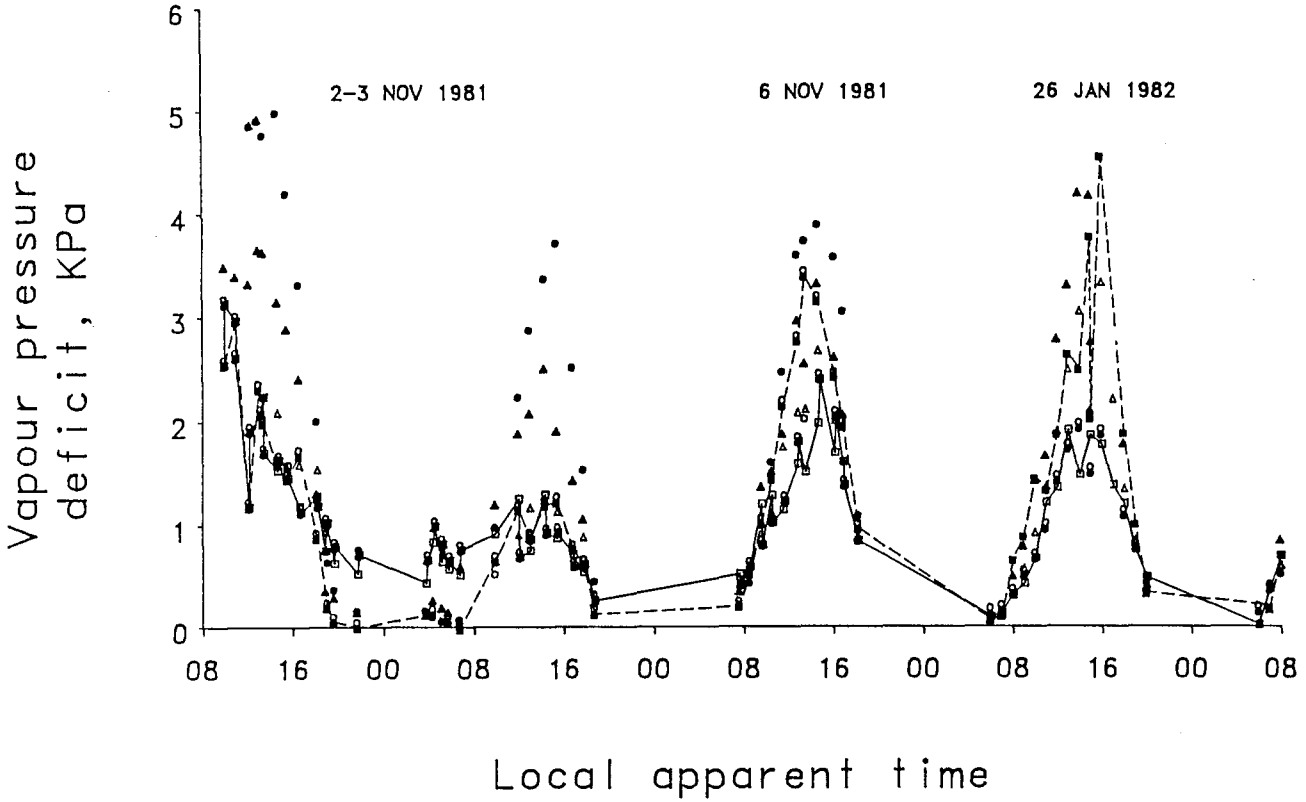


Figure 6.12. Diurnal variation in saturation vapour pressure deficits at different levels in the canopy at Jakkalsrivier. Dots are values for 150 mm on the unburnt site and filled triangles, those for 150 mm on the burnt site. Circles are vapour pressure deficits at 2,0 m on the unburnt site, filled squares, connected by dashed lines, are values for leaf-to-air vapour pressure deficits at 150 mm on the burnt site, and open squares, leaf-to-air deficits at 1,2 m on the unburnt site.

6.3.3.4. Temperatures and water vapour Daily courses of leaf, air and soil temperatures are illustrated for 2, 3 and 6 November 1981 and 26 January 1982 in Figs. 6.10 and 6.11. The water vapour status of the air at different levels is illustrated by the daily course in saturation deficits at different levels in Fig. 6.12.

In January, soil surface temperatures on the burnt site exceeded 60°C around solar noon, and were over 50° for several hours on every day of record (Fig. 6.10). At 50 mm below the surface, temperatures exceeded 25°C for 5-8 hours in the day, cooling only after nightfall. In January, the temperature of this level reached around 35°C. Surprisingly, temperatures around noon at the surface on the unburnt site, though mostly lower and usually erratic, were often nearly the same as on the burnt site. At -50 mm, however, day temperatures were consistently lower than on the burnt site with 6°C difference in the maximum in January.

The relationships in surface temperatures and those at 50 mm below the surface were reversed at night. At 150 mm below the surface, however, temperatures on the burnt site were higher than on the unburnt site both during the day and at night.

Temperatures and water contents in the free air at 2,0 m were effectively the same as those at 1,2 m in the sparse canopy of mature Leucadendron xanthoconus, except that vapour pressure deficits were marginally less in the former. On 26 January 1982, air temperatures in the mature canopy exceeded 30°C briefly, and vapour pressure deficits increased to 2-3 kPa. Leaf temperatures at 1,2 m tracked ambient air temperatures very closely. By contrast, the foliage of Leucadendron seedlings at about 150 mm on the burnt site was subject to a relatively extreme environment. Here, air temperatures often exceeded 30°C and on 26 January briefly exceeded 40°C. Leaf temperatures during the day were, however, consistently 2-6°C lower than air temperature. Thus in November leaf temperatures exceeded 25°C between about noon and 17h00 but were usually at less than 30°C. On the January day, leaf temperatures exceeded 30°C. Because of the high temperatures, vapour pressure deficits were considerably greater at seedling level on the burnt site than in the

mature canopy. However, the marked cooling of the leaves of the seedlings reduced the leaf-to-air vapour pressure deficits and in this respect the contrasts between mature canopies and regenerating canopies were much less marked (Fig. 6.12). Despite this, the leaf-to-air vapour presure deficits on the burnt site did tend to exceed 3,0 KPa around midday, and this was likely to have caused stomatal closure through longer periods of the day than would have been the case in adult plants (cf. Tenhunen et al. 1982). Possible relative effects of this kind on transpiration and carbon assimilation do not appear to have affected survival and growth of seedlings, as discussed later in Chapter 7.

The microclimate at 150 mm on the unburnt site had the most severe temperature regime, air temperatures in the day being consistently 2-6^{o}C higher than at the same level on the burnt site, with vapour pressure deficits correspondingly greater. This would probably be due to the poor ventilation in mature vegetation and the trapping of radiant energy in the canopy.

Patterns of soil temperatures for November and January were also similar. Although average soil surface temperatures were higher during the day on the burnt than on the unburnt sites, extremes were similar. This reflected the variations in surface temperatures as shading of the thermocouple site under the canopy varied through the day. Conduction of heat in soil is strongly affected by contents of water and organic matter, decreasing as these increase (Monteith 1973). At the time of measurement, the soils at the two sites had similar moisture contents (Fig. 6.2). The burnt site had more than twice the organic matter content in the A horizon than the unburnt (4,9% vs 1,8%) and this would tend to slow heat penetration because of the relatively high specific heat of organic matter. The higher night time temperatures at -150 mm on the burnt site, compared with the unburnt, indicate nevertheless that despite somewhat lower net radiation, the absence of a dense canopy had allowed greater soil heating.

6.3.4. Effects of shading on growth in Leucadendron xanthoconus

6.3.4.1. Germination Shading had no substantial effect on germination, though shading appeared to delay germination slightly. Eighty-nine to 94 per cent or more of all seeds had germinated after 150 days. In the controls and the trays with 30% shading, 70 and 69% of seeds germinated after 45 days, respectively. In the 60 and 90% shade treatments, 54 and 59% had germinated by this stage.

6.3.4.2. Growth Relative growth-rates during the 52-day period ending 7 January 1984 ranged from 15,6 $mg.g^{-1}.d^{-1}$ in the most heavily shaded plants, to 19,2 and 20,9 $mg.g^{-1}.d^{-1}$ in the 60% shaded plants and the controls, to 32,0 $mg.g^{-1}.d^{-1}$ in the plants with 70% sunlight. During the subsequent 98 days the rates were 6,67 for the controls and for the plants in 90% shade, and 13,6 and 14,5 for plants in 30% and 60% shade. During the 57 days ending 11 June 1985 the 90% shaded plants grew at 1,64 $mg.g^{-1}.d^{-1}$, the 60% shaded plants at 5,0 $mg.g^{-1}.d^{-1}$, the controls at 11,9 $mg.d^{-1}.d^{-1}$, and the 30% shaded plants at 12,5 $mg.g^{-1}.d^{-1}$.

Results are summarised in Table 6.12. At the major harvest on 15 April 1985, total plant masses were quadratically related to shading, the largest plants (7,1 g) being those being 30% shaded and the smallest, 0,506 g, being the most heavily shaded. The intermediate plants were about half the size of the largest (Table 6.13). Despite the small sample sizes, differences in size were statistically significant from the first harvest onward, although fully lit plants were initially the largest. The final order of plant size was maintained from the second harvest onward.

At this stage, plant heights were also quadratically related to shading, but the tallest plants were those in 60% shade and the shortest, those fully lit. Plants with 30% shade grew proportionately more in mass than in height, compared with controls (2,30 times and 1,82 times, respectively). In 60% shade, plants grew disproportionately in height, i.e. 2,28 times the controls, as opposed to 1,15 times in mass. The effect was even more marked, obviously, in

plants in 90% shade. Plants subjected to the latter two treatments were markedly etiolated.

6.3.4.3. Carbon allocation Root:shoot ratios were significantly affected by shading but the relationship between shading and growth of roots was complex. The highest ratio was found in plants with 60% shading, and the lowest in those with 90% shading. However, the ratios in the plants receiving 30% and 60% shade did not differ significantly from those in the controls. The ratio of total foliage mass to plant mass was also significantly affected, with the two heaviest shading treatments having significantly lower ratios than the others, but with no significant differences otherwise.

Root mass was quadratically related to shading, the highest root mass being found in plants with 30% shading. The most heavily shaded plants did not develop any roots coarser than 2 mm. Otherwise, the amount of roots in the different categories was also quadratically related to shading. Proteoid roots formed the greatest fraction of total root mass in the shaded treatments, with 60% shading inducing by far the greatest proportional development of proteoid roots.

Foilage area was greatest in plants with 30% shading (246% of those in full sun), next in 60% shading (166%), and least in 90% shading (34%). Thus would indicate extreme intolerance of shade (cf. Grime 1979, fig 6).

The proportion of fine roots to foliage mass was greatest in plants with full sunlight, and did not differ significantly among the other three treatments. However, the ratio of total absorbing roots (fine plus proteoid roots) to foliage was quadratically related to shading and significantly the greatest in the 60% shading. But the etiolated plants did not differ significantly in this respect, nor did the fully lit differ from the 30% shading. In the latter cases, the differences in fine root to foliage ratios were compensated for by differences in proteoid root biomass. This was even more apparent for the ratio of the mass of absorbing roots to leaf area, which was significantly reduced only in the heaviest shade.

6.3.4.5. Leaf conductances to water vapour The measurements in June

Table 6.12. Summary of the results of the trial to test the effect of shading on growth in Leucadendron xanthoconus. Mean values for plants harvested on 15 April 1985, 284 days after treatment began. Analyses of variance showed significant differences among treatments in all cases. The Tukey-Kramer test was used for multiple comparisons, because data were unbalanced. Arcsine transformations were used for fractions, and total plant masses were normalized by log transformations. Superscripts indicate which pairwise comparisons were statistically significantly different at P = 0,05, and which not.

	Unshaded	Shaded		
		30%	60%	90%
Height, mm.	$145,8^{c}$	$265,0^{b}$	$333,2^{a}$	$266,1^{b}$
Total mass, g	$3,09^{b}$	$7,10^{a}$	$3,57^{b}$	$0,506^{c}$
Foliage mass, g	$1,29^{b}$	$2,84^{a}$	$1,16^{b}$	$0,158^{c}$
Total root mass, g	$1,55^{b}$	$3,48^{a}$	$1,899^{b}$	$0,204^{c}$
Coarse roots	$1,88^{b}$	$0,330^{a}$	$0,147^{b}$	$0,000^{c}$
Fine roots (< 2 mm)	$0,972^{b}$	$1,41^{a}$	$0,458^{c}$	$0,0656^{d}$
Proteoid roots	$0,390^{b}$	$1,73^{a}$	$1,29^{a}$	$0,139^{b}$
Root fraction	$0,502^{ab}$	$0,489^{ab}$	$0,532^{a}$	$0,404^{b}$
Foliage fraction	$0,418^{a}$	$0,414^{a}$	$0,324^{b}$	$0,312^{b}$
Stem fraction	$0,081^{b}$	$0,109^{b}$	$0,139^{b}$	$0,261^{b}$
Specific leaf area, $g.m^{-2}$	$130,3^{a}$	$116,8^{a}$	$70,6^{b}$	$47,0^{b}$
Leaf area ratio, $g.m.^{-2}$	$310,0^{a}$	$288,7^{a}$	$221,3^{b}$	$152,7^{c}$
Fine root: foliage	$0,754^{a}$	$0,497^{b}$	$0,396^{b}$	$0,415^{b}$
Absorbing root: foliage	$1,06^{b}$	$1,11^{b}$	$1,51^{a}$	$1,30^{a}$
Absorbing root mass:				
foliage area, $g.m^{-2}$	$131,5^{a}$	$128,3^{a}$	$112,5^{a}$	$64,8^{b}$
n	6	9	11	9

showed that the shading treatments had substantial effects on vapour pressure deficits within the enclosures, mainly because air temperatures were highest in the heaviest shade and lowest in the open. The correlation between vapour pressure deficits and solar radiation levels measured under the screens had a coefficient of -0,624 (P = 0,0097). Average vapour pressure deficits ranged from 1,22 kPa in the treatment with heaviest shade to 0,950 kPa in the control. This effect was most likely due to the poor ventilation of the shaded stands, and was apparently analogous to the effect on microclimate of the canopy of mature vegetation in the field.

Leaf stomatal conductance was linearly related to vapour pressure deficit, with r^2 = 0,416, b_o = 13,9, b_1 = -0,78, F = 9,96, and P = 0,007. Thus, the plants in the heaviest shade had lowest conductances, averaging 2,24 $mm.s^{-1}$, and those in the open, the highest, 6,68 $mm.s^{-1}$. However, there was little or no difference between conductances observed in plants in the two lighter degrees of shading (6,9 and 4,8 $mm.s^{-1}$ for 40% and 30% respectively) and the controls. Light and humidity were thus confounded in this experiment. But there was no evidence that the shaded plants gained from a more favourable moisture regime relative to those fully lit; the reverse was rather the case.

6.4. Discussion and conclusions

The effects of fire on the physical environment of plants depend on the structure of the prefire canopy, especially its stature and density, on the immediate impact of the fire, especially the proportion of vegetation combusted, and on the subsequent rate of recovery of the vegetation, other factors being equal.

The effect of changes in the vegetation canopy on microclimate and water balance are complex. Effects on the energy balance of the site arise from changes in the amount of solar and far infrared radiation absorbed by the canopy and the amounts lost from it by radiation in the far infrared, by convection and by evaporation. In general, the amount of incoming solar energy intercepted by the canopy is

exponentially related to leaf-area index (Monteith 1973; Roberts and Miller 1977). Interception is also affected by the inclination of stems and foliage, this relationship varying with the altitude and azimuth of the sun. Empirically, Miller (1983) found that an extinction coefficient of 0,7 adequately described interception of solar irradiance by vegetation canopies. Data in Grace and Marks (1978), for laboratory experiments on light interception by Calluna vulgaris, are fitted well with negative exponential curves with extinction coefficients of 0,60-0,70. Assuming a coefficient of 0,70 to hold for fynbos, we calculate a leaf area index of 2,7 $m^2.m^{-2}$ for the unburnt vegetation at Jakkalsrivier, with an overstorey index of 0,4. At 12 months after burning, the estimated leaf area indices at sites 1, 2 and 3 were 0,7, 0,3 and 3,0 respectively. These are close to the values estimated from point-quadrat data (Chapter 5).

The elimination of the vegetation canopy by fire (though short-lived on the phreatic site) is accompanied by certain changes in the micro-environment. The higher reflection coefficients on the burnt site result in a lower net radiation but because the vegetation cover is low most of the energy that is absorbed enters the soil and must be dissipated by downward conduction, convection, and upward long-wave radiation. While the surface soil layer of 250-300 mm has sufficient moisture for evaporation, latent heat will also be lost. A net heating of the soil is evident in the higher temperatures observed on the burnt site at 150 mm below the surface, but most heat is lost through radiation, as evident in warmer surface temperatures than those on the unburnt site during the day, but cooler temperatures at night. Because wind-speeds near the ground on the burnt site were relatively high there is good cooling by forced convection and hence the relatively low air temperatures at 150 mm, roughly the height of Leucadendron xanthoconus seedling foliage. By contrast, the weak ventilation in the unburnt vegetation results in higher air temperatures at 150 mm.

The markedly higher surface soil moisture contents on the burnt site at the start of the study indicate lower actual evaporation rates; redevelopment of the canopy during the first spring appeared, however,

to reduce the surplus by the first summer (Fig. 6.2). Significantly higher moisture contents in the next winter suggest low potential evaporation rates together with low interception losses from the canopy. Moisture contents in summer are the same on the burnt as on the unburnt site; soil water potentials on the burnt site are therefore lower (because of the clay soils), suggesting higher evaporation rates, especially from soil.

Table 6.13. Mean leaf widths and orientations from random samples of 25 from seedling and adult female Leucadendron xanthoconus at Jakkalsrivier. Standard deviations given in brackets.

	Leaf width mm	Leaf zenith angles, degrees	Leaf azimuth (from N), degrees
Seedlings	3,08 (0,63)	37,1 (11,8)	200,4 (97,2)
Adult females	3,47 (0,59)	39,1 (19,1)	170,5 (107,6)
t-values	0,467	0,454	1,48

Leucadendron species are sometimes dimorphic, with seedlings having narrower foliage, or foliage differently orientated than in adults (Williams 1972), suggesting an "uncoupling" of juvenile and mature life strategies Grime(1979), so that, in this case, juvenile plants may be adapted to the rigours of the burnt site. A random sample of L. xanthoconus at Jakkalsrivier, however, showed no significant difference between seedlings and adult female plants with regard to leaf orientation (zenith angle and azimuth) and width (Table 6.13). In Elegia juncea, juvenile shoots tend to be somewhat sinuous, as opposed to the nearly straight mature shoots. Otherwise, morphology of E. juncea and Penaea mucronata regenerating on the unburnt site was identical to that of adult plants, except of course for height. These species and Erica spp. tend to have rather narrow or small leaves or equivalent organs, inclined toward vertical.

These factors contribute to a low radiation load and rapid convectional cooling (Gates 1980) and this together with relatively high wind-speeds ensured that seedling leaves seldom exceeded daytime ambient air temperatures and were usually substantially cooler. Another important factor lies in the relatively dark soils at Jakkalsrivier, resulting in rather low reflection coefficients and hence low back-radiation onto seedlings.

Around noon on the clear days selected for study, leaf temperatures of Leucadendron xanthoconus seedlings exceeded those of adult plants by 5-12^{o}C. Seedling leaf temperatures exceeded 30^{o}C during several hours in the day and approaching 40^{o}C briefly on the January day. Though the rate of maintenance respiration increases rapidly with increasing tissue temperature (Jones 1983), rate of net photosynthesis in Proteaceae as in other evergreen sclerophylls of mediterranean-type ecosystems are not markedly sensitive to leaf temperature in the range 10-30^{o}C (Mooney 1983; Mooney et al. 1983). These relatively high leaf temperatures are not expected to have a marked effect on net photosynthesis, which in any event would be moderated by stomatal response to vapour pressure deficit and light levels. Transpiration rate is proportional to leaf temperature (Monteith 1973; Jones 1983). Higher leaf temperatures increase the leaf-to-air vapour pressure deficit and hence the potential rate of transpiration which could lead to greater desiccation. However, the observations show marked relative cooling of seedling leaves by convection. This tends to negate the high vapour pressure deficits arising from high ambient air temperatures near the ground. Nevertheless, the conditions in the canopy of regenerating vegetation may cause high transpiration rates while stomata are open. However, the hypothetical tendency for excessive transpiration in Leucadendron seedlings may be negated by the tendency for stomata to close as vapour-pressure deficits increase (e.g. Tenhunen et al. 1982; Jones 1983).

Wind-speeds near the ground on the unburnt site were much reduced by friction and drag despite the low, open vegetation. Maximum speeds were below the threshold for direct mechanical damage to plants (Grace 1977) or for the saltation of sand grains (about 5 m.s^{-1}; Bagnold

1941) and neither form of damage was evident in the organs of regenerating plants. Drag coefficients of the plants at Jakkalsrivier are low anyway, because of narrow, near-vertical leaves or shoots and a tendency among many species of streamlining when canopies flex and foliage deflects to present a smoother profile to the wind.

The relatively high moisture contents and high water potentials in the surface soils during the study reflected the frequent rains and, apparently, low potential evapotranspiration at the site. Rainfall during 1981/82 amounted to some 920 mm, which is close to the annual average, but in 1982/83, it was about 690 mm, much lower than the annual average. Vapour pressure deficits, as estimated from humidity records in the Stevenson screen, were apparently higher on average in 1982/83 than in 1981/82 (1,22 kPa vs 1,17 kPa), but average plant water status did not differ.

Xylem pressure potentials in all plants were relatively high (less negative) in summer. In shrubs of the California chaparral and Chilean matorral, for example, lowest potentials range among species from -6,5 MPa or less to about -2 MPa, the variation correlating with species-specific maximum leaf conductances (negatively) and rooting depth (positively). Pre-dawn water potentials in shrubs from these areas fall to about -6 MPa or less in summer although the few deep-rooted species are more stable, with minimum pre-dawn potentials around -1,5 MPa (Chapter 2; Poole et al. 1981). Much lower ψ is found also in Australian heath shrubs (Chapter 2). Such levels of water stress were not found in the Jakkalsrivier species, with the lowest pre-dawn and midday potentials of -1,45 and -2,40 MPa being found in Elegia. The potentials measured in shrubs at Jakkalsrivier were about the same in their relatively high values and weak seasonal fluctuation as those recorded for Protea spp by Miller et al. (1983) and Moll and Sommerville (1985), in much warmer and drier environments that at Jakkalsrivier, in some cases. However, Restionaceae studied by these authors and Ericaceae or other ericoid shrubs studied by Miller et al. (1983) exhibited much lower ψ than the equivalent forms investigated at Jakkalsrivier.

Regarding pyric succession, plant ψ indicates little substantial difference between regenerating and mature plants at Jakkalsrivier. This is in marked contrast with results for chaparral, where seedlings and sprouts may exhibit enhanced or reduced water stress, but seldom no difference (Chapter 2). Jeffrey et al. (1987) have made rather similar studies on fynbos species at Kirstenbosch. There, they found no differences in the diurnal course of xylem pressure potentials in Diospyros glabra, a sprouter, and Pelargonium cucullatum, a seeder. Midday ψ Widdringtonia cupressoides, a sprouter, were, however, -0,6MPa on the unburnt sites and -1,2 on the burnt, and about the same contrast was found for Podalyria calyptrata. They suggested that the greater depression in midday ψ in P calyptrata was due to the higher transpiration rates and lower osmotic potentials observed in the older plants, implying that where differences in water relations were found that these were owing to juvenile-mature differences in plant physiology, rather than habitat contrast.

Water status as reflected by xylem pressure potential in plants of different species and habitats depends on the balance between uptake of water and loss through transpiration, which in turn is a complex function of soil moisture availability, plant form and physiology, and potential evapotranspiration rates. The persistently moist soils at Jakkalsrivier allowed plants to equilibrate at high xylem pressure potentials at night, irrespective of the season. Conditions of light, temperature, and humidity on the burnt site would be conducive to high transpiration rates, but these could be negated by stomatal control. Low annual ranges in ψ, despite the high evaporative demand, suggest that stomatal control was effective. Higher windspeeds at the top of the canopy in the unburnt vegetation would be conducive to higher transpiration rates, and this could reduce the relative effects of vapour pressure deficits on the burnt site. The effect of wind on transpiration depends in a complex way on available energy and stomatal resistance, so that wind may increase transpiration rates when stomatal resistance is low and available energy limited, but decrease it otherwise (Monteith 1973; Grace 1977). That the species included in this study may differ in their responses to environmental controls on transpiration is indicated by the relatively low midday

ψ recorded for Penaea mucronata, a sprouting shrub, and the stronger correlation between midday ψ and vapour pressure deficit in this species than the others, suggesting either shallower rooting, higher stomatal conductances, or weaker stomatal response to humidity. Thus, though the burnt and the unburnt habitats clearly had little effect on plant water status, it would be difficult to explain this without a detailed study of stomatal behaviour, at least.

Nutrient balance studies in fynbos ecosystems at the level of the catchment have shown a brief net export of nutrients during the first three months or so after fire (Van Wyk 1982). At Jakkalsrivier, ionic concentrations in streamwater in the first flood after an autumn fire increased in 1980 2,5-fold on average, compared with simultaneous values for the stream of an unburnt catchment. The anions SO_4^{2-}, HCO_3^{2-}, and Cl^- increased 4,7, 2,3 and 2,9 times respectively. Concentrations of cations K^+, Ca^{2+}, Mg^+ and Na^+ increased 3,8, 3,6, 3,1 and 2,0 times, respectively. In acid, peat-stained streams, where pH normally ranges between 3,2 and 4,0, acidity decreased by 1,5 to 2,0 pH units. In streams with a pH around 5,0, no response was observed. This is strong evidence for a short-lived but potentially important change in the nutrient status of the ecosystem which may not have been detected in my soil samples, first taken 18 months after the burn of March 1981.

At Pella, a lowland fynbos site 60 km north of Cape Town, Stock and Lewis (1986) and Brown and Mitchell (1985) have shown concentrations of available soil nitrogen as nitrate and ammonium and soil phosphorus, respectively, to increase for a few months or so after fire. These effects were most pronounced in the upper 100 mm and did not persist for more than six months.

The balance of evidence therefore is that the fire at Jakkalsrivier would have modified and enhanced the nutrient status of the soils there, by releasing elements such as potassium, calcium, magnesium and sodium, and by accelerating mineralisation of nitrogen. Levels of available phosphorus also have been enhanced by fire in other mediterranean shrublands (cf. Gray and Schlesinger 1981; Read et al.

1983; Rundel 1983). At Jakkalsrivier, however, statistically significant enhancement in soil concentrations was detected only for phosphorus. Though the soil samples detected no significant differences in concentrations of calcium and magnesium, there is tentative evidence that the climax plants studied here had increased foliar concentrations of these nutrients and this would find corroboration in Van Wyk's (1982) results; however, there is no such trend for nitrogen, phosphorus and potassium. Since the increased availability of nutrients in the soil is an ephemeral phenomenon, it could be that regenerating plants could have taken up available nutrients, but that foliar nutrients were diluted by enhanced growth. This would be in contrast with, say, Californian chaparral where regenerating plants respond to increased nutrient availabilities after fire by taking up nitrogen, phosphorus and other minerals to the point that tissue concentrations significantly exceed levels in plants on unburnt sites (Rundel and Parsons 1980). Also, foliar concentrations of mineral nutrients in many other plants vary according to the availability of nutrients in the soil (Van der Driessche 1974). But climax plants in fynbos, as in Australian heaths, have low rates of nutrient uptake and metabolism. Lewis and Stock (1978) and Stock and Lewis (1983) have shown for nitrogen in Leucadendron xanthoconus and other Proteaceae that the species lack the capacity to take up nutrients at higher than "normal" low rates, despite high concentrations in the medium to which they were exposed. Such plants, especially if regenerating from seed, may therefore not exploit the temporary flush of nutrients following fire (cf. Siddiqi et al. 1976b).

Comparisons among species in terms of their tissue nutrient concentrations must be made with caution. Species may differ in foliar concentrations expressed per unit dry mass but such comparisons neglect morphological and anatomical differences. The same species may not differ when compared in terms of concentrations expressed per unit leaf area (e.g. Mooney 1983). Nevertheless, the differences between pioneer and climax species at Jakkalsrivier are consistent and marked. Pate and Dell (1984) report similar patterns for similar categories in Western Australian kwongan (heathlands of the sandplains). The results suggest effective uptake of mineral

nutrients by the pioneer species, as opposed to climax species.

Little or no regeneration occurs under the canopy of mature fynbos at Jakkalsrivier (Chapter 4). This may be owing to predation on seed and seedlings by rodents and other consumers (e.g. Bond 1984) but the marked effects of the vegetation canopy on the microclimate including light at ground level may also be a factor. The shading experiment with Leucadendron xanthoconus indicated that germination its seed is not affected. Marked responses in the growth of seedlings were significant, with light shading such as that found in the canopy of regenerating vegetation enhancing the growth and robustness of the seedlings. Heavier shading caused etiolation and a disproportionate allocation of growth to stem and fine roots. It is improbable that seedlings growing under a mature canopy would survive intermittent summer droughts, especially since the poorly ventilated environment near the ground is marked by high air temperatures and pronounced vapour pressure deficits. Therefore, although light and other environmental factors were confounded in the nursery experiments, it is clear that the direct effects of changes in canopy structure on plant recruitment must play an important role in succession. This role may be proximal, causing the death of seedlings, or ultimate, selecting against the release of seed in the shaded environment or in favour of dormancy in released seed.

The hypotheses which relate improved availabilities of water and nutrients after fire to mechanisms of post-fire succession must be rejected for Jakkalsrivier, except in so far as pioneer species apparently rely on the nutrient flush, which evidently does occur, for completion of their life-cycles in the first 1-5 years after fire. There is no evidence for density-dependent mortality among obligate-seeding climax plants (Chapter 7). Limitation of light may play a major role in the successional process, by determining recruitment. In this connection it is important to note that sunny conditions were chosen for field studies of microclimate and plant water status at Jakkalsrivier. Day-to-day variation in soil moisture (in response to daily rain), temperature, and humidity at Jakkalsrivier is marked (Figs. 6.1-6.3). This variation would tend to

mask the effects of the vegetation canopy on temperature and humidity, as indicated by this study. But light conditions under the canopy or cloudy days would be even less favourable than shown by this study.

Jakkalsrivier represents a category of fynbos, the so-called "black-water" fynbos of the southern humid coastal mountains, which differs in many respects from the "white-water" fynbos of the west and interior (Kruger 1974; Miller 1982). Summer droughts are apparently infrequent at Jakkalsrivier, in contrast with more familiar mediterranean environments. Summer water stress, and the amelioration of it by burning, may be important in other fynbos habitats, however. The work of Miller et al. (1983) indicates that this may be so for shallow-rooted species only. On the other hand, summer drought in such environments may prove to have been the ultimate agent in selecting for drought-avoiding regeneration and other life-history traits in fynbos plants (Deall and Brown 1981; Bond 1984) and comparisons between regenerating plants on burnt sites with established plants or unburnt sites, as done in this study, will in that case reveal no difference. Similarly, if fynbos plants have evolved metabolisms adaptive in habitats with little available nutrients, a study of seedling nutrient concentrations will not show responses to post-fire nutrient flushes. Studies of the interactive influence of fire and the physical environment on plant form and growth will require a thorough understanding of the morphological and physiological traits of the species involved.

7. PLANT DEMOGRAPHY AT JAKKALSRIVIER

7.1. Introduction

The major process of succession in fynbos is periodically initiated by fire. The responses of plants to fire and to fire regime may be analysed in terms of qualitative characteristics of each species, as is done in the system developed by Noble and Slatyer (1980, see Chapter 5). As noted previously (Chapter 5), fynbos plant species of similar form tend to share similar life-history characteristics; taller seeding shrubs tend to mature at about the same age, for example. They nevertheless may differ in their age-dependent fecundities and mortalities; successive generations of species at a given site would therefore tend to fluctuate in their relative abundances according to age-dependent reproductive potentials at the time of fire, given that they had matured. The problem of predicting the effect of fire on the relative abundances of species therefore becomes a demographic one.

That the succession following fire in mediterranean shrublands involves a number of suites of species distinctive in their life-histories has been noted by many authors (e.g. in Kruger 1984). With regard to species regenerating solely from seed, Bell et al. (1983) have distinguished between fire ephemerals, which are stimulated to germinate by fire, mature early, and have short lives of between three months and four years, and obligate seeders, which mature later and have longer life spans. They noted that these life-history characteristics correlated with certain physiological characteristics. Plants in the former category have fast growth rates and high reproductive outputs. The latter group has slow growth rates and a longer time from germination to flowering. Members of these two groups were selected for study at Jakkalsrivier to provide an initial quantification of their demography in relation to fire regime.

7.2. Methods

Five species were studied, i.e. the polycarpic fire ephemeral shrubs

Aspalathus globosa (Fabaceae) and Othonna quinquedentata (Asteraceae) and the three obligate seeders of the Proteaceae, Leucadendron xanthoconus, Protea lacticolor, and P. neriifolia. These species are sympatric though O. quinquedentata and P. lacticolor tend to favour moister habitats at Jakkalsrivier.

Population densities of Leucadendron and Protea were estimated on the study sites by means of quadrat samples after fire. Quadrats of 1m x 1m were laid out at random in Leucadendron and P. lacticolor populations and were marked permanently and assessed periodically. Additional random samples of individuals of each species were selected and tagged for monitoring after fire from the post-seedling stage, by the wandering-quadrat method of Catana (1963). Samples consisted of 40 and 30 plants respectively for Aspalathus and Othonna, where rapid mortality was predicted and hence relatively small samples would suffice, and 100 for the other species. Some seedlings of Protea neriifolia were erroneously included in the initial samples of P. lacticolor and these individuals were later dropped. Quadrat samples and tagged samples could not be taken in exactly the same places, because of the effects of trampling. All plants in each sample were tagged and plants were visited at intervals of about one year from 1981 to 1985. Leucadendron xanthoconus and Protea lacticolor were monitored in the burnt as well as the unburnt vegetation. P. lacticolor was sampled in three habitats within the burnt vegetation, on a phreatic riparian site, on a drier colluvial substratum in the vicinity of a small scarp, and in an intermediate "moist" habitat. This was to gain an impression of the effect that habitat factors have on plant demographic variables.

Tagged plants were measured for height growth and classified as juvenile or mature at each visit. Growth was further assessed by harvesting a random sample of up to 25 plants in the vicinity of the sample monitored, and weighing stems, foliage, and reproductive organs. This was also done before fire for the three Proteaceae. Root masses for a subsample of three to five plants were determined at the time of the first harvest 28 months after fire. Roots could not be sampled effectively later, because it was difficult to excavate and

separate the roots of the sample plants from the dense root mass of other species in the surface soil horizons. The numbers of seed per inflorescence were determined for the samples of Proteaceae before the fire.

The populations had been sampled before fire, in 1979 and 1980, to quantify the biomass of adult plants in both 10- and 22-yr-old vegetation. All biomass samples were dried at 80°C until constant mass.

Recruitment to the populations was assessed by visual inspection at the time of censuses. Because no or little recruitment was observed subsequent to the start of monitoring, no methods were used to follow the fate of individual plants other than by observing those tagged in the initial samples.

For the tagged samples, which were not visited at regular intervals, survivorship was calculated to provide a uniform basis of comparison, by determining the maximum likelihood estimate of the daily survival rate, p_d, as

$$p_d = (n_s/n)^{1/\ell},$$

where n is the number of individuals observed at the beginning of an interval of length ℓ days and n_s is the number of survivors at the end of the interval. For intervals between visits the annual survival rate p_y was then calculated as

$$p_y = p_d^{365}$$

(Bart and Robson 1982). The overall survival rate for the entire period of observation on a given sample was corrected to a standard period of 1500 days, for direct comparison between samples. The logarithm of this variable is nearly normally distributed (Bart and Robson 1982). The standard deviation of the overall survival rate was calculated from the periodic survival rates according to Bart and Robson (1982), as follows:

$$s_{\ell n(w)} = [\sum_i (t_i/p_i)^2 . s^2_{p_i}]^{0.5}, \quad \text{where}$$

$$s^2_p = [\sum (n_i . \ell_i . p_i^2 . \exp(\ell_i 2)/(1-p_i \exp(\ell)]^{-0.5} \quad \text{and}$$

$$p_i = (n_{is}/n_i)^{1/\ell}$$

where ℓ_i = interval length in days
p_i = daily survival rate for ith period
n_i = number in sample at beginning of ith period
n_{is} = number of survivors at the end of the ith period

Tests for significance of difference between survival rates in samples at different sites were based on the statistic

$$Z = (w_1 - w_2)/(s^2_{\ell nw1} + s^2_{\ell nw2})^{0.5}$$

7.3 Results

7.3.1. Population densities Very high densities of plants established initially, with up to about 100.m^{-2} or more, and averages of about 30-60.m^{-2} (Table 7.1). This was in July and September 1981, about one year after the seedlings would have appeared.

Dead plants were present at this stage, though very few in the case of Leucadendron xanthoconus (about 0,5%), relatively many in Protea lacticolor on the moist site (13,3%), and intermediate and highly variable numbers in the case of P. lacticolor on the wet site. This indicates fairly substantial though highly variable mortality during the first year after germination.

7.3.2. Survival rates Observations on tagged samples of plants began on 27 November 1980 in the adult Leucadendron, on 5 November 1981 in the cases of Aspalathus and Othonna, on 27 November 1981 for Protea lacticolor in the unburnt vegetation, and in mid-May 1981 for the other samples.

Samples were visited three or more times subsequently, up to August and

December 1985. Periods of observation ranged from about 3,7 to 4,7 years. The dates of periodic visits are given in Table 7.2. At the end of the observation period, plants on the burn were about five to 5,5 years old, assuming germination in the late winter or early spring after the fire on 28 March 1980. In the unburnt vegetation, plants were about 27 years old.

By June 1984, only four of the tagged plants of Aspalathus, and two of Othonna survived. From November 1981 to March 1982, all Othonna plants survived (Table 7.2). At this stage (March 1982) many (50%) had flowered or were in bud for the first time. Mortality set in between March and September 1982, when about 30% died. During the interval between September 1982 and June 1984 about 77% of the balance died, and the rest died thereafter. Aspalathus was not assessed in March 1982, although mortality was observed by that time. About 43% of individuals had died by September 1982 and 64% of the remainder by June 1984. i.e. 21% survived at this stage. During the interval ending June 1984, about 90-95% of the young plants in the Proteaceae survived (Table 7.2).

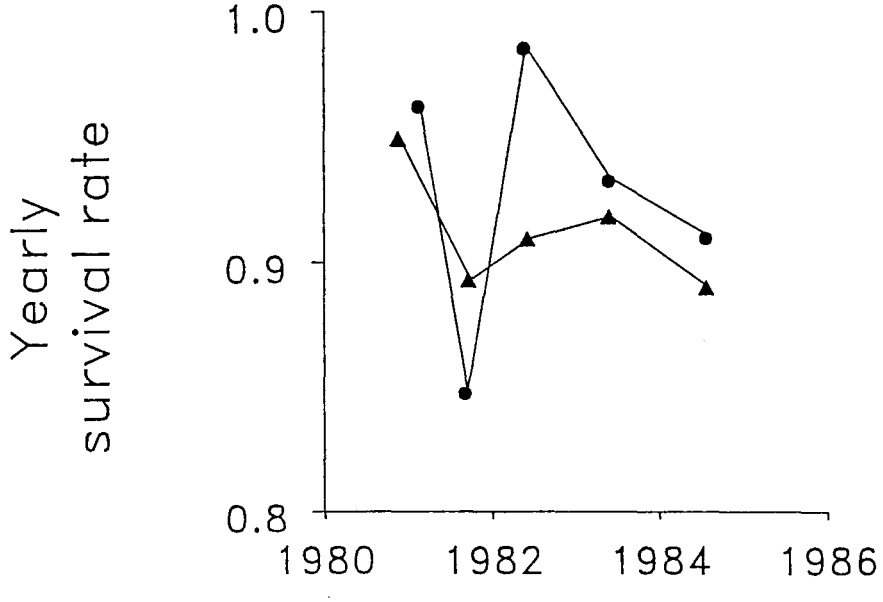


Figure 7.1. Annual survival rates in Leucadendron xanthoconus at Jakkalsrivier. Dots: young cohort on burnt site; triangles: old cohort on site last burnt in 1958.

Table 7.1. Population statistics for shrubs in the Proteaceae on the burnt site at Jakkalsrivier. n = 25 quadrats. Protea lacticolor samples classified by topographic position as dry, on shaltows soils on slopes, moist, being intermediate and wet being riparian.

Species	Site	Initial density, plants. m^{-2}					Mortality over 4,5 years,%		
		Mean	Std. dev.	Minimum	Maximum	No. of dead plants	Mean percentage mortality per quadrat	Minimum	Maximum
Protea lacticolor	dry	37,7	-			2,68	12,7		
Protea lacticolor	moist	57,1	31,3	22	129	8,76	23,7	7,3	87,1
Protea lacticolor	wet	42,5	25,5	20	138	variable	29,3	4,6	68,4
Leucadendron-xanthoconus	-	31,3	11,5	14	53	≈0	12,2	0	2,7

Table 7.2. Periodic annual survival rates for five shrub species at Jakkalsrivier. Dates at the heads of the columns are for the start observation on a given sample. Figures in brackets are the lengths of the intervals in days over which the survival rate was observed.

Date at end of observation period	Othonna quinque-dentata	Aspalathus globosa	Leucadendron xanthoconus		Protea lacticolor				Protea neriifolia
					Burnt			Unburnt	
			Burnt	Unburnt	Dry	Moist	Wet		
	81.11.05	81.11.05	81.05.14	80.11.27	81.11.26	81.05.13	81.05.14	81.11.27	81.05.15
24-27 November 1981	-	-	0,963 (197)	0,950 (362)	-	0,963 (195)	0,944 (194)	-	1,00 (196)
18 March 1982	1,00 (133)	-	-	-	-	-	-	-	-
29-30 June 1982	-	-	0,849 (214)	-	0,982 (216)	-	-	-	0,899 (215)
29 July 1982	-	-	-	0,893 (247)	-	0,955 (247)	0,985 (247)	-	-
24 August 1982	-	-	-	-	-	-		0,933 (270)	-
29 September 1982	0,711 (195)	0,566 (328)	-	-	-	-	-	-	
25-27 April 1983	-	-	0,986 (301)	0,910 (272)	0,946 (299)	0,986 (272)	0,917 (271)	0,984 (246)	0,987 (301)
21 June 1984	0,232 (209)	0,355 (209)	-	-	-	-	-	-	
11 July 1984	-	-	0,934 (442)	0,919 (441)	0,981 (443)	0,937 (441)	0,982 (442)	0,884 (441)	0,962 (422)
21 August 1985	- -	- -	0,911 (406)	0,890 (406)	1,00 (406)	0,990 (406)	0,990 (406)	- -	0,990 (426)
30 December 1985	-	-	-	-	-	-	-	0,897 (537)	-

Table 7.3. Overall survival rates over given periods of observation in Leucadendron xanthoconus and Protea lacticolor. Survival rates were calculated by the methods of Bart and Robson (1985) (see text) Protea lacticolor sites classified by topographic position (see Table 7.1).

	Leucadendron xanthoconus		Protea lacticolor				Protea neriifolia
			Burnt			Unburnt	
	Burnt	Unburnt	Dry	Moist	Wet		Burnt
n (size of initial sample)	100	100	91	99	100	100	99
n_s (number surviving at end of period)	81	74	84	86	88	69	88
Observation period, days	1560	1728	1364	1561	1560	1494	1560
Overall survival rate for interval	0,810	0,740	0,923	0,867	0,880	0,690	0,889
Estimated overall survival rate for 1500 days	0,817	0,767	0,916	0,873	0,884	0,689	0,893
Standard deviation of survival rate	0,0608	0,0734	0,0302	0,0408	0,0387	0,0670	0,0373
Mean annual survival rate	0,952	0,938	0,979	0,967	0,970	0,913	0,968

Table 7.4. Size and biomass of individuals of Aspalathus globosa and Othonna quinquedentata in July 1982, when plants were about two years old. n = 15.

	Aspalathus globosa		Othonna quinquedentata	
	Mean	Standard deviation	Mean	Standard deviation
Height, m	1,60	0,368	0,891	0,424
Total mass, g	53,2	22,7	21,2	25,3
Root:shoot (n=3)	0,22	0,053	0,34	0,133
Biomass components of shoot, %				
Stems and branches	72,7		71,2	
Foliage	22,2		24,5	
Reproductive organs	5,0		4,1	

Annual survival rates in Proteaceae ranged between about 85% and 100% during the full period of observation (Table 7.2; Fig. 7.1). Rates fluctuated somewhat from year to year but there was no overall trend (Table 7.2; Fig. 7.1). For the purposes of further analyses the survival rates among these shrubs were assumed to be constant.

Overall survival rates for the Proteaceae are shown in Table 7.3. Because the observation periods varied, the overall survival rates have been adjusted to a base period of 1500 days for the purposes of comparison. Survival rates in Leucadendron xanthoconus were 0,82 in the young plants on the burn, and 0,74 in the old plants (Table 7.3). The difference was not significantly different (P = 0,20). These rates were significantly lower than those in young plants of Protea lacticolor (P = 0,04 - 0,002 and P = 0,006 to 0,0003 for young and old Leucadendron plants, respectively), but did not differ significantly from the rate of 0,69 recorded in old P. lacticolor (P = 0,33 for both cases). The apparently lower rate of survivorship in old Leucadendron was mainly owing to the low survivorship in the male cohort, which amounted to 0,542, as opposed to 0,75 in females. Over the nearly five years of observation the sex ratio in the Leucadendron xanthoconus in the unburnt vegetation increased from 1,08 females per male to 1,50 females per male. The males which died were significantly smaller at the start of monitoring than those which survived (0,99 m tall vs. 1,15, P = 0,0009); this was not the case in females, though the plants which died were smaller on average than were the survivors (1,15 m vs. 1,23, P = 0,210).

In Protea lacticolor, the survivorship in old plants was significantly lower than in young plants (0,689 vs. 0,884 to 0,916; P = 0,02 to 0,0008; Table 7.3). There were no significant differences between the rates of survivorship observed among the samples of young plants from the dry, moist and wet habitats. However, the rate of 0,916 on the dry site was nearly significantly higher than those recorded for the other sites (0,873 and 0,884; Table 7.4).

7.3.3. Growth and maturation Shrubs were first sampled for biomass in July 1982, when they were about two years old. At this stage,

Aspalathus globosa had a mean height of 1,60 m and mass of 53,2 g while Othonna quinquedentata was an average of 0,89 m tall and weighed 25,3 g (Table 7.4). Othonna plants varied markedly in size, from 0,36 m in height and 2,9 g mass to 1,95 m and 89 g. Aspalathus plants were 1,16 to 2,53 m tall and weighed between 22,2 and 84,8 g. Of the Aspalathus, all but one was bearing flowers. Seventeen of the 23 surviving plants were in flower in September 1982; the other six had had their shoots removed by rodents. Seven of the sample of 15 Othonna plants had no flowers in July 1982.

Root fractions ranged from 0,15 to 0,22 in Aspalathus and 0,16 to 0,31 in Othonna. These species were not sampled subsequently because most plants had died.

Survival rates for P. lacticolor were higher among tagged samples than in the quadrat samples (Tables 7.1. and 7.3). This is not readily explained, but could be owing to the fact that it was not possible to sample identical habitats and that mortality was patchy. Analysis of the data for the permanent quadrats indicates that the mortality was not related to density. The correlation between mortality over 4,5 yr and initial densities per quadrat was -0,008 for the moist site and 0,329 (P = 0,11) for the wet site.

In Leucadendron xanthoconus, apparent mortality in the quadrats (12,2%) was lower than that in the tagged samples (19,0%). Some recruitment to the young plants in the quadrats was noted at different times, so that the plants in the quadrat did not represent a cohort and mortality was underestimated. This recruitment after initial establishment seldom amounted to more than one or two plants per quadrat per year, if any. The same was observed for P. lacticolor, so that mortality in the quadrats relative to that in the tagged samples must have been greater than measured. Adult shrubs of the Proteaceae in unburnt veld did not grow significantly in height during the period of observation. Mean heights for Protea lacticolor at the beginning was 2,26 m and after 4,1 years was 2,52 m; Leucadendron heights changed from a mean of 1,15 m to 1,34 m over 4,7 years. The change in the mean height was mainly owing to the fact that mortality tended to be greater in smaller shrubs.

Young tagged plants grew relatively slowly in height and mass. In July 1982, average plants of Leucadendron and Protea lacticolor were 0,21 and 0,30 m tall, respectively, and weighed 0,88 and 3,16 g,respectively. Aspalathus and Othonna were up to eight times taller and 60 times heavier at the same stage. The root fractions for the Proteaceae at this stage were 0,24 (range 0,16-0,32) for L. xanthoconus and 0,22 (0,11 - 0,34) for P. lacticolor (P. neriifolia was not sampled). These were about the same as for the fire ephemerals.

The rates differed between species and for P.lacticolor, within sites. Species may be compared in terms of periodic relative growth rates and net assimilation rates for the first five years after fire (Table 7.5). These rates are underestimates because tissue losses such as through leaf fall are not accounted for. They may also be affected by whether or not plants were harvested after onset of the early spring growth which is commonly observed in young Proteaceae. Nevertheless, the values serve for the purposes of comparison. Initially high relative growth rates in L. xanthoconus and P. lacticolor on the wet site of 3,22 and 5,03 $mg.g^{-1}.d^{-1}$ respectively declined to about 1.6 and 0,8-1,2 $mg.g^{-1}.d^{-1}$ in the later periods of observation. During these periods, highest relative growth rates were measured in P. lacticolor on the dry site and in P. neriifolia. In September 1985, at the age of about five years, P. neriifolia plants had the greatest shoot masses (45,7 g), followed by P. lacticolor on the wet site (34,3 g), P. lacticolor on the dry site (21,8 g) and Leucadendron (9,5 g). P. lacticolor on the wet site and P. neriifolia were about the same height (0,79 and 0,71 m respctively). At that time, P. lacticolor on the dry site was 0,58 m tall and Leucadendron, 0,52 m.

By July 1984, i.e. at the age of nearly three years, 0 to 7,5% of Protea lacticolor plants on the burn had flowered, the highest percentage being recorded for the moist site. At this time, 3,3% of P. neriifolia and none of L. xanthoconus had flowered. The Protea spp. flowered in autumn, and L. xanthoconus in spring. By August

1985, at five years, 10-17% of P. lacticolor had flowered, 10% of P. neriifolia, and 32% of L. xanthoconus.

Data for all Proteaceae populations are summarised in Table 7.6. There is not a consistent relationship between the different parameters of plant dimension and age, as may be seen from the data for L. xanthoconus and P. lacticolor. The local effects of habitat on plant vigour are pronounced. In L. xanthoconus, the lack of vigour in the 22-yr-old plants is probably owing in part to the fact that they were sampled from a site with soils derived from quartzite (see Chapter 3).

There is a natural tendency for the foliage fraction of shoot mass to decrease with the size of the plant (Table 7.6). A more important indicator of vigour is the leaf-area index, i.e. the ratio of leaf area to projected crown area of the plant. Leaf-area indexes vary markedly between samples with about the same foliage fraction. The 10-year-old L. xanthoconus had an unusually high LAI. This is because of its slender branches and crown, and the accumulation of older cohorts of leaves on the branches. The older shrubs do not retain older leaves as much, and evidently produce less leaves per new shoot than the younger plants.

The shrubs of Protea species have branches set at larger angles and spreading crowns, so that leaf-area indexes tend not to exceed about 2,0-3,0. The tendency is for LAI to decrease with age on a given site but in vigorous P. lacticolor LAI is maintained at least until 10 years. This decreasing ratio of foliage to stem and branches was not associated with increasing mortality in the Proteaceae.

The species treated here are serotinuous i.e. seed are retained in woody inflorescences, so that any plant may bear seed crops for more than one season. The number of seed retained per plant is broadly related to plant size, so that reproductive output is a function of vigour. This is not the case in L. xanthoconus where, despite the relatively small parent plants, the number of seed per plant was greater in the 22-yr-old cohort than in the 10-yr-old, despite the

fact that the latter plants were much larger. In P. lacticolor, the difference between the reproductive output of 10-yr-old plants on the dry and the moist sites was marked. In fact, 10-yr-old plants on the moist site had a greater reproductive output than did 22-yr-old plants on an intermediate site.

7.4. Discussion and conclusions

The results of this study emphasise the marked differences in life histories of fire-ephemeral and obligate-seeder shrubs. The fire ephemerals match the cases reported for the kwongan of Western Australia very closely, having similar life-spans and growth rates, and similar patterns of nutrition (Bell et al. 1984; see Chapters 2, 4 and 6). Their survivorship curves fit the Deevey type I model, in that mortality rates increase as individuals approach the ends of their life-spans. Populations of these species show senescence, in the terms used by Leopold (1961).

Among the obligate seeders, the small differences in survival rates between species, cohorts within species, and identical cohorts in different habitats are overshadowed by the low rate of mortality overall. Despite abundant establishment and nearly sevenfold variations in densities on quadrats in a sample, there was at most weak evidence of density-dependent mortality. Mortality in the first year after germination, deduced from the abundance of dead individuals in the quadrats at the time of the first survey, was negligible in the case of Leucadendron xanthoconus and up to about 510% in P. lacticolor. This is in marked contrast with most seedling populations of woody plants. For example, survivorship in Eucalyptus delegatensis recruited after fire was 2,9% after 72 weeks, with initial densities about the same as those at Jakkalsrivier (O'Dowd and Gill 1984). First-year mortality among recruits of shrubs after fire in chaparral has been recorded at 90-92% (Kummerow et al. 1985).

Although the annual survival rates of cohorts of Proteaceae decreased with age, the difference was not great. Therefore, the trend fits a Deevey type II survivorship, with more or less constant age-specific

mortality. The cohorts therefore do not show senescence. This is in contradiction to the type I model proposed for fynbos Proteaceae by Kruger (1983), and markedly different from the type III curve reported for Banksia ornata by Specht et al. (1958). It has yet to be established whether the survivorship rates for cohorts of Proteaceae are in fact approximately constant, or whether progressively increasing levels of exploitation of the site by the developing vegetation may lead to one or more waves of mortality such as reported for Ceanothus megacarpus by Schlesinger and Gill (1978). In Protea lacticolor, the ratio of daughter plants to parent was extremely high, i.e. 53:1 on the dry site and 41:1 on the wet site, as indicated by transect surveys after fire. If these ratios reflect mortality among the previous, parent population then the observed mortality rate was about half what would be needed to account for survival after 10 yr, and this would imply some more-or-less episodically high rate of mortality. However, this deduction is not firm, because the ratio between parent and daughter populations are complex, depending among other things on density effects on fecundity (Bond et al. 1984). However, if there is low mortality during establishment, no density-dependence in the mortality among established plants, and if reproductive output is determined by plant size, then the abundance of any post-fire population of these species will be strongly dependent on the reproductive potential of the pre-fire parent population. This would in turn depend on on the age of the pre-fire population and the history of climatic and other factors governing reproductive output during the interfire period, as well as on levels of predation on seed after dispersal.

The relationships between age and vigor and reproductive output among Proteaceae at Jakkalsrivier were confounded by habitat. The marked effects of habitat on vigour and reproductive output must interact with fire to sharpen the local distributional boundaries of species, depending on their dispersal characteristics. In Protea lacticolor, where seed dispersal is limited, early fires will markedly reduce or eliminate portions of its population which occurs on marginal sites and where growth is slow and reproductive output for, while having no lasting effect on abundance in adjacent, optimal sites. One may

readily envisage rapid contractions in local ranges and slow expansions, with changes in fire regime, with fluctuations being affected by variations in environmental conditions e.g. droughts during the inter-fire period.

8. CONCLUSIONS

8.1. Stability of fynbos

The stability of ecological systems has been defined in various ways. A straightforward definition from Woods and Whittaker (1981) holds that a community in which several species coexist with relative importances and hence their population structures remaining fairly constant over three or four generations of the longest-lived species, may be considered stable. By this definition, few or no mediterranean-type communities are stable, since they are chronically disturbed by fire and their composition is constantly changing. However, stability must be assessed relative to disturbance and it is constancy of composition under a given regime of disturbance that is of concern.

The recovery of species recorded after a single fire at Jakkalsrivier and Zachariashoek in this study indicates a remarkable stability in fynbos vegetation, if change in floristic composition is taken as a measure of relative stability. These data, unlike those reported by Van Wilgen and Kruger (1981), reveal very low real turnovers of species in fire at a given site. Much apparent turnover is due to the temporary addition of species, as well as those added because they are more easily detected after fire. Some change in the flora does occur locally in association with fire, through extinctions of rare species on the site and immigration, principally by short-range dispersal. These are probably more or less random processes. At Jakkalsrivier, in one case at least (Nebelia paleacea), a substantial local extinction was detected which possibly was not associated with fire at all. The change in composition detected on the Jonkershoek site, where Erica sphaeroidea evidently invaded a community previously nearly free of Erica species, hints at even greater changes that may occur in time, independently of fire. Clearly, additional observation and experimentation are needed to reach a position where change owing to disturbance such as fire may be properly distinguished from change owing to other factors, or perhaps simply random processes of dispersal. Severe disturbance by mass wastage of soil at

Jakkalsrivier did not result in colonisation of the site by a distinct set of pioneer species. Some of the species involved in the pyric succession are vagile and have high relative growth-rates, but these did not necessarily dominate the soil slip, and few of these were in fact found on these denuded sites. Species typical of the fynbos climax were also numbered among the colonists of the soil slips. At least at Jakkalsrivier, the fynbos flora seems to lack a set of pioneers distinct in their dominance of disturbed sites.

In fact, it is difficult to identify pioneers in this fynbos, and labelling species as "pioneer" or "climax" is no more than a device to aid discussion. The pyric successions did not involve the replacement of one set of species by another, but only the changing dominance among the autosuccessional flora as a result of different life-histories. At most, rapid changes occurred on the phreatic site studied because of the relatively abundant populations of fire ephemeral species differing in longevity.

Changes in fynbos at Jakkalsrivier in the absence of fire were relatively small, involving an attrition in shrub populations. There was no evidence of an immigration of new species over the time from about 10 to 25 and more years after fire. It does seem that, at Jakkalsrivier, on shallow infertile soils, exclusion of fire will result eventually in impoverished communities in which a few tolerant and vagile species continuoilsy replace their populations.

As discussed earlier, resilience refers to the rate at which a community recovers to some specified prior state. Resilience was assessed in terms of growth-form composition in this study, but since the floristic composition of the samples studied did not change, one may reasonably expect that quantitative analysis in terms of growth forms would reflect the dynamics in terms of species composition. The conclusion here was that all the communities studied had similar resilience, despite variations in rates of canopy development. This is not surprising, since the scale of habitat variation is smaller than the scale of prevailing fires would have been over evolutionary time, and this would tend to have selected for species of roughly similar

life histories irrespective of habitat. However, demographic studies on Protea lacticolor did indicate habitat effects on age-specific fecundities, so that an increase in fire frequency would eliminate this species progressively from less favourable habitats, leaving it to survive only in the most favourable. Such interactions between disturbance regime, habitat, and community resilience need further attention in the fynbos, particularly to assist in devising conservation policies that would properly accommodate environmental variation.

8.2. Uniformity of succession in fynbos

In general terms, pyric successions in fynbos follow similar patterns despite differences in the habitats included in this study. Regeneration by sprouting and by seeding is inhibited except during the first season or so after fire. There is a progressive loss of species, except that most persist as seed or subterranean organs, as succession proceeds. Overstorey canopies do not accumulate cover and biomass, tending to decline from 20-40 years after fire. Dense overstoreys do not develop at Jakkalsrivier, except on phreatic sites and on unusually fertile soils. This is not because of fire or other disturbance, since overstorey shrub species are abundant, and their reproductive potential sufficient to allow colonisation of any habitat in time. Rather, the sparse overstoreys, where the taller shrubs do occur, are owing to the inherent morphologies and life-histories of the species concerned. Where they do not occur, this is evidently because of physical environmental constraints.

With the exception of Erica hispidula, there is no substantial recruitment of young plants as the canopy thins.

In particular, however, the patterns differ quite strongly between the different habitats, in regrowth rates and in the relative abundance of different life forms at different stages. This study could do no more than describe some aspects of the patterns in pyric succession. Prediction would require further experimental work, though the predominant role of soil moisture regime or other factors governing

productivity is obvious.

Mountain fynbos successions evidently differ from the patterns in lowland fynbos. In the latter case, there is apparently high turnover in species, firstly between the pre-fire and the regenerating stand, and secondly during later pyric succession. This must involve the loss at the time of the burn of species recruited during succession, and the gain of some lost during succession. This indicates that the inhibition model does not hold in Lowland Fynbos, though there is no evidence of facilitation.

It is possible also that succession in Mountain Fynbos involves a variety of pathways. Thus, in fynbos on granite at Jonkershoek, Van Wilgen (1981) found that the opening of the stand of proteoid fynbos from around 30 years after fire was accompanied by a recruitment of species some of which could be considered forest precursors (see also Kruger 1984). At Jakkalsrivier however the opening of the shrub layer is not accompanied by recruitment from the forest flora, either because the physical environment precludes forest, or because some form of inhibition persists, or because the propagules of forest species are not available It is unlikely that propagules are limiting. Critical experiments to choose between the remaining alternatives would be useful. The difference could be due to the low nutrient status of the Jakkalsrivier sites or to some other physical environmental factor, since the incipient forest successions reported from elsewhere, as discussed in Chapter 2, have been on more fertile soils derived from granite or shale.

The principal conclusion, therefore, is that the model of pyric succession presented in Chapter 2 is simplistic and would need to be qualified for valid predictions in different fynbos environments.

8.3. Changes in alpha diversity

At Jakkalsrivier the richest regenerating communities, and the greatest post-fire increases in species richness, tend to be found in communities of intermediate biomass or productivity. In these

intermediate communities, the difference between species richness in unburnt and in burnt vegetation may amount to about 20 species on $4m^2$, i.e. 40% of the apparent maximum, at around 30 years after fire. The reduction in species is not associated with cover of the overstorey, as has been found in Australia, nor entirely to the disappearance of fire ephemerals. The evidence from the demographic studies, i.e. from the survivorship schedules of the longer-lived shrubs, indicated that inherent life-history traits were at least as important as species interactions in determining succession. This is despite the fact that surviviorship curves did not provide evidence of senescence by about 27 years after fire, and hence that the so-called senescent state of the old vegetation was simply the outcome of the gradual progressive attrition of plant populations (together with low rates of decay of dead material) and the inhibition of recruitment.

Because so few species in the fynbos are vagile, and because the pyric succession is not a process of replacement of pioneer species by climax species, in the classical sense, the hump-shaped diversity curve cannot be explained as the outcome of the interplay between r- and K-species. Rather, it is some expression of the factors governing the numbers of seeding species which may be assembled in the community and of the scope of the array of life-histories which may co-exist.

8.4. Effects of fire on the availability of resources and their capture by plants

The evidence from this study as well as from others on the same or similar sites is that fire in fynbos substantially affects the availability of energy, water and mineral nutrients to plants. In some cases, these enhancements may be brief and for this reason difficult to detect. In the humid environment at Jakkalsrivier, water stress was not found to affect plants in either the regenerating or the mature vegetation. Enhanced availability of nutrients could not be shown to affect successional process directly, but only ultimately in the sense that the varying nutritional environment allows the temporary co-existence of fire ephemerals, with high nutritional demands and rapid growth, and long-lived "climax" species with low

capacities for nutrient uptake and slow metabolism. The suggestion in the data of enhanced uptake of nutrients other than nitrogen and phosphorus among regenerating "climax" plants would need further study to determine whether or not this is so.

Leaf-area indices of the fynbos at Jakkalsrivier may reach as much as 3,0. In denser canopies, light attenuation is sufficient to reduce the illumination at the ground to levels below those normally required for positive carbon balance in evergreen sclerophylls. Preliminary experimental results indicate that levels of shading likely to be encountered in the field would cause etiolation sufficient to prevent establishment of seedlings. Poor ventilation of the canopy of mature vegetation and the trapping of radiant energy within it exacerbate the conditions under which seedlings must establish. The effects of herbivores and granivores on plant recruitment are arguably the prime determinant of the even-aged structure of fynbos vegetation under many conditions (Chapter 2). These were not studied at Jakkalsrivier, but it is clear that the effect of the vegetation canopy itself is likely to play an important role.

Although the availability of water did not in itself appear to affect the process of vegetation recovery and hence growth, there are clear patterns of plant biomass, growth rates, and pyric succession associated with soil water availability. The analysis of soil properties at Jakkalsrivier showed a marked difference between sites, with the pools of mineral nutrients at the phreatic site being at least twice and up to ten times or more greater than at the other sites. This was a function both of soil depth and of nutrient concentration. For whatever reason, there is a marked accumulation of mineral nutrients at the phreatic site and this, together with the effects of a more favourable water regime on nutrient availability and uptake by roots (e.g. Lamont 1982), rather than water regime per se, could account for the spatial patterns in vegetation and succession. Certainly, the nutrient demanding fire ephemerals were more abundant at the phreatic site than at others.

8.5 Responses of individual species to fire

It follows from the foregoing that the stability of the fynbos communities was due to the resilience of individual species to fire, and this was overwhelmingly because of their capacities to survive on site. Severe disturbance, such as through mass wastage of soil, may exceed the threshold that allows recovery in situ, and recovery of denuded sites will therefore be extremely slow, given the rarity of species with capacities for long-range dispersal. Presumably, severely disturbed sites will be slowly colonised unless and until the disturbance regime were to change to the point that populations of vagile species reach a level that will ensure a seed rain adequate to rapid colonisation.

The plausible vegetation replacement sequences obtained by using information on the vital attributes of individual species depend heavily on inferred information, especially about the effective longevity of sprouters and of seed banks. Such models must necessarily be very tentative until reliable information relating to these parameters becomes available, at least for examples of species in the relevant categories. Our ability to predict the outcome of disturbances outside the scope of those normally observed is dependent on research of this kind.

8.6. Fynbos and succession theory

This study centred on the immediate effects of fire on fynbos and it was natural that a reductionist approach would be followed in answering questions about the survival of species and the determinants of patterns of change. McIntosh (1980) and Finegan (1984), having highlighted opposing "holistic" and "reductionist" schools of thought regarding ecological succession, argued that the distinction was artifical and that a synthesis was necessary. Can studies in fynbos contribute to a synthesis?

An answer to this question would require more thorough studies of the mechanisms operating during pyric succession, as well as of the

consequences of prolonged exclusion of fire. At face value, the results indicate that the inhibition, and therefore reductionist (Finegan 1984), model operates under most circumstances. Therefore, the furthest that the fynbos ecologist needs to move on the road to a synthesis would be to develop a knowledge of the ecological relationships of growth-form categories, guilds, or similar functionally distinct infracommunity sets of species. This would allow adequate generalisation of the patterns of succession deducible from a knowledge of the constitution of communities in these terms. This view would be proved wrong if autogenic processes, such as biologically mediated nutrient cycling, are found to be important mechanisms governing the process of succession, especially over long periods of time.

8.7. Value of successional studies in practice

The objectives of management of fynbos ecosystems are expressed principally in terms of vegetation (e.g. Kruger and Bigalke 1984). In this respect, policies are determined by a viewpoint with regard to what forms of vegetation may potentially exist on any given site or over a landscape, and what degree and rate of change in this vegetation may be considered acceptable.

The first consideration is often expressed in a debate as to whether or not the fynbos at a site may become forest through succession over sufficient time. At Jakkalsrivier, there was no evidence of potential forest, though on other fynbos sites such replacement has become evident over a similar span of time. Management objectives involving the control of succession to forest will need to take explicit account of the variation in potential vegetation in different fynbos habitats.

There is sufficient evidence to indicate that the composition and structure of fynbos vegetation may be substantially changed by deliberate or inadvertent measures, including changes in the season and frequency of fire (Kruger 1984; Kruger and Bigalke 1984). This study focused on the effects of a single fire, and demonstrated that fire as such need cause no change in vegetation. Other factors being

equal, the vegetation at Zachariashoek and especially Jakkalsrivier was stable under a 10-year fire cycle. In the case of Jakkalsrivier, the full suite of fynbos plant forms were present, and one may conclude that a managed regime involving burns at intervals of 10 years and more would meet the requirements for species conservation. The sample survey also indicated that recovery of the species under longer cycles, i.e. about 24 years, was also complete. There appears to be wide latitude for fire frequencies in the managed fire regime in this type of fynbos. Nevertheless, some change may occur independently of fire, and this may be subtle, as the results from Jakkalsrivier indicate, or marked, as suggested by the results for Abdolskloof.

Managers monitor the changes in vegetation to assess the degree to which their objectives are met. To interpret the changes that they are sure to detect, they need to know which are owing to management and which are due to the natural and other processes that are operating beyond their control. This study contributes to such knowledge. However, proper evaluation of policies and practices by top management will require that the changes observed should be expressed in easily understood indices (Train in Cormack et al. 1979) and the interpretation of the results of this and other similar studies will need to contribute to the development of such indices of change.

Finally, effective management needs the means to predict the effects of measures applied to vegetation on dynamic aspects of resources, such as water yield and quality, species diversity, and the potential for fire in the vegetation. The quantitative analyses in this study provide data fundamental to such a capability. It is especially important that detailed information is now available from Jakkalsrivier for the humid, black-water fynbos of the southern coastal mountains. Successional dynamics in fynbos are likely to vary along gradients of site water balance, nutritional status of the soils, and of primary productivity per se (Specht and Moll 1983). Jakkalsrivier represents a relatively humid (less stressed by summer drought) and infertile site in the fynbos biome, and as such is a useful counterpoint to studies in contrasting sites, such as in lowland fynbos at Pella. Without detailed studies at several

contrasting sites is will be difficult to evaluate fully the general validity of management policies.

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ERRATUM

The following is the beginning of the first paragraph of page 467, which was mistakenly omitted in the text:

These factors affect the competitive relations among species in two ways. First, fire-to-fire variation induces fluctuational change in the vegetation like that reported by Gulmon (1979) for annual grasses though on a longer time scale, but also serving to preclude competitive exclusion of any member of the community. Second, the patterning of fire intensities of. . . .

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23. Plant Community Diversity and Dynamics in Relation to Fire

F. J. KRUGER

23.1 Introduction

Recurrent fires in vegetation are a general feature of mediterranean-type ecosystems and the profound effect of fire regimes on these ecosystems is generally acknowledged (Mooney and Conrad 1977).

Management of natural and semi-natural landscapes in these zones inevitably implies control of fire. This needs an understanding of vegetation dynamics both to enable fire control and to allow predictions of the ecological effects of fire control. The apparent interactions between fire regime and community (alpha) diversity raises important questions regarding both community ecology and practices for ecosystem conservation.

Here I have attempted to review and synthesize the information on the dynamics of mediterranean-climate vegetation in relation to fire regimes. Coexistence of plant species in the context of vegetation dynamics is considered with a view to our understanding of the effects of changes in regime. This is done principally for the mediterranean-climate zones of California, Australia, and South Africa where effects of fire regime are confounded less by human activities than in the Mediterranean Basin and Chile.

Cody and Mooney (1978) and Gill and Groves (1981) have recently reviewed information on the ecological effects of fire in these ecosystems. Some aspects of their findings are summarized in Table 1. Gill and Groves (1981) concluded that the pattern of change in vegetation after fire in heathlands and mediterranean-type shrublands in general "...is more a gradual elimination of individuals present from the outset than a replacement of initial species by new species..." and the classical succession model of "facilitation" (Connell and Slatyer 1977) does not apply. Another characteristic they noted is that "Pyric succession in heathlands comprises regeneration both from seed and from rootstocks." They maintained that "... the responses of heathlands to fires is probably one of the major features common to these different shrublands." Both reviews provided instances of the pronounced effects of different fire regimes on vegetation composition. But in spite of the overall similarities in vegetation response to fire there are important differences

Table 1. Summary characteristics of pyric succession in mediterranean-type ecosystems as described by Cody and Mooney (1978) and Gill and Groves (1981).

	Chaparral	Matorral	Maquis and garrigue	Australian heath	Fynbos
Annuals and short-lived fire ephemerals	Dominant post-fire	None	None?	Rare	Rare
Immigrant post-fire annuals	None?	None?	Often abundant	None?	None?
Geophytes	Some	?	Many	Prominent	Prominent
Persistent herbaceous perennials	Very few	Abundant (decrease post-fire)	Grasses stimulated post-fire. Rare in old stands.	Sedges, restios dominant post-fire and remain prominent	Grasses, sedges, restios dominant post-fire and remain prominent
Regeneration mode of shrub species	About 50% sprout	Most sprout, few by seed only	Most sprout, few by seed only	Both modes prominent	Both modes prominent
Timing of plant recruitment	Immediately post-fire	?	Immediately post-fire	Immediately post-fire	Immediately post-fire
Fire-stimulated germination in shrubs?	Yes	No	No	Yes	Yes
Redevelopment of canopy cover	100% in 10-20 yr	?	Closed canopy in 5 yr	100% in 10 yr	70-90% in 2 yr
Diversity trends	Species richness (S) decreases with age	?	S decreases with age	S decreases with age	S decreases with age (sometimes an initial increase)
Effect of long absence of fire	Stagnation	?	?	Stagnation; in some cases, trend toward *Banksia* or *Eucalyptus* woodland, or *Leptospermum* thicket	Stagnation; in some cases immigration of evergreen forest species

among mediterranean-type ecosystems that correspond with differences in nutrient status (Table 1).

23.2 Fire regimes

The degree to which the floras and vegetations of the different mediterranean regions converge with respect to their responses to fire must depend in part on the measure of correspondence between the respective fire regimes. Fire regimes include the following: fire type, intensity, seasonality, and frequency (Gill 1975; Gill and Groves 1981) and comparative data are not available on all components.

23.2.1 FIRE FREQUENCY

There are few good data on fire frequency as characterized by the mean period between fires and variance about the mean. Indirect evidence suggests that Australian heaths experience a relatively high frequency of fires with low variance. Coaldrake (1951) describes a regime of frequent (less than 10 year recurrence interval?) fires in the extensive sand-heaths of South Australia; Specht et al. (1958) could find no stand older than 25 years on their study site in the Dark Island heath and had to travel 16 km to find a 50-year-old stand. Siddiqi et al. (1976) worked in vegetation where fire had recurred fortuitously five years and 12-15 years after the previous burns. The oldest stand of heath that Russell and Parsons (1978) could find in Wilson's Promontory National Park, an area where fire suppression is practised, was 20 years old and burnt shortly after their study was completed. Fires had recurred about once in 6.3 years in one of the stands they analysed, and these were mainly wildfires. Coaldrake (1961) reported a prevalent frequency of about once in five years for the heathlands of the southern Queensland coastal lowlands, for the period after European settlement. Prolonged absence of fire (i.e. 32 and 80+ years) has been reported only occasionally (Hazard and Parsons 1977).

Some indication of low frequencies in South African mountain fynbos is available from State forests where suppression is practised (Kruger 1979a). Here, most fynbos may burn either every 20 years or less, and very rarely once in 40 years. Horne (1981) analysed fire records for the Groot-Swartberg, a southern mountain range where fire suppression has been practised, and found an average frequency for all fires of once in 18 years, and for fires of natural origin - if man-caused fires are ignored - once in about 40 years. Fire frequencies are greater than these in most fynbos areas under present conditions.

The picture for chaparral indicates a fairly long mean recurrence interval, with relatively large variance. Schlesinger and Gill (1978), reported that "...stands older than 35 to 40 years are extremely rare..." in the Santa Ynez Mountains. However, several of Hanes's (1971) study sites were in vegetation more than 80 years old, and Keeley (1977b) sampled a stand more than 90 years old - these ages have not been reported for fynbos, for example. At San Dimas Experimental Forest, eight fires occurred between 1895 and 1960 on the area of about 7000 ha but only the fires of 1920 and 1960 were large; thus most of the vegetation had reached an age of 40 years and a number of stands were 65 years old in 1960 (Mooney and Parsons 1973).

The incidence of fire in National Forests of the San Bernardino range, southern California, and in fynbos of the Cedarberg State Forest is shown in Fig. 1. In both these areas fires have been suppressed by fire-break systems and fire-fighting measures and therefore allow a fairly exact comparison between chaparral and fynbos ecosystems. The data clearly show that fynbos burns more frequently than chaparral.

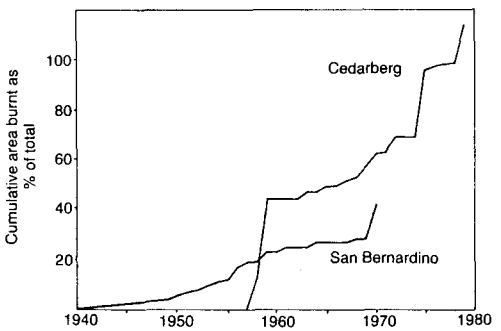


Fig. 1. Cumulative sum of area burnt from arbitrary initial dates in portion of the San Bernardino National Forest, southern California, and Cedarberg State Forest, South Africa. Derived from data in Philpot (1974) and the records of the South African Directorate of Forestry.

Fire frequencies are apparently highly variable in all of the mediterranean-type ecosystems. The upper limits of frequency are determined by vegetation structure and productivity. Thus Coaldrake (1951), Specht et al. (1958) and Kruger (1977a) have pointed out that South African fynbos and Australian heathland normally require 4-5 years before sufficient standing vegetation and litter have accumulated to carry a fire, though fires may sometimes spread into younger stands if conditions are extreme. In the chaparral, Hanes (1971) reported fire periods of 2-10 years at its lower elevational limits in the zone of transition with coastal sage, but Philpot (1977) found from an analysis of fire atlases for National Forests in the San Bernardino range of southern California that almost no large fires occurred in vegetation less than 15-17 years old. Early recurrence of fire in chaparral may depend on the nature of the herb regrowth and especially on the degree of invasion by exotic grasses. Fire appears never to be very frequent in the average natural chaparral stand. By contrast, sprouting hemicryptophytes in fynbos and Australian heath quickly re-establish a nearly continuous fuel bed that permits the frequencies of up to once in four years reported there.

The lower limits of frequency are determined by probability of ignition. Few or no cases have been reported where prolonged deferral of fire leads to changes in vegetation composition that reduce the flammability of stands, though inferred in certain instances in Australia (Jackson 1968).

23.2.2 OTHER ELEMENTS OF FIRE REGIME

Fires naturally tend to occur in the summer half-year of the mediterranean-type climate but fire seasons are in fact relatively variable. Thus, in chaparral, Horton and Kraebel (1955) reported burns that had occurred in January, March, July, August, September and November. The fire atlas for the San Bernardino National Forest shows burns from February to December, but with less than 1% of the total area burning in spring, about 30% in summer, and over 60% in autumn (Philpot 1974).

Wild-fires have been reported during any season in South African fynbos, although there appears to be a summer peak (Kruger 1979a). In the Cedarberg, 14% of the area burnt was by spring wild-fires, 52% in summer, and 32% in autumn (Andrag in Kruger 1979b). Horne (1981) found for the Groot Swartberg that 24% of wild-fires were reported in spring and 51% in summer (21% and 60% respectively for lightning fires). There is some indication of a greater incidence of large winter fires in the southern coastal mountains than elsewhere, and therefore of regional variation in the seasonality of fires in fynbos (Kruger 1979a).

Thus, in both chaparral and fynbos the seasonal timing of fire can be unpredictable from year to year with considerable variance within about a six-month range. The same should apply for Australia and A M Gill (personal communication 1980) reports maximum occurrence from spring to midsummer for heathlands in eastern Australia. This significant variability in fire season is to be expected. With regard to South Australian heath, Specht et al. (1958) have noted that "Times of high fire risk do not necessarily correspond with times of climatic stress on the vegetation. Several hot, windy days are sufficient to dry the surface and to make the fire risk high despite high soil moisture reserves." The fact that conditions for spreading fires are strongly controlled by current weather, and only partly correlated with season, has also been emphasized by McCutcheon (1977) and this observation would be valid for all mediterranean-type ecosystems.

The scant data available show that chaparral fires are distinctly more intense in terms of energy release rates (see Rothermel and Philpot 1973 cf. Bands 1977; Gill and Groves 1981) and hotter in terms of flame temperatures in the canopy and soil surface and shallow sub-surface temperatures (Rundel 1982) than fynbos or heathland fires. The deep ash-beds found after incineration of biomass in chaparral fires (e.g. Vogl and Schorr 1972) are not found after average fynbos and heathland fires (Kruger, unpublished).

Variation in the frequency of fire on any given site allows variation in the amount of fuel that accumulates and is available for each fire. This with variability in season and weather would cause considerable variation in fire intensity and in temperatures at the fire front. This has not been properly investigated, though Gill and Groves (1981) indicate the likely magnitude of variation. Gill (1981a) has also shown how intensities vary by up to a factor of five within a given fire, simply because of different rates of spread around the perimeter.

23.3 Pyric succession

23.3.1 SUCCESSION AS A SELF-REPLICATION OF STANDS: AUTOSUCCESSION

Plant succession after fire in mediterranean-type shrublands consists largely of the regeneration and development through their respective

life-cycles of the species present before the fire (Specht et al. 1958; Hanes 1971), and studies have shown that the burnt stand retains its floristic identity, i.e. is more similar to the pre-fire stand than to others in the area (Russell and Parsons 1978; van Wilgen and Kruger 1981). Hanes (1971) called this "autosuccession". However, most succession studies have relied on comparisons among stands apparently alike aside from fire history, rather than on successive observation of permanent sample sites. Studies of the latter kind usually show that recovery in composition is not complete. In fynbos, Adamson (1935) found that 16 of an original 92 species had not reappeared within 6.5 years after fire. Van Wilgen and Kruger (1981) found after a repeat survey of 33 permanent plots in fynbos burnt six years previously that the floristic composition of each plot had apparently changed by an average of about 50%, even though the species richness per plot and the total flora encountered in the sample had changed little. Despite observation error in both cases, changes were real and significant. Horton and Kraebel (1955) showed floristic changes both in dominants and in overall composition of the annuals and herbaceous perennials after successive fires in chaparral of the San Bernardino mountains (some change being due to immigration of an exotic species); their records also indicated that shrubs such as Ceanothus crassifolius could respond differently to successive fires on the same site; seedlings were abundant after the first (summer) fire, absent after the second (in spring).

The relative abundance of species may also change after different fires because of differences in one or more components of fire regime. Specht et al. (1958) recorded major differences in the relative abundances after burning of seedlings of early-maturing and late-maturing species in adjacent heath stands, one six years old when burnt, and the other 10 years old; the ratio of late-maturing to early-maturing species was 3:1 in the former case, 30:1 in the latter. Bond (1980) found significant and major (up to 12-fold) reductions in Proteaceae and dicotyledon seedling densities after fire in senescent fynbos stands, compared with mature stands. Relative abundances of seeding species (those regenerating solely from seed) in fynbos are markedly affected by season of burn with the pattern often being one of successful regeneration after summer or autumn fires, but low success, or loss of populations, after winter or spring fires (Jordaan 1965, 1981; Bond 1980), a pattern apparently also found in some chaparral species (Horton and Kraebel 1955). These reports are from comparative data (same fire burning adjacent stands of different ages, for example) but show how fire-to-fire variation in period, season and other regime components on the same site can affect initial stand composition.

Thus, though sclerophyllous shrublands tend to retain their identity despite burning there is at least some progressive or fluctuational change in species composition after successive fires. Contributing to this change are (a) the effects of season of the burn, (b) interval between fire (see below), (c) the interaction between timing of the fire and subsequent weather (Horton and Kraebel 1955; Specht et al. 1958), and (d) by analogy with Australian eucalyptus forest understoreys (Floyd 1976; Gill 1981a), intensity of fire.

23.3.2 TRENDS IN COMMUNITY DIVERSITY

Most studies show that old stands contain less species than they do in the immediate post-fire phase but the reported decline in diversity is not necessarily a uniform progressive change from a maximum in the first year

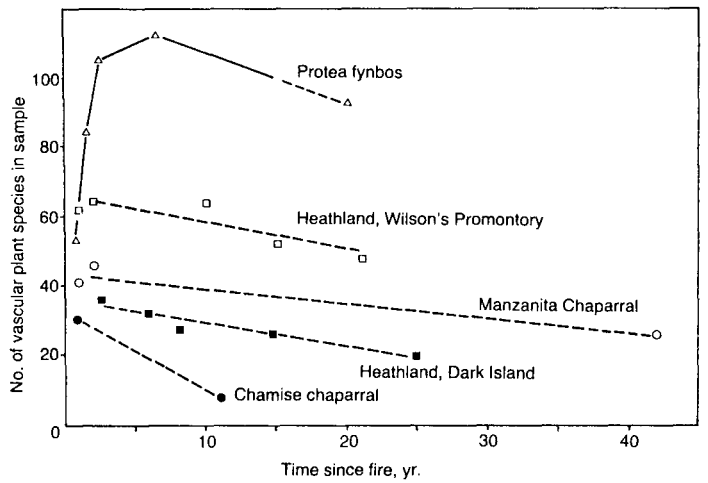


Fig. 2. Trends in community diversity with pyric succession. Data from Adamson (1935), Specht et al. (1958), McPherson and Muller (1969), Vogl and Schorr (1972), and Russell and Parsons (1978).

after fire (Fig. 2). The trend of increasing richness in the first few years to levels beyond pre-fire richness reported by Adamson (1935) has also been found in Australian heathland or heath understoreys (Bell and Koch 1980; Posamentier et al. 1981). In these cases, some or all of the increasing trend is spurious, owing to difficulties of detecting or identifying plants in the early stages of regeneration. Results are often difficult to interpret because of sampling techniques. For example, Posamentier et al. (1981) sampled plots of 0.08 ha by means of 16-20 0.2 x 0.5 m quadrats. With such small quadrats, some increase in numbers of species recorded must be owing to changes in frequency, rather than new appearance of species in the plot. In general, the progressive loss of species from the stand involves both the rapid disappearance of relatively short-lived plants, usually "fire ephemerals" (short-lived fugitive species that appear soon after fire and depend on the fire for regeneration - Gill 1981a) and gradual suppression of understorey species by overstorey species (e.g. Specht et al. 1958; Hanes 1977). The wet-heaths of Australia, richer in species than other heaths and dominated by sprouters, lose less species during succession (e.g. Russell and Parsons 1978). In Australian heathland and South African fynbos species are lost gradually during succession, but in chaparral most species that do so (about 40% of the flora) disappear relatively rapidly, in the first five years (see review in Hanes 1977; Keeley et al. 1981). This latter pattern applies to coastal sage scrub as

well (Westman 1981). In fynbos, α diversity can increase later in succession (more than 30 years after fire), apparently owing to regeneration of understorey species as the canopy opens with senescence in the overstorey (van Wilgen 1981). An increase has also been reported for Californian coastal sage scrub at about 20 years after fire, but is not associated with an opening of the overstorey, rather the immigration of tolerant herbs (Westman 1981). At 40 years, α diversity is reduced once more, despite a sparser overstorey.

23.3.3 DYNAMIC RELATIONS BETWEEN UNDERSTOREY AND OVERSTOREY STRATA

Specht and coworkers (Specht and Morgan 1981; Chapter 7, this volume) have derived a useful construct to describe the successional relations between the overstorey and the understorey strata in mediterranean communities. Briefly, sclerophyllous vegetation recovers rapidly after fire until a climatically determined maximum foliage projective cover is reached, normally within two to five years. This rapid recovery is owing to the regrowth of the understorey; once the maximum foliage projective cover is reached, the slower overstorey species begin to dominate and the cover of the understorey declines sharply. An inverse linear relationship between overstorey cover and understorey cover then obtains, while the equilibrial foliage projective cover is maintained. The number of active plant species on the site is also in an inverse linear relation to the overstorey foliage projective cover.

Several points are of interest in this regular relationship. First, the overstorey apparently begins to influence the understorey already when sparse, i.e. with a foliage projective cover of 30-40%, normally much less. This may reflect unusual light sensitivity among understorey species, or the early onset of competition below ground. Second, the overstoreys in different shrublands vary considerably in their rates of recovery. In the Dark Island heath, the overstorey reached about 30% foliage projective cover in about three years and was still increasing at 20 years. In the fynbos, overstorey cover was less than 10% at three years, and increased very slowly afterward. By contrast, chaparral overstorey shrubs recover their pre-fire canopy cover within five to 7-9 years (Hanes 1977; Keeley 1977c). Though Specht and others (Specht et al. 1958; Specht and Morgan 1981; Chapter 7, this volume) argue that the relation between understorey and overstorey is competitive, the curves for fynbos show a decline in understorey cover well before the overstorey has reached the level of 30% or so that apparently caused a decline in the understorey of Australian heath, for example. This implies effects due to competition for different resources (water and/or nutrients, instead of light), or different life-history strategies (earlier senescence, in fynbos understoreys). Also, the pattern of senescence in the overstorey accompanied by recovery in the understorey reported by van Wilgen (1981, 1982) shows that the inversely linear progression may not continue indefinitely. In any case, this overstorey-understorey relationship promises a useful basis for comparison of successional patterns and processes among the different mediterranean-type ecosystems, and a basis for extrapolating from local experiments.

23.3.4 CONSEQUENCES OF PROLONGED ABSENCE OF FIRE

The potential for replacement of mediterranean-type shrublands by alternative vegetation types if fire is excluded is a controversial matter

and empirical studies are few. First, prolonged absence of fire may lead to cyclic succession where shrubland dominants alternate or replace themselves as gaps occur through population senescence or death of large individuals, as in Australian heath or in fynbos (Specht et al. 1958; van Wilgen 1981, 1982). This has not been suggested for chaparral. This pattern would fit the inhibition model of succession proposed by Connell and Slatyer (1977).

Second, senescence among the dominants of the mature stand may allow less abundant species already present to propagate and gain prominence - the tolerance model (Connell and Slatyer 1977). In chaparral (of the "climax" zone) Patric and Hanes (1964) have suggested that a "scrub oak chaparral" can develop over about 50 years, through the death of certain typical chaparral species such as in the genus Ceanothus and persistence and seed-establishment by Quercus dumosa, Prunus ilicifolia, and Rhamus ilicifolia (see also Horton and Kraebel 1955). In northern California, Sampson (1944) has suggested replacement of chaparral by grass with time. In Australian heath, Hazard and Parsons (1977) deduced that in certain parts of their study area, Banksia and Leptospermum, unable to regenerate without fire, were slowly being replaced by Leucopogon (Epacridaceae), seedlings of which were able to establish in old vegetation.

In other cases, senescence of the dominants appears to allow immigration of species of an alternative cover type - perhaps the facilitation model applies (Connell and Slatyer 1977). Van Wilgen (1981) has described a measure of immigration by tree species such as Kiggelaria africana of senescent fynbos on relatively fertile granite soil at Jonkershoek after 25-35 years of protection against fire. These species that are seen as precursors of evergreen rain forests. Del Moral et al. (1978) report a slow replacement of heath by mallee eucalypts and Burrell (1969, in Hazard and Parsons 1977) and Hazard and Parsons (1977) show how typical mixed heath can sometimes be replaced by Leptospermum thicket.

In some cases, the vegetation seems simply to stagnate, where there is gradual mortality among long-lived dominants but little immigration or re-establishment. This would fit the inhibition model, and has been reported for chaparral (Horton and Kraebel 1955; Hanes 1977). Stagnation appears to occur in fynbos on quartzites. Bond (1980) could find no successful establishment in a recent sample survey in his senescent stands. A recent survey in 35-year-old vegetation in the Kogelberg showed that though 90% of the dominant Leucadendron population was dead, no seedlings or young plants were present nor were any immigrant shrubs or trees to be found (Kruger, unpublished).

Presently, no useful generalizations seem possible about the likelihood of and patterns in vegetation replacement in the absence of fire.

23.4 Secular changes in vegetation under different fire regimes

Pyric succession in the process of vegetation change between successive fires. The longer-term changes in vegetation induced by a change from one regime to another has hardly been studied, but for experimental work in garrigue by Trabaud (1973) and in fynbos transitional to grassland by Trollope and colleagues (Downing et al. 1978). Also van Wilgen (1981, 1982) reports results from comparative studies in frequently and less frequently burned vegetation.

These studies show pronounced changes in structure and diversity with different fire frequencies. Frequent fires in garrigue and transitional fynbos favour perennial grasses. Frequent fires in fynbos at Jonkershoek

induce richer plant communities than otherwise, even though some shrub species are eliminated (van Wilgen 1981), and Campbell and van der Meulen (1980) have shown how where the climax is a tall-scrub, increased fire frequency increases understorey graminoid species, whereas where the climax is a graminoid fynbos, greater frequency increases both graminoid and woody species. Despite these changes, there was no great change in species composition overall.

Our empirical knowledge of the relation between fire regime and secular vegetation change is therefore very limited, though many speculative models have been inferred (e.g. Cooper 1922; Jackson 1968; Hanes 1977).

23.4.1 CHANGES IN STRUCTURE: SPROUTERS VERSUS SEEDERS

One aspect of the effects of changes in regime that has claimed attention is that of balance between sprouters and seeders. Perennial species that regenerate vegetatively when burnt (sprouters) form a relatively stable component of the stand and are relatively little affected by a single fire, but stand composition in terms of sprouters and seeders can be changed by changing fire regime. The most evident effect is that of too-frequent fire. In fynbos and Australian heath seeders tend to be eliminated because they cannot mature, and sprouters favoured because their propagation is stimulated by too-frequent fire (Specht et al. 1958; Siddiqi et al. 1976; van Wilgen 1981, 1982) and the same holds by implication for chaparral (Hanes 1971; Keeley 1977a) but considerable variation in the relative abundances of sprouting and seeding shrubs is evidently not explained by such obvious fire effects.

Table 2. Regeneration mode in some typical mediterranean-type shrub taxa (data from Wells 1968; Rourke 1972; Williams 1972).

	Number of species	
	Sprouting	Seeding
CHAPARRAL		
Arctostaphylos	16	59
Ceanothus	12	46
CAPE FYNBOS		
Bruniaceae[a]	4	8
Ericaceae[a]	4	46
Leucadendron	7	73
Leucospermum	4	36[b]

[a] Flora of Jakkalsrivier, Lebanon only: Kruger, unpublished.
[b] At least three of these species show some tendency to resprout from epicormic buds - Rourke 1972.

Among trees or shrubs about half or more of any regional flora comprises sprouting species (Keeley 1977a; Kruger 1977b; Gill and Groves 1981), though large genera characteristic of the floras tend to have more seeders (Table 2). However, mature stands vary considerably in the ratio of seeders to sprouters, both between and within regions and in terms of both floristic composition and ecologial dominance (Tables 3 and 4). In chaparral, stands may consist nearly entirely of sprouting Adenostoma fasciculatum (80% or more of cover - Hanes 1977); by contrast, Schlesinger and Gill (1978) studied several nearly pure stands of Ceanothus megacarpus, a seeder; in one 21-year-old stand C. megacarpus comprised 98% of individuals and 100% of canopy cover. In Australian heathlands, sprouters appear to predominate. Specht (1981) lists data for seven stands in which sprouters account for between 54% and nearly 100% of above-ground plant biomass, except in an atypical Leptospermum stand where sprouters were absent. Seventy-three per cent of the shrub species in vegetation surveyed by Russell and Parsons (1978) and all 26 species in the Banksia woodland analysed by Whelan and Main (1979) regenerated vegetatively. There are nevertheless numerous cases, at least in the south-east, where typical heaths are dominated by seeders such as Banksia ericifolia, Casuarina distyla, Hakea gibbosa, H. sericea and H. teretifolia (Siddiqi et al. 1976; A M Gill, personal communication 1980).

Two related ecological explanations have been proposed for this variation. Keeley (1977a) argued that the relative success of seeders depends on the availability of "post-fire openings" in the regenerating vegetation, where seedlings could establish and grow free of competition from sprouters. Thinning of a stand of sprouters is progressive in the interval between fires. Live and dead fuel accumulates, and the longer a fire is deferred, the greater its intensity and the greater the mortality in sprouters, and the more openings after fire. Chaparral seeders are relatively long-lived and maintain fecundity (see below) so that abundant seed is available for regeneration in the openings. Seed stored in the soil is well insulated against fire. Thus seeders have the advantage in the open regrowth that occurs after rare fires, as opposed to the competitive conditions in the relatively dense regrowth of sprouters found when fire recurs soon, and the ratio of seeders to sprouters therefore increases progressively with decreasing fire frequency. Coexistence of the two forms requires a variable fire frequency, including long fire-free periods.

Specht (1981) also emphasizes the competitive advantage enjoyed by sprouters during post-fire regeneration. Available moisture determines the density (foliage projective cover) of Australian heath, and therefore the more humid the environment, the less gaps for seeders, and the less their importance in the climax stand. Thus, the relative abundance of sprouters correlates positively with foliage projective cover so that seeders are virtually absent from humid sites. The relative prevalence of either mode of regeneration is a consequence of site productivity and hence availability of gaps for seeders, rather than of fire response.

Both Specht and Keeley argue for the crucial role of competition for gaps in the evolution of sprouters and seeders. In South African fynbos patterns in the relative abundances of sprouters and seeders are not readily apparent. Fynbos stands, including those on moist sites, have a number of species of both types, though often dominated by seeding shrubs that may cover half or more of the ground; sprouting shrubs are seldom if ever so dense (Kruger 1979b; Tables 3 and 4) and the pattern that Specht (1981) reports for Australian heathlands is not found. Furthermore, senescence in the dominant serotinous seeding shrubs results in reduced

Table 3. Species from representative stands of chaparral, heath and fynbos classified according to mode of post-fire regeneration.

	Chamise chaparral (McPherson and Muller 1969)	Manzanita chaparral (Vogl and Schorr 1972)	Australian heath Wilsons Promontory (Russell and Parsons 1978)[a]	Protea fynbos (Kruger 1979bb)	Sympieza fynbos (Kruger 1979bb)
Age, yr since fire	1,11	1 2, 42	1 - 20	17	18
Seeding trees and shrubs					
- seed storage on plant	0	0	2	1	2
- seed storage in soil	3	3	3	14	9
Sprouting trees and shrubs					
- subterranean regenerative buds only	1	8	29	16	7
- aerial regenerative buds present	0	2	1	0	0
Seeding chamaephytes or sub-shrubs	4	20	0	3	2
Sprouting chamaephytes or sub-shrubs	0	0	10	2	1
Hemicryptophytes (sprouting perennial herbs)	0	1	16	14	22
Geophytes	2	2	15	18[c]	8[c]
Annuals	19	25	0	1[c]	0[c]
Uncertain and other	0	0	8	1	1
Total	29	61	84	70	51

a Species regeneration modes determined from Specht (1972) where necessary.
b Species regeneration modes determined from Van der Merwe (1969) and Kruger, personal observation.
c More species would probably have been found by sampling soon after fire.

Table 4. Relative importance of species of different modes of regeneration, recorded for various stands of chaparral, fynbos and Australian heath, and expressed as relative contribution of each category to cover or estimated biomass: data for most abundant species, representing a sum of 90% of total cover or biomass.

	Manzanita chaparral (Vogl and Schorr 1972)	Chamise chaparral (Mooney et al. 1977)[a]	Protea nerifolia fynbos (Kruger 1979b)[b]	Protea nitida woodland (Kruger 1979b)[b]	Erica fynbos (Kruger 1979b)[b]	Sympieza fynbos (Kruger 1979b)[b]	Dark Island dry heath-land (Specht 1979)[c]	Leptospermum heath (Russell and Parsons 1978)
Age, yr since fire	≥ 42	>20?	17	7	19	18	9	20
Seeding trees and shrubs								
- seed storage on plant	0	0	48	0	0	0	18	2
- seed storage in soil	7	33	0	11	36	54	16	0
Sprouting trees and shrubs								
- subterranean regenerative buds only	89	60	43	24	9	2	38	76
- aerial regenerative buds present	0	0	0	37	0	0	0	0
Herbaceous perennials - seeding	0	ND	0	0	0	0	0	12
Herbaceous perennials - sprouting	0	ND	0	19	47	35	11	6
Uncertain	0	0	0	0	0	0	9	5

abc Information on regeneration mode from Hanes (1971), Van der Merwe (1969) and Kruger, personal observation, and Specht (1972) and Specht et al. (1958), respectively.

seed banks and a decline in daughter populations after fire, with prolonged deferral of fire (Bond 1980); the balance between seeders and sprouters can therefore respond strongly to both an increase (see above) and a decrease in fire frequency. A general explanation of the mechanisms underlying this pattern therefore requires a demographic approach, that will predict the relative recruitment and mortality of sprouters and seeders respectively under the varying conditions that determine gap formation.

The prevalence of the sprouting habit among dominant shrubs in Australian heathlands could be a recent artifact of the high fire frequencies, at least in recent times (see above). However, this is unlikely because seedling shrubs have survived in areas with low foliage projective cover despite high fire frequency (Specht et al. 1958, for Dark Island heath). Specht et al. (Chapter 7, this volume) show that water availability (moisture index values) does not reach as high levels in fynbos as in Australian heath, and thus the range of foliage projective cover values is truncated at the upper end. By this argument, there is greater potential for seeders in fynbos overall than in Australian heathland and hence their greater abundance and diversity in the former.

Sprouting hemicryptophytes and other persistent perennial herbs are more diverse and abundant in South African fynbos and Australian heath than in other mediterranean-type ecosystems (Kruger 1977a). In fynbos these plants were more abundant and diverse on frequently burnt sites than on less frequently burnt areas, and were also favoured in a measure by the opening of the canopy that occurs with long deferral of fire (Campbell and van der Meulen 1980; van Wilgen 1981). Nevertheless, this component is usually prominent irrespective of fire history.

In garrigue, perennial grasses are sparse in old, unburned stands but become abundant when vegetation is frequently burned (Trabaud 1973). In chaparral, perennials such as Stipa lepida, Paeonia californica and Marah macrocarpus persist at all stages of development, but are invariably sparse; their response to fire frequency is unknown, but their relative density post-fire is low compared with that of annuals and short-lived herbs and sub-shrubs. The vines (Convolvulus, Marah) may often have high cover after fire but populations do not increase (Horton and Kraebel 1955; Keeley et al. 1981; Westman 1981). This is a major contrast between chaparral and most other northern mediterranean-climate shrublands, and Australian heath and South African fynbos, and seems to render the post-fire environment more competitive in the latter case.

23.5 Plant demography and succession

Simple, essentially qualitative information on plant life histories and analysis of stands in such terms may be sufficient for models that predict the broader patterns of vegetation replacement, as in the "vital attributes" model of Noble and Slatyer (1981). But quantitative, demographic data are required to understand and predict the course of post-fire succession, as well as the effects of different fire regimes on the relative abundances of species.

23.5.1 PERSISTENCE AND REGENERATION IN SPROUTERS

Though most plants in a stand persist and regenerate through sprouting there are few quantitative data that relate survival and regeneration mode and rates to fire regime or to other physical and biotic environmental

factors, except for the work of Horton and Kraebel (1955) and J E Keeley and colleagues (Keeley and Keeley 1981; and references therein) on the demography of seeding and sprouting in the chaparral shrubs. The prevailing dominant sprouter in chaparral, Adenostoma fasciculatum as well as certain others such as Ceanothus leucodermis are relatively plastic in their sprouting and seeding habits (Keeley and Zedler 1978), and often experience a relatively high mortality in fires (e.g. 46% - Horton and Kraebel 1955; Keeley and Zedler 1978) and high seedling recruitment, though mortality among less frequent sprouting species is low (e.g. Horton and Kraebel 1955). In Adenostoma, the proportion of the regenerating population in seedlings ranged from about 16% to 55% and increased linearly with decreasing total shrub cover at four years on different sites ($r = 0.70$, $P = 0.01$, for data in Keeley and Keeley 1981). By contrast, in Australia and South Africa, survival rate in fires of sprouters seems uniformly high. Beadle (1940) reports survival rates of 92-100% among common Australian heathland shrubs and trees. The near-zero mortality in Protea nitida (Haynes 1976) is probably indicative of the situation in fynbos. Specht et al. (1958) recorded no seedlings after fire for the dominant sprouters at Dark Island.

Aside from fire ephemerals, all mediterranean-type ecosystems have persistent herbaceous perennials of great longevity. This, with quick responses to burning, allows prolonged coexistence with dominant shrub forms and reproduction in the sometimes long-deferred post-fire environment. For example, Dixon and Pate (1978) report putative ages of up to 54 years for Drosera erythrorhiza and greater ages (>100 years) have been found in Watsonia pyramidata (Kruger 1977b). Geophytes remain semi-dormant between fires (e.g. certain Orchidaceae in fynbos - Hall 1959; Paeonia, Brodiaea and others in chaparral, Horton and Kraebel 1955). Perennial grasses also persist. In the Mediterranean region, Brachypodium ramosum is greatly reduced in abundance in well-developed stands but flourishes immediately after fire (Specht 1969; Trabaud 1973). Naveh (1974) describes other examples. Perennial grasses of a similar habit are sometimes also found in chaparral (Melica and Stipa - Horton and Kraebel 1955). In fynbos, grasses such as Merxmuellera rufa are conspicuous in the first season or two postfire, flowering profusely and having vigorous leaf rosettes. Between fires it is scarcely detectable, each tuft showing perhaps one or two brief leaf-blades (Kruger, unpublished). In fynbos, perennial herbs apparently outlive seeding shrubs (Campbell and van der Meulen 1980; van Wilgen 1981).

The demography of such species is poorly known. Data for survivorship of fire, vegetative propagation, and seedling establishment for Watsonia pyramidata show pronounced population response to fire (Kruger 1977b) but in Brodiaea, Convolvulus and other California geophytes there appears to be little change in population despite prolific growth and flowering after fire (Stone 1951; Horton and Kraebel 1955; Keeley et al. 1981).

23.5.2 SEED-BANK DYNAMICS

Westman (1979) has proposed that a large proportion (58%) at least of the herbaceous flora of chaparral depends on immigration of seed after fire from herbs in open coastal sage stands. This is unlikely, given the distances involved, the relative weakness of wind dispersal in general (Harper 1977; Cook 1980), and the very rapid appearance of herbs after fire (Keeley et al. 1981). Some species, which between fires grow on tracks and other open sites, may progressively invade the post-fire habitat, but most apparently rely on seed already present (Horton and Kraebel 1955; Vogl and Schorr 1972; Christensen and Muller 1975; Keeley et al. 1981). Among seeding species of both herbs and shrubs the pattern appears to be one of limited dispersal and survival in situ through dormancy (Wicht 1948; Specht et al. 1958; Hanes 1977). Keeley (1980, in Keeley et al. 1981) suggests that "fire annuals" of the chaparral behave like fugitive species but since exposure of any chaparral site by fire is inevitable there is little selection for long-range dispersal. The high species turnover between the fire ephemeral floras listed for different sites by Hanes (1977) bears this out (see also Keeley et al. 1981). At least in fynbos and Australian heathlands we find that the dominant or prominent shrubs are also adapted for short- rather than long-range dispersal (Williams 1972 for Leucadendron; Berg 1981; Bond 1980).

Soil-stored seed is apparently the norm for chaparral species (Hanes 1977) but many shrubs of Australian and South African heathlands differ from their Mediterranean and New World counterparts (aside from Coniferae), in the high incidence of serotinous species that retain viable seed stored in protective organs on the parent plant (Gill and Groves 1981). Serotiny is found mainly in Proteaceae but also in Myrtaceae (Eucalyptus - Beadle 1940; Callistemon and others - Kruger, unpublished), Casuarinaceae (Beadle 1940), Ericaceae (Erica sessiliflora - Baker and Oliver 1967) and Bruniaceae (Brunia spp., Berzelia spp. - Kruger unpublished). Also, serotiny has evolved differentially and, apparently, independently in different lineages of the Proteaceae (Banksia and Hakea in Grevilloideae; Isopogon, Protea, and Leucadendron in Persoonioideae). This therefore reflects evolutionary convergence rather than phylogeny.

The seed of these shrubs are relatively large (10-760 mg), and rich in nitrogen and phosphorus (van Staden and Brown 1977; Chapter 10, this volume) with concentrations respectively 8-100 times and 30-500 times the levels found in leaves of the same plants; 65-83% of seed or embryo dry mass is in protein and oil (Kuo et al. 1982; see also van Staden and Brown 1977).

In such species seed ripens over 9-24 months (e.g. Protea repens, Jordaan 1949; Kuo et al. (1982) for Western Australian species) and is held dormant until the organ or the parent plant dies, usually from fire. Seed may be held for 3-9 years or more, (e.g. in Callistemon, Leucadendron, Protea - Kruger, unpublished) but shows no prolonged dormancy after release and imbibition (e.g. Banksia ornata, B. ericifolia, and B. serratifolia, Specht et al. 1958; Siddiqi et al. 1976; Leucadendron spp., Williams 1972) though some species require stratification to overcome seed-coat dormancy (Deall and Brown 1981). An extreme case is found in Leucadendron platyspermum, where seed germinates in the cones before falling to the pyrogenic seed bed (Williams 1972). Because seed is short-lived after release the mortality schedule and age-specific fecundities of the parent plants are critical in determining post-fire daughter populations: Bond (1980), for example, has shown how post-fire regeneration in stands of senescent Protea punctata was markedly depressed relative to that in a burnt mature stand.

Large, rich seeds are not confined to serotinous species (e.g. Williams 1972 for Leucadendron) and is a trait adaptive for seedling establishment in a competitive post-fire environment (Grundon 1972; Kuo et al. 1982) but serotiny as such would be one trait adaptive for large-seeded species in the face of predation in an otherwise resource-poor environment (Gill 1981b). Serotiny is however also a means for precisely cued release of seed onto the post-fire seed bed as well as a predator satiation mechanism (Gill 1975, 1981b).

The dynamics of canopy-stored seed have been little studied in mediterranean-climate shrubs but Gill (1981b) has indicated for Banksia ornata that annual loss is less than 2%, and that the balance of seed remain viable. By contrast, soil-stored seed of Ceanothus and Arctostaphylos in chaparral have an annual attrition rate as high as 90%, though the soil seed-bank was nevertheless 100 times or more greater than the post-fire seeding population (Keeley 1977b). Thus, serotiny is associated with a low annual production of high-quality seed with low turnover and well-cued germination, whereas soil seed-banks require high fecundities to balance annual attrition, but with the advantage that the species can persist in situ as seed for some time after death of the parent plants as well as maintaining a soil reserve after post-fire germination.

Seed banks are characteristic of successional vegetation and hence of areas subject to widespread disturbance generally (Grime 1979; Cook 1980). In mediterranean-type ecosystems they are perhaps unique in that the composition of the seed bank closely reflects the species assemblage of the current vegetation; in other situations the similarity between species as dormant seeds and those of the plant cover steadily diverges with successional change (Oosting and Humphreys 1940; Harper 1977; Cook 1980).

The cues for germination among the species of these seed banks are complex and varied, including release from allelopathic inhibition in certain California herbs and shrubs (McPherson and Muller 1969; Christensen and Muller 1975), the pyrogenic heath pulse as a predictive trigger for stimulation of dormant soil-stored seed (Quick 1935; other references in McPherson and Muller 1969), change in soil temperature regime (McPherson and Muller 1969), contact with charcoal for some chaparral herbs (Wicklow 1977), or simply release of serotinous seed on the death of the parent (see above). Persistent seed-banks are a necessary correlate of such opportunistic adaptations (Grime 1979).

The relative abundance of seed of different species in a stand will vary with the length of the fire-free interval because of differences in life span and fecundity schedules between species and differences in decay rates of seed pools. Thus the composition of the seed stock available for germination after fire will vary (Specht et al. 1958). Because of complex germination controls the responses to any given fire will vary with intensity (Gill and Groves 1981) and season of the burn (W J Bond, personal communication 1981). Therefore the interaction between the composition of the seed bank and fire regime should cause considerable variation in the relative abundance of plants. Our predictive knowledge of the effect of fire regime on mediterranean vegetation will depend greatly on understanding the dynamics of seed banks and controls in germination.

23.5.3 MORTALITY AND SENESCENCE IN SEEDING SHRUBS

Among seeders, populations each consist by and large of a single cohort dating back to the last fire. Marked differences are found among these shrubs with respect to life spans and patterns of mortality, or survivorship curves.

Among seeding shrubs the first growing season after fire is usually crucial. Specht (1981) has shown direct correlations between rate of establishment (seedling survival) and the duration of surface soil moisture exceeding 40% content, and this bears out observations by Horton and Kraebel (1955) and many others. Once plants have survived the first season, different patterns of mortality are found in the absence of fire (Fig. 3). The survivorship curve for Banksia ornata suggests typical

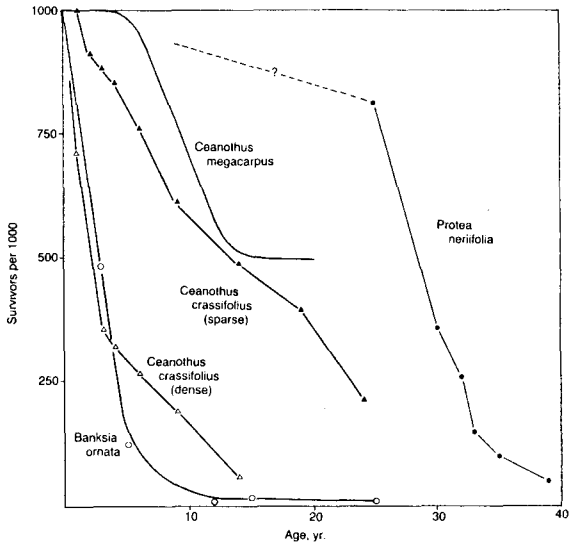


Fig. 3. Survivorship curves for a selection of mediterranean-type shrubs. Based on data in Specht et al. (1958), Horton and Kraebel (1955), Schlesinger and Gill (1978), and unpublished records of the South African Directorate of Forestry.

density-dependent mortality, with populations falling from about 74,000 plants ha^{-1} at establishment to 9000 and about 1200 at five and 15 years after fire respectively (Specht et al. 1958). In Ceanothus megacarpus rapid, apparently density-dependent thinning occurred in the first few years after fire but both dense and sparse populations then apparently remained stable at about 5000 plants ha^{-1} (Horton and Kraebel 1955). Schlesinger and Gill (1978) report a different pattern for Ceanothus megacarpus, with mortality greatest about five to 12 years after fire and populations stabilizing at about 16,000 to 30,000 plants ha^{-1}. Overall, populations thin at a relatively slow rate, so that individual shrubs are smaller at a given density than would be predicted from the two-thirds thinning rule (e.g. Schlesinger and Gill 1978).

Few data are available for fynbos but the curve for Protea neriifolia apparently represents dominant seeding shrubs. Populations have little mortality until late in life (> 25 years), and then decline rapidly. This is classical population senescence in Leopold's (1961) terms.

Thus, density-dependent mortality (self-thinning) in the maturing and mature populations appears to be exceptionally low in shrub dominants of both chaparral and fynbos. Chaparral dominants maintain vigour. Even small shrubs (small diameters, low biomass) maintain height growth and their position in the canopy, despite dense crowding (Keeley and Keeley 1977; Schlesinger and Gill 1978). Growth and reproductive output rates are maintained (see Keeley and Keeley 1977, 23-year-old versus 90-year-old populations of Arctostaphylos spp.). But marked thinning from abundant

post-fire populations and relatively limited life-spans (40-60 years) are evident for certain chaparral dominants, especially Ceanothus species (C. crassifolius, C. oliganthus, Hanes and Jones 1967; Hanes 1977; Keeley (1975) suggests the members of subgenus Euceanothus). Keeley (1977b) contrasted this pattern with that in Arctostaphylos glauca (low mortality, long life, few seed, few seedlings) and suggested that they represented alternative life-history strategies.

In relatively short life-spans of fynbos and Australian heathland species such as Protea neriifolia (Fig. 3) and Banksia ornata are notable. In fynbos, long-lived species like Leucadendron argenteum are those that have evolved protective mechanisms such as thick bark to ensure some survival among any cohort in most fires. They tend to occur in areas with low fuel accumulation rates because of aridity (Rourke 1972) or perhaps high fire frequency; life-history strategies are apparently entirely different.

The longest-lived seed-regenerating shrubs occur in chaparral. Davis (1973) and Keeley (1975) have described stem morphological features in long-lived seeding chaparral shrubs in the genera Arctostaphylos ("bark-striping") and Ceanothus ("stem channeling") which they suggest are adaptations for long life-spans, in that the ratio between photosynthetic tissue and supportive tissue (hence maintenance costs of carbon) is reduced (Keeley 1975). These features are absent from fynbos and Australian heath shrubs.

Reproductive output in terms of biomass in chaparral shrubs amounts to about 8-11% of total annual shoot increment (stem plus leaves plus reproductive tissues) (Mooney et al. 1977) or a maximum of about 25% in a "good" year (Keeley and Keeley 1977). Data for Banksia ornata in Specht et al (1958) indicate that reproductive tissues accounted for about 40-60% of net annual plant increment between the ages of nine and 28 years. Even if large allowance is made for leaf fall and other loss of increment it is clear that current allocation of biomass to reproduction is much greater in the Banksia than in the chaparral shrubs. This would seem to hold for fynbos seeders as well (cf. Protea repens in Kruger 1979c). Seed of these shrubs are particularly rich in nitrogen and phosphorus (see above) and the contrast in terms of mineral nutrient budgets could be more pronounced than for carbon. Thus, short lives in fynbos and Australian heathland shrubs may be owing to different resource allocation strategies that limit allocation to growth and support, relative to chaparral shrubs.

Senescence among serotinous shrubs and trees implies a high likelihood of local extinction with long intervals between fires or at least partial displacement by species with dormant seeds and by long-lived vegetative shrubs (Specht et al. 1958; Bond 1980).

All of the sclerophyllous shrublands include fast-growing perennial seeding shrubs and sub-shrubs that have intermediate life spans, which exploit the post-fire environment (Table 5). These apparently have low competitive ability and are eliminated as resources are appropriated by the longer-lived species. However, some such as Aspalathus in fynbos have very dense populations, low self-thinning, and marked senescence. It is not clear that the population dynamics in such cases are driven by competition though depletion of limiting resources such as phosphorus may limit life-spans (Chapters 12 and 13, this volume).

23.5.4 PRIMARY JUVENILE PERIODS AND FECUNDITY SCHEDULES

Information on the ages at which germinative perennials first produce seed is essential to understanding their responses to fire regime. No

Table 5. Examples of seeding shrubs with different life-spans in three mediterranean-type ecosystems. Primary juvenile periods shown in brackets[a].

Short-lived shrubs and sub-shrubs (4-10yr)	Lotus scoparius (Fabaceae) (2-3 yr)	Aspalathus spp. (Fabaceae) (2-4 yr)	Acacia suaveolens (Fabaceae)
	Lupinus longifolius (Fabaceae) (2-3 yr)	Othonna quinquedentata[b] (Asteraceae) (2-3 yr)	Boronia falcifolia (Rutaceae)
	Nama parryi (Asteraceae) (2-3 yr)	Ursinia crithmoides (Asteraceae) (2-3 yr)	Epacris pulchella (Epacridaceae)
	Senecio douglasiana (Asteraceae) (2-3 yr)		Persoonia shirleyae (Proteaceae)
Intermediate shrubs (10-50 yr)	Artemisia californica (Asteraceae) (3 yr)	Erica spp. (2-4 yr)	Acrotriche serrulata (Epacridaceae)
	Ceanothus oliganthus (Rhamnaceae) (< 5 yr?)	Protea neriifolia[b] (4-6 yr)	Adenanthos terminalis (Proteaceae)
	C. tomentosus (Rhamnaceae) (< 5 yr?)	Protea repens (3-4 yr)	Banksia marginata (Proteaceae) (c. 5 yr)
	Eriogonum fasciculatum (Polygonaceae) (< 5 yr)	Leucadendron floridum, L. macowanii (Proteaceae) (3 yr)	Baeckea ericaea (Myrtaceae)
	Salvia mellifera (Lamiaceae) (3 yr)	Leucadendron comosum (4 yr)	Acacia longifolia (Fabaceae)
		Leucadendron muirii (6 yr)	Gompholobium minus (Fabaceae)
Long-lived trees and shrubs (> 50 yr)	Arctostaphylos glauca[b] (Ericaceae) (< 10 yr)	Protea laurifolia (5-7 yr)	Banksia intergrifolia
	Ceanothus crassifolius (Rhamnaceae) (< 10 yr)	Leucadendron argenteum (7-9 yr)	Leptospermum laevigatum (Myrtaceae)
		Leucospermum conocarpodendron (Proteaceae) (7-9 yr)	
		L. praemorsum (9-11 yr)	

a From Adamson (1935); Horton and Kraebel (1955) ; Specht et al. (1958, 1977); Van der Merwe (1969); Keeley (1975, 1977a); Hazard and Parsons (1977); Keeley and Zedler (1978); Moll et al. (1980).

b Species showing marked senescence.

studies have focused on this parameter in plants of mediterranean-type ecosystems but several report observations. The general pattern is for short-lived and intermediate shrubs to mature within 2-4 years (Horton and Kraebel 1955 for Artemisia californica; Adamson 1935 and van der Merwe 1969 for fynbos species). The relationship between age of first seeding and longevity is therefore approximately as found by Harper and White (1974), but the correlation is poor and mediterranean-type shrubs are usually precocious. Flowering and fruiting is advanced even among longer-lived dominants (Table 5). This is particularly so for fynbos shrubs. Rourke (1980), for example, reports several Protea species in cultivation as flowering within two years after germination; the median juvenile period in 42 species was four years. Observations suggest that plants in the field are not much delayed in this respect (Table 5).

Few observations are available for chaparral dominants, but they appear slower to mature, requiring 8-10 years or perhaps more (Table 5).

No data appear to be available to show patterns of age-specific seed output (fecundity schedules). Biomass accumulation graphs for Banksia ornata in Specht et al. (1958) show accelerating fruit production per plant from about nine years of age to between 20 and 25 years, with some indication of declining annual production as 25 years age is approached. Certainly these authors imply a reduced annual reproductive output between 28 and 50 years. In fynbos, it is not clear that reproductive output per plant declines as senescence approaches (Bond 1980).

Seeding chaparral dominants maintain reproductive vigour with advancing age and Keeley and Keeley (1977) found greater fruit output in a 90-year-old sample of Arctostaphylos glauca than in an adjacent 23-year-old stand.

In chaparral, sprouting shrubs also maintain their vigour and reproductive performance as they age (e.g. Arctostaphylos glandulosa in Keeley and Keeley (1977)). In fynbos, tall sprouters such as Protea nitida appear to maintain reproductive effort (Kruger, personal observation) but many shoots of the lower sprouter such as Protea cynaroides and P. speciosa appear to lose vigour within a decade or so after fire, and flowering per plant declines (Rourke 1980); the shoot systems are rejuvenated by defoliation.

23.6 Conclusion

The regions discussed here share similar regimes in that fires are of intermediate frequency and intensity; fire does not occur just about once a year as in grassland, nor at long intervals (> 100 years) as do conflagrations in coniferous or ash-type eucalyptus forests; simultaneously, fires are sufficiently intense so as to open the site effectively (more so than in grasslands, wooded savannas or eucalyptus woodlands), yet do not preclude vegetative survival of a proportion of plant individuals. These regimes may have the special characteristic of allowing more diverse modes of regeneration (various seeding and sprouting strategies) than do the regimes of grassland or forest. Comparative studies would highlight aspects of the dynamics of mediterranean-type ecosystems especially worth studying.

Although fire regimes in mediterranean-type ecosystems are predictable they are stochastic. All components of fire behaviour vary within one fire on any site, and so do intensity, frequency and seasonality in time. Interactions between the fire event and current and post-fire conditions compound this variability.

nutrient distribution, of charcoal distribution (see Wicklow 1977), post-fire erosion, and similar factors (Chapter 22, this volume) induces microsite variability and enhances pattern diversity (internal beta diversity). These effects with the temporal partitioning of resources over time that is allowed by pyric succession must play a role in maintaining plant species diversity. This role has not been studied explicitly but since managers are and will be affecting the fire factors that are relevant here, appropriate studies are urgently necessary. The Australian experience, where regular, frequent, low-intensity controlled burns markedly affected the richness and character of understorey species in eucalypt forests, to the point of modifying ecosystem nutrient cycles and forest health, is indicative of likely problems (see Gill et al. 1981).

The longer fire cycle in chaparral, with high fire intensity, would very likely account for the marked contrast between chaparral pyric succession and that in fynbos and Australian heath, while maintaining the full diversity of herbaceous species. Presumably, chaparral cannot burn so frequently that tufted grasses such as Stipa and other perennial herbs would become prominent, as grasses do in Quercus coccifera garrigue (Trabaud 1973). A regime of infrequent, intense fires in fynbos and Australian heathland would favour seeders if the fire period does not exceed the life-span of serotinous seeders, but the small annual and biennial flora would continue to be limited by nutrients. In any event, under the "normal" regime sprouting herbs and shrubs are abundant and the competitive post-fire environment not suited to annuals and short-lived perennials.

The research interests of ecologists and resource managers are largely coincident now. Alternative fire-management options must be selected on the basis of the predicted effects of different regimes on community structure and diversity. For this the effects of variations in regime must be simulated on the basis of our knowledge of the dispersal ecology, germination requirements, and demography of constituent species. Even the question of finding the "natural" regime is a matter for deduction from demography (cf. Keeley 1977a), in the absence of proxy records.

A basis for general principles must be found in geographic patterns in the structure and response to fire of vegetation. These patterns could be made tractable by approaches such as that of Specht and Morgan (1981), if linked with energy and water balance controls on vegetation dynamics (Chapters 2, 7 and 8, this volume).

Keeley (1977b), in his study of responses of chaparral shrubs to fire, proposed that each represents a different strategy, or demographic model. Gill (1981a) has outlined three different approaches to modelling vegetation-fire dynamics - species' response classification, species replacement models, and demography, each successively more complex. Presumably, convergence in plant life-history strategies will render manageable the problem of generalizing from our knowledge of a few species. Nevertheless there is considerable scope for work on the demography of representative plant species since present knowledge is simply inadequate for necessary generalizations. Studies to determine patterns in the distribution of strategy-types or fire life-form classes (Gill 1981a) are necessary to reduce apparent vegetation complexities to intelligible patterns.

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Chapter 5 Fire in Fynbos

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INTRODUCTION

Fires in fynbos are frequent, spectacular and alarming. They often cause considerable economic loss, as when 21 houses were lost in the Betty's Bay fire of 1970. Great fires, such as those in the region between Swellendam and Port Elizabeth in 1869, are cardinal in the history of land management in the zone and the lessons from them are embedded in the manager's lore. To the biologist the consequences of fire often seem disastrous. It is hard for an observer to imagine that the blackened waste to be seen after a fynbos fire is merely a stage in the cycle of regeneration and development of such rich and attractive communities.

The consequences of prevalent fire in the fynbos biome are varied, both ecological and economic. Costs include direct losses of assets such as timber plantations during fires, as well as the continuing costs of protecting those assets (Kruger 1979a). Indirect costs of unmanaged fire include those arising from invasions by exotic trees and shrubs - for instance, reduced catchment water yields, increased hazards of wild-fire, reduced ecological diversity, and loss of aesthetic values. Potential benefits of a managed fire regime include maintenance of natural biotas, cost-effective fire control, and enhanced water yields (Bands 1977; Kruger 1977a). The history of attitudes, ideas and policies regarding fire have been reviewed elsewhere (Wicht and Kruger 1973; Bands 1977). This chapter is a review of ecological studies and observations, as a step toward a basis for rational fire management of the fynbos biome.

All of the five Veld Types in the fynbos biome (Huntley, this volume, chapter 1) contain communities that are burnt periodically and recover subsequently, but they are not uniform with regard to the incidence of fire, nor in their responses to fire. Strandveld, for example, is likely to carry fire less often than the other types, because of the sparse canopy and the relative abundance of succulents. A comprehensive account of the ecological effects of fire in the biome is not possible, because our knowledge does not extend that far. This account centres on the mountain fynbos (Acocks's (1975) Veld Types 69 and 70), about which there is most information. Where possible, facts are adduced to show how the communities or biota of the other Veld Types resemble the mountain fynbos or differ from it, with regard to the ecological effects of fire.

CHARACTERISTICS OF FIRE REGIME AND FIRE BEHAVIOUR

FUELS, CLIMATE AND WEATHER

Fynbos communities can accumulate large quantities of fuel for fire. This fuel comprises well-dispersed, but nevertheless bulky, inflammable material in the intermingled herb and lower shrub strata sometimes up to 1,5 m above soil level but usually less than 0,75 m above soil level (Table 1). Emerging from this are taller shrubs (usually up to 3 to 5 m tall) whose crowns burn if conditions are suitable. In the herb and lower shrub layer fuel quantities of between 4 and 40 t ha^{-1} have been recorded (Kruger 1977b; van Wilgen 1982).

Table 1 Some physical characteristics of samples of fynbos plants that provide flammable and less flammable (*Leucadendron laureolum*) fuel, compared with a California chaparral dominant, *Adenostoma fasciculatum* (from Countryman and Philpot 1970; le Maitre 1980).

Species	Physical properties of fuel				
	Mean height m	Mean crown volume m^3	Mean biomass g m^{-2}	Mean fuel density[a] g m^{-3}	% available fuel[b]
Leptocarpus hyalinus	0,39	0,025	511	1546	100
Restio egregius	1,13	0,424	2166	1913	100
Sympieza articulata	0,66	0,054	642	1092	50
Leucadendron laureolum (male)	1,62	5,05	1399	868	30
L. laureolum (female)	2,15	4,13	2910	1296	23
Adenostoma fasciculatum	1,70	2,82	2220	1392	39

[a]Ratio of crown mass to crown volume.
[b]Arbitrarily determined as the proportion of crown mass in leaves and in shoots with diameter less than 6 mm.

The physical and chemical characteristics of this fuel are poorly known. Concentrations of secondary chemical products are usually high, and many aromatic species are found. The essential oils content of leaves in *Agathosma betulina* (round leaved buchu) and *A. crenulata* (long-leaved buchu) (Rutaceae), for example, ranges from 1,4 to 4,0% of oven-dry mass (Blommaert and Bartel 1976). The stems of restionaceous plants, an important fuel component, are usually covered in a thick layer of cuticular wax. The indications are, therefore, that the chemistry of fynbos fuels favours combustion rate (King and Vines 1969). The physical properties of the main fuel layer are determined by the nature of the predominant narrow-sclerophyllous shrubs which have leaves of widths and thicknesses of about 1 to 2 mm and fine, much-branched shoots. Tufted and rhizomatous Restionaceae and often various sedges and grasses add to the relatively fine textured, highly combustible fuel mix. It is worth noting, however, that most components of available fuel in fynbos have minimum dimensions greater than about 1 to 2 mm, and are therefore coarser on average than those of grassland and savanna and this most likely explains the normally lower rates of fire spread, despite high fire intensities.

The amount and character of fuel varies considerably among vegetation types. Thus, in the restioid-ericoid zone (Taylor 1978) the fuel may consist almost entirely of about 4 to 6 t ha^{-1} of restioid material whereas in sclerophyllous scrub various life forms contribute (Table 2; Kruger 1977a). Naturally, fuel quantity varies also with succession after fire (Table 2 and Figure 6). Fires occur in 2 yr old vegetation under exceptional circumstances (Martin 1966). Four years' regrowth is usually necessary to sustain a spreading fire (Martin 1966; Kruger 1977a) and the vegetation must be somewhat older to burn readily under average summer conditions. Also important in determining the frequency of fire is the rate of accumulation of litter and standing dead material, which can comprise large proportions of above-ground biomass (Table 2). Martin (1966) has shown in field experiments that flammability of mature fynbos is largely due to the abundance of this dead component. In many fynbos communities litter and standing dead material begin to accumulate from the third year onwards, with death among 2 yr old shoots of Restionaceae that, unlike grasses and sedges, do not decompose readily. Other factors being equal, fire intensity increases with age of the vegetation as do height and depth of flame fronts. The large fires listed in Table 3 all occurred in very old vegetation (unburnt for 15 to 40 yr).

Table 2 Available fuel in fynbos stands of different ages and approximately similar sites at Jonkershoek[a] (from van Wilgen 1982).

Vegetation age, yr	Above-ground biomass and available fuel, g m^{-2}					
	4[b]		21		37	
Biomass component	Biomass	Available fuel	Biomass	Available fuel	Biomass	Available fuel
Tall shrubs	0	0	3130	1050	1600	430
Low shrubs	73	73	115	72	557	305
Graminoid and restionaceous plants	468	468	112	112	41	41
Forbs	84	84	182	182	36	36
Litter and standing dead	43	43	1430	1250	5330	3500
Total	668	668	4969	2666	7564	4312

[a]Available fuel defined arbitrarily as leaves and shoots with diameter less than 6 mm.
[b]Average for two stands.

Table 3 Some properties of selected large fynbos fires (data from Bands 1977; Department of Forestry records).

Locality of fire	Area km^2	No. of ignition points	Date	Duration days	Predominant age of veld yr
Hottentots-Holland Mtns	112,0	2	Dec 1942	18	15-20
Hottentots-Holland Mtns	171,3	2	Jan 1958	16	ca 16
Du Toits Kloof Mtns[a]	180,0	5	Feb/Mar 1971	17	10-20
Krakadouwpoort, Cedarberg State Forest[a]	27,0	ca 5	Dec 1972	4	ca 38
Krakadouw-Groot Koupoort, Cedarberg State Forest	59,5	1	Feb 1975	5	ca 40
Kouga Mts Baviaanskloof State Forest	187,0	1	May 1975	10	20-30
Sneeuberg, Cedarberg State Forest	135,0	1	Dec 1975	6	15
Heksberg, Kouebokkeveld Mts	300,0	1	Feb 1976	10	30-35
Langeberg Mts Garcia State Forest[a]	26,8	9	Mar 1977	4	15-20
Middelberg-Boskloof Cedarberg State Forest	107,0	1	Jan 1979	8	ca 15

[a]Causes include lightning.

Fynbos fuels impose a certain character on the fire regime. They are coarser and more dispersed than grassland fuels, and therefore do not burn as fast or as frequently though productivity may be similar. On the other hand, compared with chaparral fuels in southern California, for example, where fine fuels are concentrated in the crowns of shrubs (Countryman and Philpot 1970), the fynbos fuel bed is evenly dispersed, and inclined to burn more frequently, mainly owing to the presence of persistent hemicryptophytes (grass, sedges and restionaceous plants).

The nature of fynbos fuels and the characteristic weather and climates combine to favour a fire regime unique in southern Africa. Pertinent features of weather and climate are the following:-

1 Southeasterly winds occur frequently in summer. These may blow for several successive days, are usually strong, gusting to 30 m s^{-1} or more in the lee of mountains, and averaging 12 m s^{-1} or more over 24 hr (Schulze 1965; Kruger 1974). They bring moisture in orographic clouds to certain montane locations but usually desiccate most surfaces traversed because the air is warmed and dried adiabatically as it descends. Major fires occur on "southeaster" days in the southwestern Cape, from the Peninsula northwards.

2 Fohnlike bergwinds often precede cyclonic weather systems, especially in winter. Dry subsiding air moves off the interior plateau of South Africa in response to strong coastward pressure gradients. Standing waves arise as the air is drawn across the coastal ranges, and strong downwash in their lee results in warm, turbulent winds where the waves reach the surface. Phillips (1931), Tyson (1964) and le Roux (1969) describe the pronounced anomalies in winter air temperatures and relative humidities associated with the onset of bergwinds. Wicht and de Villiers (1963) and le Roux (1969) have shown that major fires occur usually in winter during these conditions in the southern Cape, between Hermanus and Port Elizabeth. The devastating fires described by Brown (1875) occurred in summer but during bergwinds. The fire of May 1975 in the Kouga, for example (Table 3), spread largely under bergwind conditions, when air temperatures exceeded 30°C in spite of typical winter weather before and after the fire.

3 Summer heat favours conflagrations in fynbos of inland mountain ranges. Large fires in the Cedarberg in 1975 and 1979 (Table 3) occurred during periods of 7 to 10 days during which maximum air temperatures ranged from 35 to 45°C, minimum relative humidities between 5 and 20%, and turbulent, erratic winds prevailed (Kruger and Haynes 1978).

It is likely that weather conditions that favour large fires occur rather irregularly, perhaps only once or twice per year at a given place, and not necessarily in midsummer.

CAUSES OF IGNITION

Figure 1 depicts some data on the causes of fires in the fynbos zone. Most fires in areas close to population centres (as in the case of the Cape Peninsula) are presently caused by human activity. On the other hand natural causes of fire are important in remote areas (see for example Table 4), no doubt because these areas are less subjective to man-made fires. The Cedarberg is subject to a relatively intensive fire protection system, and is visited by only about 10 000 to 15 000 people annually, so that fires owing to human agency are less likely and natural fires more likely than for example on the Peninsula. Horne (1981) reports a similar pattern in the Groot-Swartberge.

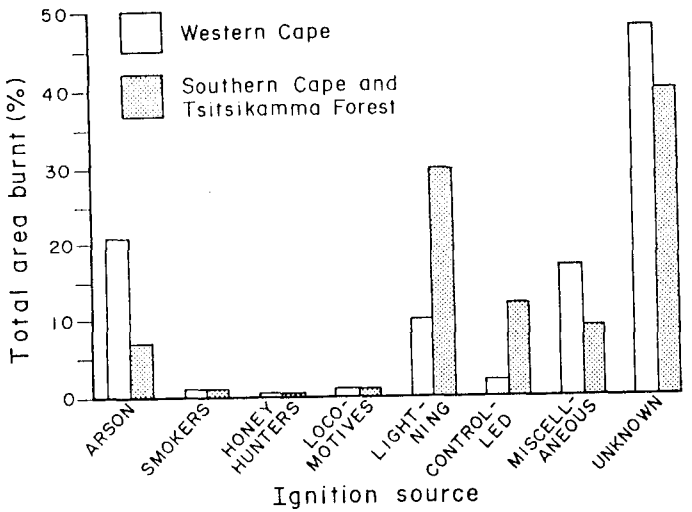


Figure 1 Classification of total area of unafforested State Forest land burnt in 1966/67 to 1975/76 according to ignition source (total area reported = 1 473 km^2) (Kruger 1979a).

It is difficult to determine the cause of a given fire. Nevertheless, there are documented eye-witness accounts of fires of natural origin (Wicht 1945). Fires due to lightning strikes are reported throughout the fynbos region, in spite of the relatively low frequency of lightning storms (about five thunderstorms annually at typical Cape weather stations; Schulze 1965). Although lightning is one-tenth as frequent or less in the western Cape as it is in the areas prone to thunderstorm activity (Kroninger 1978), the flash density is nevertheless adequate to explain the relatively high incidence of lightning fires reported in forestry areas. An annual flash density of 1,0 km^{-2} is equivalent to a record of 1 300 ground strikes within the 20 km range of a flash counter. This, at Citrusdal for example, is equivalent to about 400 strikes yr^{-1} which seems more than sufficient to cause a fire within the 1 300 km^2 area every few years.

Falling and rolling rocks arising from natural scarp retreat and earth tremors (which, according to Theron (1974), occurred in the southern Cape about 53 times over the past 50 yr) cause fires under suitable conditions of weather and fuel (Wicht 1945; van Wyk and Kent 1974).

FREQUENCY OF FIRES

Fire frequency can be expressed in terms of the number of years between fires at a site. The probability that the area will burn is the inverse of this return period. Thus, in a certain mountain range the vegetation on any given site may burn out once in 20 yr on average; the probability of fire is therefore 0,05 yr^{-1}.

Some indication of low fire frequencies can be obtained from records for areas protected against fire. An analysis of fires recorded in the Cedarberg from 1957 to 1975 (from the map in Andrag 1977) showed that about 50% of the total area was burnt in 1957 to 1959, 11% during 1960 to 1969 and 30% during 1970 to 1975; about 17% escaped fire during this period. Roughly 30% of the total area burnt twice or more. Almost all burns were wildfires. Records for the southerly slopes of the Groot-Swartberge indicate a frequency of natural fires of about once in 40 yr, though the actual frequency observed was once in 18 yr when fires of natural and human origin are considered jointly (Horne 1981). Frequencies on dry north aspects, transitional to karoo, were lower. Fire has been excluded for more than 30 yr from only relatively small areas such as Langrivier at Jonkershoek, and then usually by means of an elaborate firebreak system.

The frequency of fire in these protected areas can probably be taken as a lower limit for fynbos ecosystems under present conditions. Also, under past pre-colonial conditions, when fires, natural or otherwise, would have spread much more readily in the absence of manmade barriers, it is unlikely that such low fire frequencies occurred.

FIRE SEASON

The fine fuel component of fynbos communities includes dead material, the moisture content of which tends to follow that of ambient air. Thus, most mature fynbos will burn in warm, sunny conditions, whatever the season. It is not surprising therefore that wild-fires are reported in all seasons in any fynbos area (Figure 2). Nevertheless, most large fynbos fires occur in summer (Table 4) (Horne 1981), except that in the southern Cape coastal zone large fires occur frequently in winter (le Roux 1969). Martin (1966) refers to a fire of August 1955 as "... one of the most severe in the Grahamstown district".

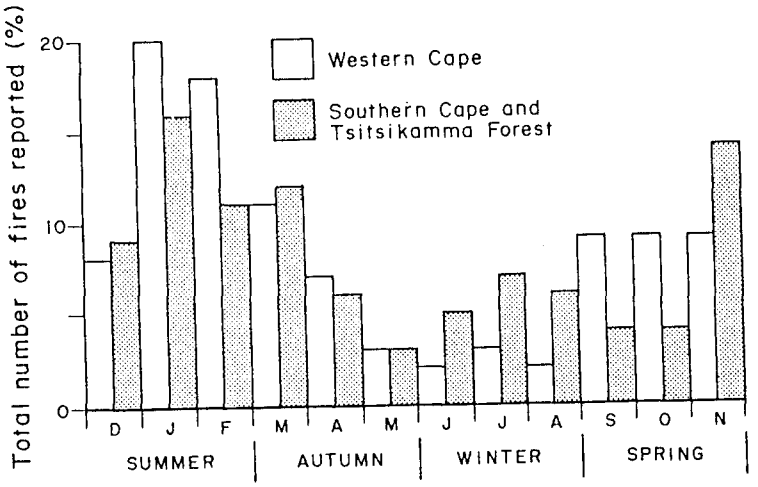


Figure 2 Seasonal incidence of fires on State Forest land in the fynbos biome during 1966/67 to 1975/76 (Kruger 1979a).

Table 4 Incidence and extent of wildfires in the Cedarberg State Forest (79 000 ha) during the period 1958 to 1974 inclusive (Andrag 1977).

Cause	Number of fires reported					Mean area per fire km^2	Proportion of total burnt area %
	summ.	aut.	win.	spr.	total		
Lightning	9	4	1	5	19	3,2	17
Rolling rocks	5	2	0	5	12	15,5	52
Escape from prescribed burn	0	0	1	3	4	8,8	10
From outside	0	3	0	1	4	1,7	2
Negligence of public	1	2	0	1	4	6,5	7
Honey hunters	0	1	0	0	1	18,2	5
Unknown	2	3	3	1	9	2,9	7
Total	17	15	5	16	53		
Mean area per fire (km^2)	10,9	7,5	1,8	3,2	6,8		
Proportion of total burnt area (%)	52	32	0	14			

The season of incidence of lightning fires could be a pointer to the possible seasonality of natural fires in fynbos. However, Department of Forestry reports for the 10 yr 1966/67 to 1975/76 show that while most large lightning fires occurred in summer, they occurred in all months but June and July (Horne 1981).

The relationship between season and frequency of fire is depicted hypothetically in Figure 3. This hypothetical model is no doubt an over simplication but probably reflects the essential trend.

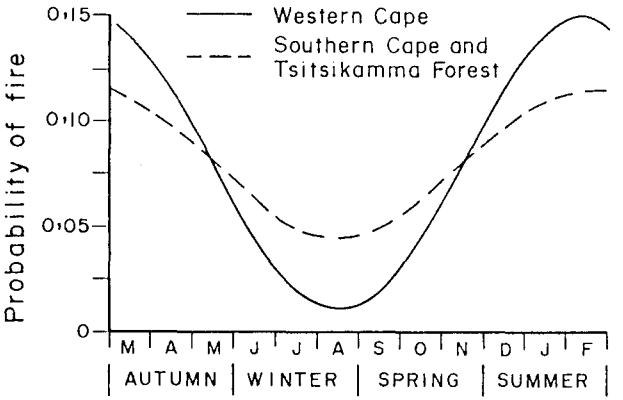


Figure 3 Hypothetical seasonal fire frequencies for the fynbos biome. Solid line represents a "western" fire regime and dashed lines, an "eastern" fire regime. Probability is calculated as the reciprocal of the interval in years between fires (Kruger 1979a).

FIRE INTENSITY AND BEHAVIOUR

There are few studies of fire intensity and behaviour in fynbos. Table 5 contains estimates of energy release rates from typical fynbos fires.

Fynbos fires are not exceptionally intense (though apparently more so than in grasslands), and have rates of advance rather slower than, for example, those in humid grassland with similar amounts of available fuel. Nevertheless, because the vegetation is tall and because of its structure as a fuel bed, flames tend to be rather high (2 to 5 m) and flame fronts deep (1 to 6 m). These fires are consequently difficult to control, especially in the prevailing rugged terrain.

Behaviour characteristics of very intense fires, such as powerful fire-whirls and long-range spotting, are not the rule in most fynbos fires. However, under hot windy conditions and highly combustible fuel loads, rapid rates of advance (over 4 km hr^{-1}) with moderate spotting (fires carried 200 m or more) have been

Table 5 Intensities for fynbos fires. Estimated values (from Bands 1977) for what are thought to be prevailing conditions. Observed values measured on plot trials in the Kogelberg (le Maitre 1980).

	Intensity categories			
	Low	Intermediate	High	Instantaneous maximum[a]
Estimated				
Available fuel ($g\ m^{-2}$)	300	700	1 000	-
Rate of spread ($m\ s^{-1}$)	0,07	0,38	1,11	-
Byram index ($kJ\ s^{-1}$)	360	3 300	18 900	-
Observed on plots				
Available fuel ($g\ m^{-2}$)	1 204	1 042	1 087	1 087
Rate of spread ($m\ s^{-1}$)	0,22	0,35	0,47	2,0
Byram index ($kJ\ s^{-1}$)	5 130	7 278	9 990	42 700

[a]Estimated on the basis of the maximum forward rate of spread on the plot ie 2,00 $m\ s^{-1}$ as opposed to the average of 0,47 $m\ s^{-1}$.

reported. The large fynbos fires (such as those listed in Table 3) almost all occur under relatively rare, severe weather conditions (see above).

Temperature changes produced by fire near and in the ground have important effects on plant nutrients and soil microbial populations (Dunn and DeBano 1977) and, presumably, have consequent effects upon vegetation dynamics. However, there are few data for fynbos. Martin (1966) recorded subsurface and surface soil temperatures during experimental burns in small plots (5 x 5 m) in heathland near Grahamstown. The vegetation had an average height of about 0,6 m. Temperatures were measured by means of a thermocouple and small capillary tubes filled with various organic compounds of different melting points. The burn in a plot with undisturbed vegetation produced a maximum temperature of 550°C at the surface; high temperatures persisted only for about 10 s and were close to normal within 480 s. Sub-surface soil temperatures however did not rise greatly, and menthol (melting point 43°C) at a depth of 12,5 mm did not melt. A second plot when cleared of "dead brushwood" produced a maximum surface temperature of 350°C. Taylor and Kruger (1978) reported temperatures in a burn in 4 yr old fynbos, measured by means of pellets that melt at different temperatures. Maximum temperatures observed at the soil surface at 36 random locations ranged from 149 to 371°C, with the mode at 316°C. At two stations, temperatures were measured at 0,45 m and 0,90 m: a maximum of 316°C was recorded in all cases.

EFFECTS OF FIRE REGIME ON VEGETATION STRUCTURE AND DYNAMICS

SUCCESSION AFTER FIRE

Kruger's (1977b) account of plant succession serves as a basis for what follows. Development of fynbos communities after fire must vary considerably with differences in vegetation type and environmental variables. For example, Levyns (1935a) describes an unusual succession in coastal renosterveld where the vegetation was successively dominated by a different seeding species in each of the first three years after fire. A seeding species of *Aspalathus* dominated in the fifth year, but Levyns assumed this was likely to decline and to be replaced by *Elytropappus rhinocerotis* (renosterbos). Temporary dominance by pyrophytic perennials is found sometimes where *Aspalathus* spp proliferate after fire (Dahlgren 1963). On humid mountain slopes in the Jonkershoek area the post-fire community can comprise a nearly pure stand of a 1,5 m tall, robust grass, *Pentameris thuarii*, which is replaced by mixed fynbos after 4 to 6 yr (Kruger, 1982). However, successional changes in dominants seem to be exceptional. Field observations and information in Mitchell (1922), Levyns (1929b), Adamson (1935), Wicht (1948b), Martin (1966) and Taylor (1969a, 1978) indicate that most mountain fynbos communities follow an essentially similar course of succession after fire, although there clearly is variability within the mountain fynbos in terms of both floral properties and time scale. The major features abstracted from these sources are outlined below.

Immediate postfire phase

Although fire intensities in fynbos range widely, burns are seldom so intense as to kill sprouting species. Regeneration of all or most of these species occurs within the first twelve months after fire. Hemicryptophytes appear within days or weeks at most, and some are able to flower and set seed within this phase. Since hemicryptophytes are important in most communities, initial recovery is rapid. Fire lilies and almost all annuals reproduce in this phase.

It is also in the first 12 months after fire (ie usually in the first winter or spring) that successful germination and establishment occurs, apparently mainly from seed stored on the parent plants prior to the fire, or in the soil. Martin (1966) has suggested that seed of *Erica* spp is short-lived and must be imported to the site, and he, Adamson (1935) and Kruger (1972) have observed that germination and establishment of some *Erica* spp is delayed until more than 12 months after the fire. This may be due to the delay while seed is carried onto the site but could also be due to special requirements for germination that are met only after some development of the community. Time may be necessary for recovery of mycorrhizal associates of *Erica*, for example (Martin 1966). On the whole, it does not seem that immigration of species is an important process of postfire succession. Once established, young plants apparently suffer relatively little mortality (Martin 1966).

Youth phase (up to 4 to 5 yr)

Fynbos is quickly dominated by restionaceous and graminoid plants and sprouting shrubs (Figure 4), the herbaceous plants reaching a maximum biomass of up to 8 000 kg ha^{-1} in the first 4 to 5 yr. In this period, canopy cover reaches about 80% of preburn levels (Martin 1966, Figure 5). The remaining sprouting species attain reproductive maturity. Opportunistic shrubs, including succulent Mesembryanthemaceae (Adamson 1935), mature and die, but longer-lived shrubs begin to emerge from the canopy. The vegetation becomes flammable at about 4 yr.

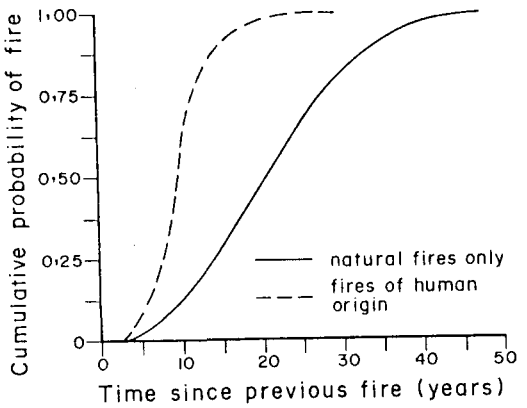


Figure 4 Hypothetical fire frequencies, expressed as cumulative probabilities of occurrence over any given area, as a function of time since previous fire (the burning rotation). Solid line represents a probability function for an area where fires of human origin are at a minimum, and broken line that for an area with many fires of human origin.

Transitional phase (up to about 10 yr)

Most plant species attain reproductive maturity in this phase. Tall shrubs emerge from the canopy and adopt the ascending branch habit.

Mature phase (up to 30 yr)

Tall shrubs attain maximum height and full, rounded form, with maximum flowering activity. Seeding low shrubs (eg *Erica* spp) begin to die, litter accumulates more rapidly and lower herbaceous strata are reduced in importance and negligible establishment of germinules occurs. Although germination may be quite prolific in winter, few or no seedlings survive (Wicht 1948b).

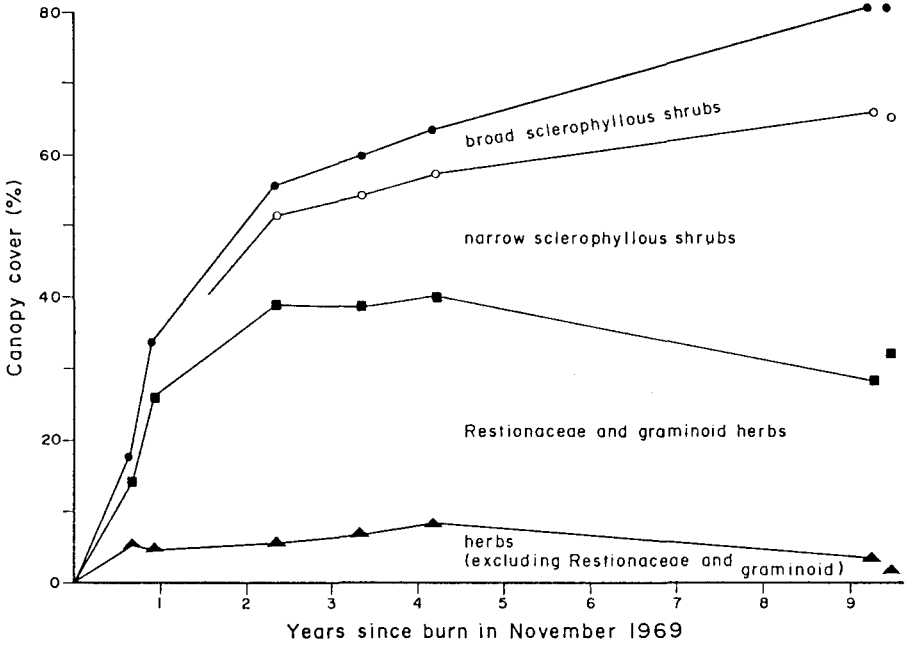


Figure 5 Change in vegetation cover after fire in a broad-sclerophyllous open scrub at Jakkalsrivier, Grabouw. Data points at extreme right represent cover before the burn, at age 11 yr (Kruger 1982).

Senescent phase

Mortality among seed-regenerating shrubs accelerates, foliage on survivors is reduced to tufts at tips of branches, and crowns become open. With the opening of the canopy, some seed regeneration may occur. Litter and dead shoots continue to accumulate. On special, limited sites that are both fertile and have moist soils, immigration of forest precursors may occur.

Thus, postfire succession in most fynbos communities is notable for rapid initial recovery owing mainly to growth of perennial graminoid herbs and sprouting shrubs. Although germination after fire may be delayed in some instances, species richness in the plant community is at a maximum in the immediate postfire phase and after. Adamson's data suggest some turnover in species in the first few years, but thereafter there is a steady reduction in diversity, particularly in the moist sites. Dominance concentration, perhaps initially intermediate, falls in the late youth phase when species are roughly equal in height, and then increases to a maximum in the mature phase.

Postfire growth rates of different fynbos communities vary widely (Figure 6). Initial growth rates are highest on moist

sites, lowest on dry (Kruger 1977a) but above-ground biomass attained at maturity seems to depend on whether or not tall, long-lived shrubs (*Protea* spp, *Leucadendron* spp) are present; if so, biomass continues to accumulate fairly rapidly for 30 yr or more and may reach 75 t ha^{-1} (van Wilgen 1982). Live biomass reaches a maximum at about 20 yr in the *Protea* scrub at Jonkershoek; older stands comprise 54 t ha^{-1} of dead material of the total 75 t ha^{-1} (van Wilgen 1982). Low heathlands on dry aspects, by contrast, accumulate only about 10 to 15 t ha^{-1} (Kruger 1977a). These differences in postfire growth rates also indicate probable differences in successional patterns, such as different rates of recovery to the prefire condition, and rates at which species composition will change.

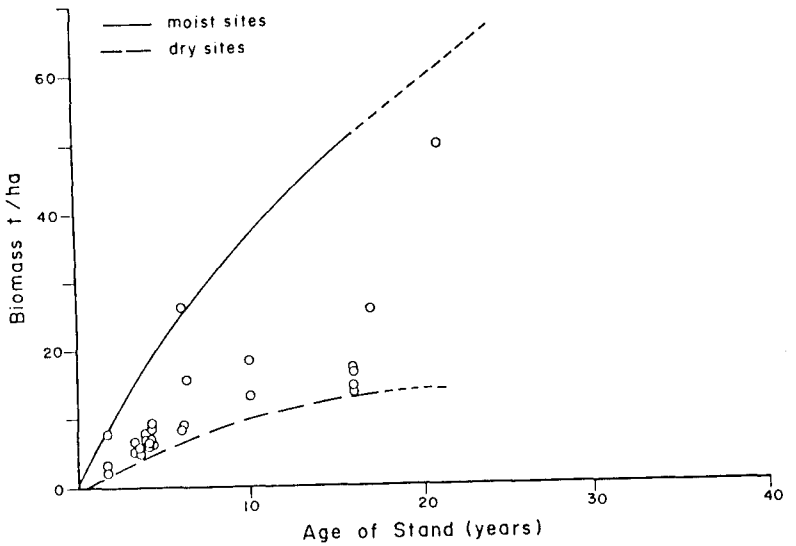


Figure 6 Change in above-ground plant biomass with succession after fire in fynbos communities. Biomass as total standing crop ie live plants, standing dead and litter (Kruger 1982).

EFFECTS OF FIRE INTENSITY

Studies on the effects of fire regime on vegetation structure and dynamics have so far focused on the effects of rotation and season, with scant attention to intensity effects. That extreme intensities have important effects is confirmed by field experience and the few extant studies available. On humid, cool sites, for example, field observation indicates that light burns fail to consume sufficient litter and vegetation to create a satisfactory seedbed for good germination and establishment. Observations show that young *Mimetes hottentoticus* plants are established only in mineral seedbeds, and fail on peaty surfaces especially if littered (Kruger and Lamb 1978). This is possibly related to water repellency on organic and humic soils as Bond (1980) has reported that high intensity burns are necessary to oxidize and volatilize the organic compounds which cause repellency and maintain an unfavourable moisture balance. Elsewhere, growth of shrubs regenerated from seed has been seen to respond strongly where soils had previously been oxidized by very intense burns which is presumably analogous to the "ashbed" effect reported in *Eucalyptus* forests (Humphreys and Craig 1981). Other effects of high intensity burns could be seen after the unusually hot fire in the Cedarberg in January 1975 (Kruger and Haynes 1978). This fire, which was hot enough to cause considerable flaking and cracking of quartzite boulders, consumed the organic soil layers of bogs and seeps, virtually eliminating plant life from such sites. On other sites most sprouting herbs such as Restionaceae and Gramineae were killed, although mortality among adults of sprouting woody plants such as *Protea nitida* (1 to 3,5%) (Haynes 1976) was relatively low. Recovery was marked by abundant regeneration from seed among most taxa, so that the vegetation was initially dominated by seeding grasses (eg *Ehrharta ramosa*) and shrubs and semi-shrubs in the Asteraceae, and local colonies of hard-seeded *Aspalathus* spp. Re-establishment from seed of species of Restionaceae indicated that communities would return approximately to their original composition, though their initial growth was slow. This sequence of events, unusual in fynbos, seems to be due mainly to this exceptionally intense burn.

Fire intensity as a factor influencing vegetation structure and dynamics could perhaps be viewed as follows. High intensities will have several important effects. Abnormally high mortality among sprouting plants is likely (eg Trollope (1973) reports reduced grass basal cover due to "hot" fires), to the advantage of seeding species. Also, germination of hard-seeded species will be favoured. Growth of all plants will be favoured by the ashbed effect, but the net consequence of abnormally high intensities would be a change in composition toward an increased woody plant component, especially seeding shrubs. Abnormally low intensities will apparently have an opposite effect, favouring graminoid and restioid herbs over woody elements. The effects of average intensity fire would be intermediate between these two extremes.

EFFECTS OF FIRE FREQUENCY

The gross effects of fire frequency are usually the most easily seen and most frequently commented upon of regime effects. The marked contrast between vegetation at Jonkershoek subject to 6 yr burning and that subject to fires once in about 15 to 20 yr has been reported by van Wilgen (1981b, 1982). The 6 yr regime changed structure profoundly from a tall shrubland with aboveground biomass of about 50 t ha^{-1} to a low herbaceous shrubland with biomass of around 6 to 8 t ha^{-1}.

Most fynbos retains relatively abundant, mainly sprouting shrubs whatever the fire frequency, but in marginal fynbos zones, burning frequency can be a critical determinant of vegetation composition. Trollope (1973) and Downing et al (1978) have shown this in the case of grassland in the Dohne Sourveld of the Amatole Mountains invaded by "macchia," ie scrub of fynbos species in the genera *Cliffortia* and *Erica*. The shrubs are easily reduced and some finally eliminated by repeated burning at short intervals of 2 to 4 yr. Martin (1966) also noted that certain fynbos communities near Grahamstown could be converted to perennial grassland by frequent fires. Trollope (1970) has reviewed the general problem of invasion of grasslands along the margin of the winter and all-year rainfall zones by "macchia" elements, ie mainly shrubs of genera such as *Cliffortia* (Rosaceae), *Erica*, and *Euryops* and other Asteraceae, and how these may be checked by burning on a short rotation. Similarly, where marginal grassland and grassy fynbos types have become altered and dominated by *Elytropappus rhinocerotis* through certain grazing and burning regimes the original grassland, often dominated by *Themeda triandra*, can be regained successfully in many cases if the veld is rested from grazing and burnt at intervals of about 4 yr and less (Levyns 1956; Moffett and Deacon 1977).

The influence of low-frequency burning as such has not been studied. Campbell and van der Meulen (1980) and van Wilgen (1981b, 1982), however, have reported effects of prolonged deferral of fire. In fynbos protected for 37 yr tall *Protea* shrubs were reduced in cover and abundance owing to high mortality with senescence and low seedling recruitment, as opposed to their dominance in 20 yr stands. The opening of the stand was apparently accompanied by a recovery among undergrowth species, including rhizomatous restionaceous plants, sedges and grasses. These graminoids are considerably reduced in old vegetation dominated by tall shrubs, relative to their condition in frequently burnt vegetation. Thus, in the Langeberg foothills at Swellendam, Haynes and Kruger (1972) reported a marked reduction in basal cover of graminoid and restionaceous plants in 47 yr old stands, relative to that in 4 yr old vegetation of firebreaks burnt on a 6 yr rotation (Table 6). Bond (1980) reported similar effects.

Fynbos communities are complex in their life form composition and, as already shown, in the range of plant responses to fire regime. Generally, fire frequency effects relate to the following:-

1 The demographies - especially primary juvenile periods, age-specific seed productions, and life spans - of the dominant seeding shrubs (Jordaan 1949). Many of these shrub species are precocious - *Protea repens* (sugar bush) flowers within 3 to 4 yr. Nevertheless the numbers of *P. repens* and *P. neriifolia* (oleander-leaved protea) are severely reduced by burning at average intervals of 6 yr (van Wilgen 1981b). Therefore, reproductive potential may be limited at early maturity because of delayed ripening of seed (Jordaan 1949) or similar factors. Seeding shrubs of a smaller stature, such as *Erica* and *Cliffortia*, are less readily decimated by frequent fire (van Wilgen 1981b).

Few data are available on age-specific reproductive potential. Lombaard (1971) has shown that *P. repens*, for example, carries sufficient viable seed per individual at age 10 to 12 yr to replace the parent population. With senescence (at about 25 to 50 yr in tall *Protea* spp) the number of reproductive individuals in the population declines markedly. Bond (1980) showed how, after the same fire, seedling densities in 40 to 45 yr old stands of Proteaceae are much less than in 20 yr old stands, because populations have declined more than the individual fecundities have increased with age and though these Proteaceae retain viable seed on the plant it is short-lived when released. It is not clear when reproductive effort and success per individual culminates and this problem requires further study.

2 Extreme frequencies may have nonreversible effects on vegetation and result in new stable vegetation equilibria. For example, high frequencies may cause local extinction as in the case of *Erica* spp and *Cliffortia* spp in the Amatole Mountains (Downing et al 1978). On the other hand, long periods between fire, in excess of 50 to 100 yr, could allow establishment of forest precursors such as *Kiggelaria africana* (wild peach) (van Wilgen 1981b), although such communities are rarely observed except on sites unusually favourable in fertility and moisture status (McKenzie et al 1977; van Wilgen 1981b). In most cases it seems that

Table 6 Comparison between basal cover of vegetation protected from fire for 47 yr and that of 4 yr old vegetation in a firebreak burnt on a 6 yr rotation on the Swellendam State Forest. Statistics from a paired sample of 10 line transects, located in a physiographically uniform area (Haynes and Kruger 1972).

	Mean basal cover, % (with standard error)	
	Firebreak	Protected vegetation
Total	6,59 ± 0,70	3,39 ± 0,95
t	2,75 ($P \leq 0,05$)	
sprouters only	6,30 ± 0,70	2,76 ± 0,89
t	3,09 ($P \leq 0,05$)	
Graminoid and restionaceous plants[a,b]	4,09 + 0,39	2,29 ± 0,90
t	5,34 ($P \leq 0,01$)	

[a]Two transect pairs that fell on open patches in the protected vegetation, dominated by Cyperaceae, omitted from the analysis.
[b]Includes sprouting plants.

variations in frequency will instead govern the relative abundance of different plant forms. This is illustrated hypothetically for the case of seeding and sprouting species in Figure 7. High frequencies favour sprouters, especially graminoid plants, as discussed earlier. Intermediate frequencies allow succession to proceed to a stage dominated by tall shrubs, to the long-term disadvantage of sprouters. Low frequencies allow succession repeatedly to proceed beyond the onset of senescence among seeding shrubs and there is an equilibration of postfire recruitment at relatively low densities because of declining reproductive potential of parent populations as discussed. Sprouters persist in the more open vegetation, but their composition no doubt changes from an assemblage characterized by species adapted to frequent defoliation to one where dominant species are those which survive and grow under a regime of infrequent defoliation. Thus, the spectrum of species is retained but the relative abundances change.

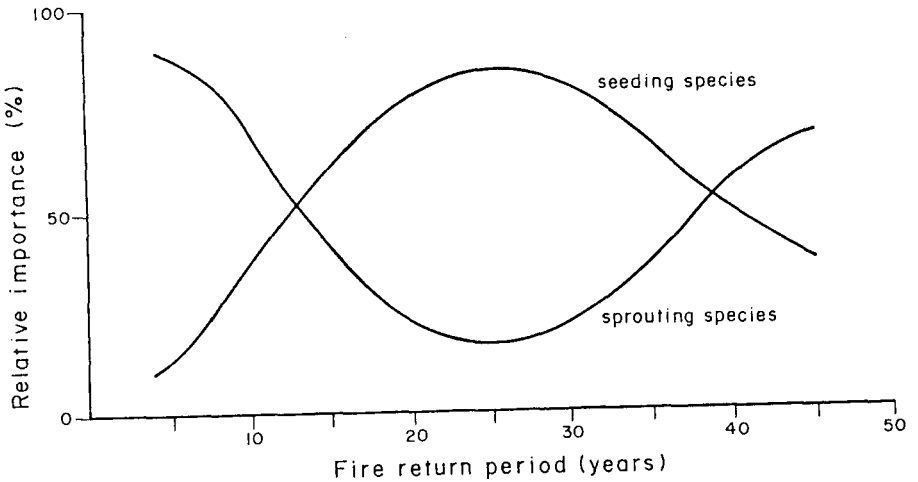


Figure 7 Hypothetical illustration of different proportions of community biomass in sprouting and seeding plants that may result under different average fire frequencies.

3 The effect of fire frequency is governed by feedback controls among frequency, rates of accumulation of biomass and fire intensity. Fires in short succession have low intensities and spread slowly because insufficient time elapses for vegetation to grow and accumulate the fuel necessary for intense fires. Thus ignition probabilities decline, fires that do occur are less intense and smaller than otherwise and the average fire frequency will tend to decrease.

4 Habitat patchiness, especially in the rocky mountain fynbos landscapes, causes spatial heterogeneity in distribution of fire and a pattern that includes patches where fire tends to occur less frequently, allowing existence of species that would not tolerate the mean fire frequencies experienced on the prevailing landscape elements. Even where the landscape is uniform and fires intense, patches are often left unburnt more or less at random (Martin 1966). Where frequencies are high this effect is more pronounced and will allow survival in refuges of species that are exterminated elsewhere. Recolonization from such refuges would be more rapid than from outside the area experiencing high frequencies.

5 Current views hold that maximum species diversity would be found under intermediate burning frequencies (Connell 1978; Huston 1979). Van Wilgen (1981b) found most plant species per sample quadrat in fynbos burnt once in 6 yr, lowest in that burnt once in 20 yr, and intermediate in that protected from fire. As he pointed out, however, many species in the 20 yr vegetation are dormant, as seed or underground organs, for example, and the full richness can only be measured over time. Pyric succession must be accounted for in assessing the role of fire frequency on diversity, and highest richness would exist, hypothetically, at intermediate frequencies. The relatively high richness observed in very old stands was due to immigration of species including forest precursors and appears to represent a special case.

EFFECTS OF FIRE SEASON

The influence of season of burn is related to the seasonality of growth and reproduction in species of any given plant community, as illustrated by examples described above. Phenology of fynbos communities is complex (Kruger 1981) so that a uniform response among species in any given community is not to be expected. Nevertheless, burns in late summer or autumn (February to April) are considered to be "natural" in the fynbos environment, so that vegetation subject to burns in this season should remain relatively stable (Jordaan 1949, 1965). This is because sprouting plants are dormant or nearly so at the height of the summer drought, and because dormant viable propagules are then available on site.

Out-of-season burns could have many effects on composition and structure. First, where veld is burnt when certain species are in active growth, survival and regrowth of resprouters could be reduced because they are defoliated when reserves are depleted and these are drained further by resprouting: there is some evidence of this effect in *Watsonia pyramidata*, for example (Kruger 1977b, 1978). Because species differ phenologically, response to season of burn will vary interspecifically and this could lead to compositional changes. For example, temperate grasses, which tend to grow in autumn through to spring, could be favoured over tropical grasses by autumn burns, and vice versa with spring burns. Restionaceae and Cyperaceae, which grow

predominantly in spring, would also be favoured by early spring burns because even if emerging shoots and leaves are scorched, regrowth from intercalary meristems is immediate and rapid, and ought to have the advantage of exploiting resources under conditions of low competition. Presumably, the same advantages would accrue to sprouting shrubs. These advantages would be greater the earlier the burn because of the relatively small effect on energy and nutrient reserves.

Secondly, insofar as fire permits or induces germination and subsequent establishment, season of burn can have pronounced effects on populations regenerated from seed. Most successful germination and establishment apparently occurs in winter through to early spring, and this is favoured by summer and autumn burns. Germination does occur after early spring burns, but establishment can be severely hampered by ensuing summer drought and by pathogens favoured by warm, moist spring conditions, leading for example to losses through damping off. Other seasonal effects could arise from differences in microclimatic change and exposure to weather, especially the effect of strong winds in removing ashed nutrients and in shifting soil.

Whatever the case, both Jordaan (1965) and Bond (1980) have indicated how "unseasonal" fires can have a profound influence on populations of Proteaceae. Bond showed that other dicotyledons responded similarly, and, clearly, other strong seasonal effects must be expected. Thus, repeated late summer or autumn burns ought to favour vegetation dominated by seeding shrubs, while repeated spring burns would favour vegetation where graminoid and restionaceous plants and sprouting shrubs are more prominent. Species whose phenology is closely attuned to survival of summer drought through dormancy and rapid exploitation of moist conditions in autumn and early winter would also be favoured by late summer and autumn burns. Thus Levyns (1929b) reported that petaloid monocotyledons were favoured over grasses by an April burn. Also important is the fact that geographic variation in vegetation and phenology may play a subtle role in the interaction between fire season and vegetation structure and dynamics. Thus Williams (1972) has noted differences in flowering phenology between western and eastern species of *Leucadendron*, which ought to be reflected in different reproductive responses to fire in different seasons.

INVASIVE PLANTS AND THE EFFECT OF FIRE REGIME

The fynbos biome is characteristically prone to invasion by exotic shrubs and trees of species that are preadapted to the local environment and to fynbos fire regimes. This is probably the most pressing environmental problem at present. Of 23 terrestrial plant species listed by Hall and Boucher (1977) as alien weeds in the fynbos biome just four are sprouting shrubs. Of the remainder, 16 are trees or shrubs that rely on seed for regeneration and reproduction. Their life cycles reflect adaptations to fire regime that are important in considering problems of control (Roux and Middlemiss 1963; Taylor 1969b; Kruger 1977b; Fugler 1979; Milton 1980). In every case, long-range seed dispersal to safe sites in more or less undisturbed fynbos (by birds and other animals in aril-bearing *Acacia* spp such as *A. cyclops* (rooikrans) and *A. melanoxylon* (blackwood), and by wind in the case of *Hakea* spp (episodically after bradysporous parent plants have been killed) and *Pinus* spp (usually seasonally)) marks the initial phase of establishment of a sparse population, as in the case of *Pinus taeda* in the southeastern United States (Spring et al 1974). When the initiating population matures, numbers proliferate in response to repeated fire until the natural vegetation has been replaced or nearly so. On the other hand, fire is successfully employed in efforts to control these plants.

Three models seem appropriate in analysing the role of fire in this problem. Firstly, precocious bradysporous *Hakea* spp are relatively easily controlled by a combination of clearing (or killing by other means) and burning. Seed once released from follicles remains dormant until moisture is taken up but germinates or dies thereafter. Seeds and young plants up to ca 24 months are heat-sensitive. Hence, seed released when parents are killed, or the seedlings and young plants, or both, are readily eliminated or reduced several orders of magnitude in density by a burn within 24, but preferably 12 months. Managers prefer to defer burning until seed has germinated because young plants are more sensitive to the heat of a fire than is seed. Any further deferral of fire and any accidental fire before clearing operations would negate control efforts (Taylor 1969b; Fenn 1980).

Secondly, less precocious pine species offer somewhat more flexible approaches. Primary youth periods are 6 yr or longer and young saplings are susceptible to fire, though most adults survive moderate fires. Thus, frequent fire must be used near sources of seed to prevent spread by killing immature plants (Kruger 1977b). However, fire does not effectively eliminate adult populations which must be killed by other means for proper control.

Finally, hard-seeded *Acacia* and other leguminous species require other methods. They are often extremely precocious, with primary youth periods of as little as 24 months and once established, are virtually immune to fire. Fires simply stimulate germination of soil-stored seed. No fire recurs soon enough to kill plants before maturity and, in any event, not all seed germinates after fire, some persisting until the next opportunity. Thus, the postfire seedling population must be killed repeatedly with herbicides and the soil seedbank eventually depleted in this manner.

Coastal Renosterveld communities, on nearly neutral, heavy-textured soils of shales and granites, are prone to invasion by Mediterranean herbs after fire or other disturbance, and these species, which include *Anagallis arvenis* (scarlet pimpernel), *Avena fatua, Briza maxima, B. minor, Koeleria cristata* and *Vulpia bromoides* (Levyns 1929b), are often also invasive in other mediterranean-type ecosystems (Gulmon 1977). Levyns (1929b) has shown how these species, absent from the undisturbed community, become abundant after fire. On the whole, responses of herbaceous invaders to fire have not received attention because they have not yet presented any great management problem.

EFFECTS OF FIRE REGIME ON FORAGE PRODUCTION AND QUALITY

It seems that fire has been used by pastoralists to improve forage in fynbos (Wicht and Kruger 1973; Bands 1977) since their advent some 1 500 or more years ago (Schweitzer and Scott 1973). Grazing with burning is still practised through much of the fynbos biome, both in the mountains and on the coast. This is typified by the practice of patch-burning, where the herder or his overseer sets fire to any patches of vegetation that will burn. This is usually done toward the end of the wet season and prior to the introduction of the livestock. Because of the mosaic pattern produced and because of the experience of the practitioner in judging weather and fuel conditions, no single fire spreads far. The veld is thus patterned in a fine-grained, very irregular mosaic, and any stand of vegetation is burnt once in about 4 to 8 yr. This practice was almost invariably (and is occasionally still) associated with transhumance, stock being alternated seasonally between fynbos and other pastures (karoo or stubble fields and ley pastures on wheatlands). This is probably owing mainly to climatic influences, but also possibly to calcium and other nutrient deficiencies in fynbos forage (Louw 1969).

The principal value of fire in the context of pasturage lies in its effect in making relatively high quality material more readily available by removing the obstructive bed of unpalatable material and stimulating new growth. Fresh young growth even of Restionaceae is palatable, but only for a few seasons after fire. These direct effects of fire on forage production and quality and their variability have nowhere been measured. Fire regime can be manipulated to change the structure and composition of certain fynbos types to induce a more or less permanent change to more productive pasture, especially in marginal fynbos in the year-round and summer rainfall zones. Van Rensburg (1962) has indicated how short-rotation burning can induce a vigorous grass cover. The stands of *Themeda triandra* in firebreaks at Jonkershoek further attest to this. Nonetheless, fire-induced grassland or mixed grassland, which may at one time have been the predominant formation on the coastal forelands (Acocks 1975), can be obtained only under particular combinations of climate and soil such as in renosterveld in the lowlands and certain Waboomveld in the uplands, and are not found on the extremely acid substrates of the prevailing forms of mountain fynbos. Here, the most that is obtained is the elimination of tall shrubs and a predominance of low shrubs with Restionaceae, Cyperaceae and sclerophyllous grasses.

EFFECTS OF FIRE REGIME ON FAUNAL STRUCTURE AND DYNAMICS

The changes in structure and composition induced by fire profoundly affect fynbos vegetation as a habitat for animals. As already indicated, a series of very marked successional stages follow one another rather slowly. Corresponding faunal changes have been little studied and can be discussed only in broad terms, mainly with reference to birds and mammals.

IMMEDIATE POSTFIRE EFFECTS

Although there is little evidence for dramatic animal mortality during a fire, dramatic changes in the faunal component occur as a consequence of the fire. Some species flee the fire and do not return to the unfavourable habitat while others disappear soon afterwards because they are unable to adjust to the change in resources. Forms which depend on the later stages of plant succession are particularly seriously affected. They are instantaneously deprived of habitable environment by fire. Sugar bird *(Promerops cafer)* is an example. It relies on elevated inflorescences of Proteaceae for nectar and insects (Mostert et al 1980) and because dominant shrubs of this kind are usually seeders, no resources are available to sugar birds for the first 4 to 8 yr after fire in most cases. More important, however, are their nest-site requirements which include a sheltering canopy (Burger et al 1976), not available until the stand is well developed, ie from about 8 yr onwards (and unavailable again when shrubs open up with senescence).

There are, on the other hand, examples of almost immediate postfire immigration. Some may be passive, as in the case of parachute spiders. However, reports of immigration for exploitation of ephemeral food resources in the postfire environment are common. Levyns (1929b) discusses foraging on recently burnt plots by various animals. Among those observed were "...buck, a hare, and several tortoises...". She also noted selective foraging patterns on the regrowth. *Anthospermum aethiopicum* seedlings, for example, were preferred and *Elytropappus rhinocerotis* seedlings were avoided. Especially nutritious food resources such as seed released from plants, corms, cormlets and other structures among geophytes, and sprouts are used by a wide variety of transients including genera of birds such as *Francolinus*, *Serinus* and *Streptopelia* and others discussed below. Baboons have been found to forage over a new burn (R C Bigalke, personal observation, 1974). However, it is not clear whether these immigrants are responding to increased productivity, or whether it is simply the open habitat that favours certain foraging strategies. Martin (1966) for example noted "...a minute spider, spinning threads from tip to tip of ...burnt stalks..." to occur commonly on the site of a recent wild-fire, also on cleared areas along pathways though it was absent from undisturbed vegetation. Species able to make effective use of resources which increase in abundance after a fire include rodent moles. Levyns (1929b) found activity of *Georychus capensis* to increase markedly on burnt plots and suggested that this was due to greater availability of underground storage organs of geophytes. Whether the resource did in fact increase in abundance or in quality, or simply became more accessible, was not clear (Wicht 1948b).

EFFECTS OF FIRE SEASON

Most major fynbos fires tend to occur in summer and autumn in the west, and in winter in the southern coastal zone. Comparative effects of fire on fauna in these and other seasons have not been studied. Late summer and autumn fires probably do not disrupt nesting or the birth and rearing of young in at least many bird and mammal species. Those in spring may be expected to do so, perhaps affecting animal density and even species composition, if repeated regularly. On the other hand the establishment of territories in winter, for example by greywing francolin *(Francolinus africanus)* (R C Bigalke, personal observation, 1974), precedes nesting by several months and could be affected by loss of cover following autumn fires.

Herbivore food supplies may be improved more by repeated spring burns, favouring restionaceous and graminoid plants (including tropical grasses) and sprouting shrubs, than by fires in summer and autumn. The timing of patch burning to improve pasturage for livestock - it is usually carried out towards the end of the wet season - perhaps results from recognition of this fact.

Since intervals between fires are usually much longer in fynbos than in other vegetation types, the long-term effects on fauna of burning in a particular season can perhaps be expected to be less marked than elsewhere.

EFFECTS OF FIRE FREQUENCY

Limited data, mainly from trapping studies on small mammals, are available. Habitats of 12 different aged stands (0 to 38 yr) have been sampled in various areas of montane fynbos, mostly at Jonkershoek State Forest, some of them by more than one worker (Toes 1972; Lewis 1978; Willan and Bigalke 1982). Their combined results (Table 7) summarize species composition in newly burnt (less than 1 yr old), young (2 to 6 yr), mature (10 to 17 yr) and senescent (30 to 38 yr) habitats. No sampling was undertaken in vegetation of intervening ages. Species richness is lowest in newly burnt sites, attains a peak in 2 to 6 yr old fynbos (youth phase, start of transitional phase again, declines in mature stands and is again higher in senescent vegetation (30 to 36 yr old)).

A similar trend is evident in the results (Table 8) from the first few years of a long-term trapping study in transitional coastal renosterveld at the Duthie Reserve, Stellenbosch (Bigalke and Pepler 1979). Although the reserve represents a small "island" habitat surrounded by seriously disturbed vegetation and probably has abnormally dense mammal populations as a result (Halpin and Sullivan 1978), succession is likely to resemble that in other fynbos communities. A single pioneer species appeared in the first year while in the second four were present. There were six or seven in each of the succeeding five years, with some changes in species composition. These are discussed further below. In terms of abundance, a slow increase leads to peak values

Table 7 Small mammal species present in relation to postfire age of southwestern Cape mountain fynbos (* indicates presence) (data from Toes 1972; Lewis 1978; Willan and Bigalke 1982).

SPECIES	Postfire age of vegetation (yr)			
	Newly burnt (< 1)	Young (2-6)	Mature (10-17)	Senescent (30-38)
Otomys spp		*	*	*
Rhabdomys pumilio		*	*	*
Mus minutoides	*	*		
Dendromus melanotis		*		
Dendromus mesomelas			*	*
Aethomys namaquensis		*	*	*
Acomys subspinosus	*	*	*	*
Praomys verreauxi				*
Crocidura flavescens		*		*
Crocidura cyanea		*		
Myosorex varius		*	*	*
Totals	2	9	6	8

Table 8 Small mammal species presence and abundance (% trap success) in Duthie Reserve, Stellenbosch, in relation to postfire age of the vegetation (* indicates presence) (Bigalke and Pepler 1979).

SPECIES	Postfire age of vegetation (yr)						
	1	1-2	2-3	3-4	4-5	5-6	6
Otomys spp			*	*	*	*	*
Rhabdomys pumilio	*	*	*	*	*	*	*
Acomys subspinosus		*					
Mus minutoides		*	*	*	*	*	*
Dendromus melanotis			*	*	*	*	*
Rattus norvegicus			*	*		*	
Crocidura flavescens					*	*	*
Myosorex varius		*	*	*	*	*	*
Totals	1	4	6	6	6	7	6
Abundance (% trap success)		3,6	16,7	50,4	22,6	25,7	

Table 9 Relative abundance (% trap success station-night^{-1}) and biomass (g station-night^{-1}) of small mammals in south-western Cape mountain fynbos in relation to postfire age of the vegetation. Absolute numbers trapped are given in brackets (Willan and Bigalke 1982).

SPECIES	Postfire age of vegetation (yr) 2	4	10	14	38
Otomys spp	0,7 (1)	14,4 (62)	7,3(22)	8,3(15)	8,3(15)
R. pumilio	8,6(18)	8,4 (36)		1,7 (3)	8,3(15)
M. minutoides	4,3 (9)				
D. melanotis	2,9 (6)				
D. mesomelas			2,7 (8)		1,7 (3)
A. namaquensis	10,7(23)	0,9 (2)	0,7 (5)		1,7 (2)
A. subspinosus		2,8 (12)	1,7 (5)		1,7 (2)
C. flavescens		0,2 (1)			
C. cyanea		0,2 (1)			
M. varius		0,7 (3)	5,3(16)	6,7(12)	15,0(27)
Totals	27,2(57)	27,6(117)	17,7(56)	16,7(30)	36,7(64)
Biomass (g station-night^{-1})[a]	9,9	19,0	9,1	9,7	14,3

[a]Calculated from mean masses for each species

in the fourth year after the fire and to subsequent stabilization at lower levels.

Changes in population density are shown Table 9 by samples trapped in montane fynbos of postfire ages 2, 4, 10, 14 and 38 yr (Willan and Bigalke 1982). Total abundance was higher in young (2 and 4 yr) than in mature (10 and 14 yr) habitats, but was highest in old (38 yr) fynbos. However total biomass is highest in the 4 yr old community, then declines and rises to a second, lower peak in senescent fynbos (Table 9).

To summarize, small mammal populations are disrupted by fire but small numbers of a few pioneer species are encountered within the first or second years. Peak density, biomass and diversity appear to develop during the youth phase when canopy cover is rapidly increasing and herb biomass reaches a maximum. Then when the vegetation is in the transitional and early mature phases these parameters decline. Finally, senescent fynbos seems to support more species and a higher total density than the preceding successional stages although biomass may not be as high as in the youth phase.

The generality of these trends remains to be tested and detailed explanations await further work. Geographic and altitudinal differences are to be expected in the timing, nature and magnitude of successional processes. A study by Bond et al (1980) in the southern Cape suggests that at least rodent species diversity (H), an index measuring both the number of species and equality of representation of the individuals of each species, may depend largely on vegetation structure. They found an inverse relationship between species diversity (but not population size and specific composition) and the proportion of foliage in the 0,4 to 0,6 m layer above the ground. Two tentative hypotheses are proposed: that the vertical distribution of plant material, irrespective of its form or nature, is significant in rodent niche partitioning and that rodent species diversity can be predicted from foliage profiles.

These authors go on to predict low diversity, associated with a high proportion of total foliage below 0,6 m, in young fynbos after fire. This should increase as upper layers develop and perhaps decrease with senescence of the plant community many years after the fire. The data in Tables 9 and 10 partly confirm these expectations but the high species richness, density and biomass in senescent stands do not fit the pattern.

Habitat preferences of some species can be invoked to explain their appearance at particular stages in the postfire succession. Thus *Rhabdomys pumilio* (four-striped field mouse) is omnivorous and therefore fitted for a pioneering role. Its early presence can also be related to its preference for "grassy" ground cover, which includes Gramineae as well as Cyperaceae and Restionaceae (Bond et al 1980). These authors found numbers of *Otomys* spp, specialized herbivores, correlated with dense, shrubby vegetation. This factor presumably explains its absence from young postburn vegetation where one would expect it to find adequate nutritious plant material. Insectivorous shrews of the genera *Myosorex* and *Crocidura* also seem to require well-developed vegetation cover. Thus *Crocidura* was first trapped in the fifth year after the fire at Duthie. This may depend on the accumulation of sufficient litter to support a good invertebrate fauna, as well as on microclimatic factors and cover preferences.

Further data on mammals are restricted to general observations on medium-sized herbivores. Many are attracted to young fynbos. Thus grey rhebuck *(Pelea capreolus)* and - near rocky sites - klipspringer *(Oreotragus oreotragus)* are commonly seen on burns. In the eastern parts of the fynbos region, within their geographic range, mountain reedbuck *(Redunca fulvorufula)* are similarly attracted and mountain zebra *(Equus zebra)* are thought to respond in the same way. Antelope probably migrate over fair distances to reach fresh burns but the extent of these movements is unknown. The improved accessibility and enhanced nutritive value of vegetation on young burns may stimulate reproduction and enhance survival and so affect population densities.

The dependence of some birds on mature fynbos for food and especially for nesting sites has already been mentioned. Cody (1975) found bird species richness in fynbos to be directly related to structural diversity of the vegetation. Casual observation shows birds to be rare on recently burnt sites and successional changes in the avifauna must be expected to parallel development of increasingly complex vegetation structure. There may be a decline in species richness as well as in density in mature or senescent stands. Winterbottom (1972) found that "Dense Protea" (apparently late mature or early senescent fynbos) had only 6 dominant bird species while in "Fynbos" there were 12.

Maintenance of a range of different aged stands of fynbos would seem to be necessary to maintain a complete spectrum of animal species, population densities and biomasses.

ADAPTIVE RESPONSE OF ORGANISMS TO FIRE

It is difficult from observations of responses of modern biota to fire to determine which responses indicate adaptation to the fire environment and which are in fact preadaptive (Frost, this volume, chapter 13). In this chapter the characters of several species are described to indicate how these favour survival and growth in the fynbos fire environment, not distinguishing between preadaptations and adaptations except to draw attention to characters which could have emerged solely as responses to the particular fynbos fire regime. In the case of vascular plants, floras are analysed to give some indication of the relative importance of certain response types in the species assemblages of different forms of fynbos.

MICROORGANISMS

We are not aware of any studies which provide information immediately relevant to the question of responses among microorganisms to fynbos fires. This is a considerable problem. Firstly, it is clear that microorganisms play a crucial role in nutrient cycling and nutrition, especially in nutrient deficient, impoverished soils where mutualistic relations between microorganisms and higher plants are apparently fundamental to nutrient uptake from the soil (Lamont 1981; Malajczuk and Lamont 1981). It is therefore vital to understand how fire influences the activity of microorganisms (Dunn and DeBano 1977). Secondly, higher plant population dynamics are at least partly influenced by the immediate effects of fire on community composition of and postfire succession in pathogens such as the soil root-rotting fungus *Phytophthora* spp (Parmeter 1977; Malajczuk and Glenn 1981). Thirdly, there clearly are characteristic fire-response patterns among microorganisms which must be studied for any worthwhile understanding of fire-related aspects of ecosystem function (Dunn and DeBano 1977). Finally, since there are large net losses of nitrogen from the ecosystem in any fire it is particularly important to know the responses of nitrogen-fixing organisms, free-living or otherwise, to fire and the postfire environment.

HIGHER PLANTS

Many fynbos areas support abundant mosses and lichens on the ground or on rocks and on stems of woody perennials. This component of the flora is known to respond strongly to fire elsewhere (Gimingham 1972) and field observations suggest there are local parallels. No information is available for fynbos, however, and the account which follows, drawn largely from Kruger (1977b), is confined to vascular plants.

Species traits and responses to fire

Scorching avoidance

Individuals of a few species of erect shrubs survive fire with all or most of their crowns intact while those of others around them are killed or obliged to sprout. In some cases, shoots and foliage are possibly protected by the shape of the crown, which apparently deflects the heat of the fire, while cambium is protected by thick bark (eg *Protea laurifolia* (laurel protea), *Leucadendron argenteum* (silver tree), *Leucospermum conocarpodendron* (tree pincushions)) (Wicht 1945). Rourke (1972) discusses this habit in tree pinchushions, but states that "...regeneration takes place from the apical branchlets...". Wicht (1945) implies the same. This is slightly misleading since individuals that survive fire are those in which at least some apical meristems survive to produce the new shoots of the coming season; strictly, regeneration does not occur. Some low, spreading shrubs with dense, matted crowns, such as *Protea effusa* and *Leucadendron glaberrimum* also survive. Although the perimeters of their crowns may be scorched, the foliage and shoots are relatively nonflammable and few plants burn out. These species do not have the capacity for vegetative regeneration, a proportion of each population is killed in every fire, and populations therefore usually consist of several cohorts. They do not survive very intense fires except through seed regeneration. Consequently, they are favoured by factors that maintain above-ground biomass and thus fuel at moderate levels, and respond well to fairly frequent, light fires.

Seed production

Species that rely entirely on seed for survival are found mainly among shrubs (trees are almost exclusively sprouters, with the notable exceptions of *Widdringtonia cedarbergensis* (Clanwilliam cedar) and *W. schwarzii* (Willowmore cedar)). Some hemicryptophytes, eg *Chondropetalum hookeranum* (Restionaceae) and *Ehrharta ramosa* (Gramineae), are killed by fire, so that with the limited number of annuals, there are also a few herbs which return through germination. Thus, although fynbos floras are dominated by species which sprout, there is a significant proportion of seeders (Mitchell 1922; Wicht 1945; van der Merwe 1966b) (Table 10).

Survival among seeders is enhanced by a variety of mechanisms. Among these is bradyspory, the retention of seed on the plant for release when the parent dies (Wicht 1945). In *Leucadendron*, 49 of 82 fynbos species retain seed in conelike fruiting heads up to at least 8 yr in some species (Williams 1972), and a similar feature is found among many species of *Protea*. Here seed is released from dormancy when the plant or the organ dies, as after fire, and germination follows soon after. This mechanism seems to protect effectively protein- and energy-rich seed against the heavy predation experienced on the ground in mature vegetation (Bond 1980). Other species, in

Table 10 Two fynbos floras classified by Raunkiaer life form and mode of regeneration after fire.

Life form	Swartboskloof[a]		Jakkalsrivier[b]	
	No of spp in class		No of spp in class	
	Vegetative regeneration	Regeneration from seed only	Vegetative regeneration	Regeneration from seed only
Phanerophyte	84	67	43	110
Chamaephyte	76	63	33	50
Hemicryptophyte	70	1	128	11
Geophyte	67	0	111	0
Therophyte	0	16	0	7
Unclassified	1	3	6	9
Total:	298	150	321	187

[a]From van der Merwe (1966b).
[b]From unpublished Directorate of Forestry records.

Proteaceae, Rutaceae, *Cliffortia*, *Aspalathus* and other taxa release seed or fruit on ripening, and these have biochemical inhibitors or hard testas or pericarps which promote dormancy and longevity (van Staden 1966; Brown and van Staden 1971, 1973; van Staden and Brown 1972, 1973; Williams 1972). Circumstantial evidence shows that this seed can remain viable on or in the soil for about 15 yr or longer (Boucher and McCann 1975; Rourke 1976). These often require heat as a scarification mechanism (Blommaert 1972; Williams 1972). Many species, as in Ericaceae and Asteraceae, produce a superabundance of small seeds, some at least of which (eg *Elytropappus glandulosus*) (Levyns 1935b) are moderately long-lived in the soil. Laboratory studies showed a life of 7 yr. Percentage survival and germination among such seeds needs to be relatively small to replace parent populations. Whether or not species rely on postburn dispersal of seed to the site from outside has a strong bearing on how communities are maintained in a fire environment. Levyns (1929b) reports cases where circumstantial evidence in her experiments indicated germination from soil-stored seed. Wicht (1948b), from his experience in a detailed replicated burning trial, inferred that most seeds that germinated on burnt plots "...were not derived from adjacent unburnt areas". Bond (1980) has noted how Proteaceae seed fails to disperse beyond the boundaries of a burn. Short-distance dispersal seems the prevalent pattern in species with large long-lived seed, and in any species with isolated subpopulations. However, Martin (1966), for example, has suggested that some *Erica* spp rely on dispersal to the site after fire. This important question requires further investigation.

Vegetative regeneration

The full array of vegetative regeneration modes in mediterranean-type fire environments is found also in fynbos communities. It includes the following: (i) epicormic sprouting for dormant buds protected by thick bark of the stem (Figure 8), in a few species like *Protea nitida*, *Maytenus oleoides* (mountain maytenus) and *Heeria argentea* (rockwood) (Wicht 1945); (ii) sprouting from dormant buds in lignotubers or similar organs at or below the soil surface, which is perhaps the most common mode among shrubs and is associated with typical, multi-stemmed growth forms like Australian mallee (Mitchell 1922; Wicht 1945; Martin 1966); (iii) sprouting from rhizomes at or near the soil surface, as in most grasses, sedges and restionaceous plants such as *Pentaschistis*, *Tetraria* and *Restio* spp, but also in a few dwarf shrubs, eg *Protea acaulos* (Rourke 1980), and (iv) survival and

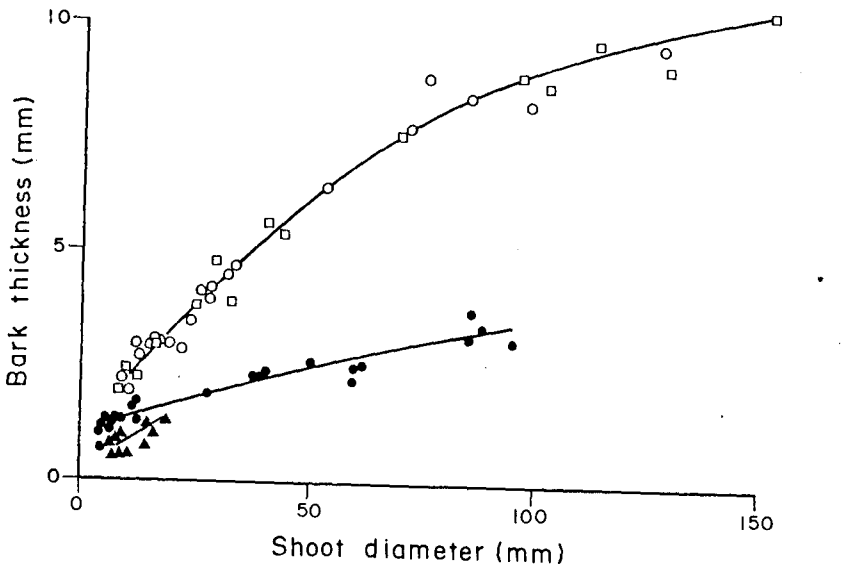


Figure 8 Bark thickness in relation to shoot diameter in various fynbos Proteaceae. Dots represent values for *Protea repens* (sugar bush), a species where individuals are killed by fire, and triangles, *Leucadendron salignum* (geelbos), where the shoots are killed and plants sprout from lignotubers. In *Protea nitida* (squares) and *Leucospermum conocarpodendron* (tree pincushions) (circles) shoot systems tend to survive fire; the former regenerates by epicormic shoots, the latter does not. Data from populations sampled at Jonkershoek (Kruger 1982).

growth from dormant buds on underground storage organs (geophytes), as in Liliaceae, Haemodoraceae, Iridaceae, Orchidaceae, *Drosera*, *Oxalis* and various Asteraceae *(Berkheya, Gerbera, Osteospermum)* (Mitchell 1922; Levyns 1929b; Adamson 1935; Wicht 1945, 1948b; Martin 1966).

Flowering responses

Martin (1966) has classified plants regenerating after fire according to their flowering responses, as follows: (i) species that flower shortly after fire and rarely or not at other times, including typical "fire lilies" in the Haemodoraceae *(Cyrtanthus contractus* (fire lily), *Haemanthus canaliculatus)*, Liliaceae *(Androcymbium leucanthum)*, Iridaceae *(Moraea ramosissima* (geeltulp)), Orchidaceae and other families (Mitchell 1922; Levyns 1929b, 1966a; Wicht 1945, 1948b; Hall 1959); (ii) species that flower in abundance shortly after fire, less frequently afterwards, for which Martin notes a graded series in the intensity of responses; *Watsonia pyramidata* is an example (see below); (iii) species in which flowering does not occur immediately after burning, but is enhanced relative to unburnt stands in the second and third years *(Themeda triandra, Restio triticeus)*; (iv) species in which flowering is depressed after fire and normal in subsequent years *(Phylica axillaris)* and (v) species that are neutral to fire *(Dierama pendulum, Leonotis leonurus* (wild dagga)). Thus, in some cases the fire response may well be adaptive (as in "fire lilies") while in others, especially shrubs, the response appears to reflect increased vigour as a response to defoliation and/or removal of senescent tissue that is costly to maintain, as in *Protea scabra*, *P. speciosa* and other *Protea* spp (Rourke 1980), and very likely in most sprouting shrubs (except, for example, *Asparagus* spp). Among many monocotyledons (eg *Watsonia pyramidata)* and some dicotyledonous shrubs (eg *Cliffortia linearifolia)* (Martin 1966) vegetative reproduction is also enhanced by fire. In some cases, at least among geophytes, it has been suggested that flowering but not vegetative activity responds to burning (Wicht 1948b), but observations by Levyns (1929b) agree with the general field experience that most sprouting plants grow more luxuriantly on burnt than on unburnt sites.

Interestingly, annuals appear to respond similarly to clearing and to burning, at least in the study reported by Levyns (1929b), though few or none grow and reproduce in unburnt vegetation. Levyns (1929b), comparing cleared and burnt plots, showed that the flowering responses among geophytic monocotyledons were owing to fire effects rather than simple clearing. Unfortunately she could report no results from ash and fertilizer trials. Martin (1966) discounted the direct effects of fire on plant reproductive effort, as opposed to clearing, but his experiment confounded burning and clearing.

In some instances, fire may induce much earlier flowering (eg *Asparagus capensis* and *Cyrtanthus contractus)* although flowering seasonality in most species is not affected (Mitchell 1922; Martin 1966). On the other hand, there is evidence that the nature and intensity of the responses depend partly on the season of the burn (eg *Watsonia pyramidata*, see below).

Juvenile periods

The time required for plants to reach reproductive maturity after regeneration following fire varies from about 1 to 10 yr (Table 11). Species which sprout, including some shrubs, often flower within 12 months (this is the secondary juvenile period), though others may require up to 24 months *(Rhus lucida, Hibiscus aethiopicus, Leucadendron salignum* (geelbos), *Podalyria myrtillifolia* and others) (Mitchell 1922; Wicht 1948b; Martin 1966) and sometimes 36 months (eg *Brunia stokoei)* (Kruger and Lamb 1978). Primary juvenile periods (time elapsed between germination and flowering), at least among shrubs, are more variable but most species reach reproductive maturity within 8 yr (Kruger 1979b). Some species are precocious, as in *Anthospermum aethiopicum*, reported as flowering in the second year after fire (Martin 1966), and *Erica mauretanica*, flowering after 30 months (Mitchell 1922). Van der Merwe (1966b) reports that some *Protea repens* individuals flowered in the third year. Rourke (1980) presents observations on the age at first flowering in cultivation among members of *Protea* (Figure 9). The median juvenile period among 42 seeding fynbos species is 4 yr. Species that required 6 yr or more to flower were among those that are usually slow-growing and occur in special habitats with a degree of protection from fire, eg rock outcrops and ledges *(P. magnifica* (bearded protea) - 6 yr), cool, moist upper montane sites *(P. stokoei* - 5 to 12 yr), extremely arid localities *(P. glabra* (Clanwilliam protea) - 10 yr) or crest ridges of high peaks *(P. rupicola* - 16 yr).

There is usually a lag between the age at which the first plants flower and the majority flower. In *P. eximia* (broad-leaved protea), for example, precocious individuals flower at 2 yr but most flower after 3 yr. Observations on cultivated plants may not reflect performance in the field; nevertheless, Williams (1972) and Taylor (1977) report field observations on some species of *Leucadendron* and these show that juvenile periods

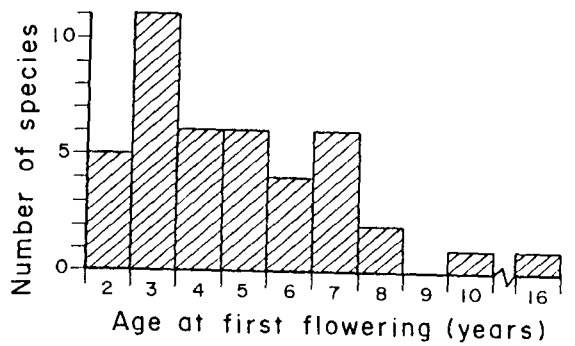


Figure 9 Frequency distribution of youth periods in cultivated fynbos *Protea* spp (Rourke 1980).

Table 11 Primary juvenile periods of some seed-regenerating fynbos species: percentage of population at given age with ripe seed (Kruger 1978).

Species	Age of sample (yr)							
	1	2	3	4	5	6	7	8
Erica sessiliflora	0	0	0	0	1,0	21,0	-	-
Leucadendron concavum	0	0	0	0	37,5	-	-	-
L. salicifolium	0	0	0	0	1,0	64,0	100,0	-
L. xanthoconus	0	0	0	0	0	5,0	45,0	-
Protea lacticolor (moist site)	0	0	0	1,0	6,0	19,0	85,0	-
P. lacticolor (dry site)	0	0	0	0	0	1,0	28,0	-
P. mundii	0	0	0	0	0	1,0	7,0	-
P. stokoei	0	0	0	0	0	0,8	14,2	-
Roridula gorgonias	0	0	0	0	17,0	73,0	-	-

under field conditions are not markedly longer than in cultivation. Their field observations for *Leucadendron* indicate juvenile periods of 3 yr *(L. floridum, L. macowanii)*, 4 yr *(L. platyspermum)* and 6 yr *(L. muirii)*.

The balance of evidence, therefore, shows that seeding fynbos shrubs of habitats exposed to frequent fire are highly precocious except where individuals have the capacity to survive fire *(Leucadendron argenteum, Leucospermum conocarpodendron)* or where moist conditions or sparseness of vegetation due to rockiness or aridity makes for infrequent fire, at least locally *(Protea glabra, P. magnifica, P. stokoei, Leucadendron praemorsum)*.

Many Proteaceae and other taxa require up to 12 months after flowering for seed to ripen. Thus, if the production of viable seed rather than flowering is viewed as marking the end of the juvenile phase then 1 yr should be added to the figures quoted above.

Features of life cycles in relation to fire

There are no comprehensive and detailed studies on the life cycles of representative fynbos species which would serve to illustrate possible adaptive groups, but information assembled mainly from unpublished sources provide a useful picture. The account that follows is drawn largely from Kruger (1977b).

Herbaceous plants whose responses are most often noted are the geophytes. The extreme instance is the so-called "fire lily" type noted above. Hall (1959) showed that the incidence of geophytic Orchidaceae was strongly associated with recent fire. Tagged samples of 10 species were all most abundant and active in the first one to four spring seasons after a burn, and virtually absent thereafter.

Some information on *Watsonia pyramidata* (Kruger 1977b, 1978) illustrates geophyte life cycles and responses to fire. In this species, corm discs are produced annually, are highly resistant to decay and remain in chronological sequence in the soil. Two new corms are almost invariably produced when a ramet flowers. It is therefore possible to excavate clones and examine their genealogy with some accuracy. Clones have a great longevity, several older than a century being found in random samples. Individual ramets are also long-lived, with a maximum observed age (before first flowering and clonal reproduction) of about 35 yr. In unburnt populations, about 5% or less of all ramets flower annually. If burnt in autumn (and possibly also in late summer), populations respond strongly, at least half of all ramets producing inflorescences. Populations burnt in spring do not respond. Since each inflorescence produces about 700 seeds and flowering induces vegetative reproduction, fires in the "right" season obviously have a strong impact on *Watsonia* populations. Seedlings germinate freely in the following winter and spring, and contractile roots draw the new corm to an average of 26 mm below the soil surface within 12 months. Corms apparently grow for 4 to 8 yr or more before first flowering. Thus *W. pyramidata* has various adaptive features of survival value in an environment subject to fire, although fire may well not have been the key factor in the natural selection process. Long-lived clones with deeply buried meristems enable continued occupation of a site in the variable, sometimes long, interval between fires. Reproduction in the favourable postfire environment is enhanced by synchronous and marked population responses, a behaviour that probably also favours pollination, and relatively low predation on fruit and seeds. Contractile roots ensure burial and good protection of the perennating bud against climate, predators and fire.

There is little information on short-lived opportunistic shrubs which are often conspicuous after fire, disappearing or becoming rare thereafter (Levyns 1929b; Adamson 1935; van der Merwe 1966b). Some have hard, apparently long-lived seed (eg *Aspalathus chenopoda* and *Chrysanthemoides monilifera*) but many, especially the Asteraceae such as *Euryops abrotanifolius* and *Othonna quinquedentata*, have small seed that may be highly dispersible and short-lived. Levyns (1929b), discussing this characteristic among *Pelargonium* spp, notes seed burial mechanisms and suggests linkage with dormancy and longevity as adaptive.

The *Protea repens* and some allied species serve as examples of seeding shrubs with longer life cycles. *P. repens* itself is easily killed by fire but seeds germinate readily and there is usually little mortality among young plants. Plants require about 4 to 8 yr to reach reproductive maturity after establish-

ment (Jordaan 1949; van der Merwe 1966b), and bradysporous capitula retain a reasonable supply of viable seed. In a 19 yr old stand at Jonkershoek, for example, all plants carried capitula 2 yr old and older, and most had retained seed for at least 4 yr (Kruger 1978). Lombaard (1971) has shown in stands about 10 to 12 yr old that current seed production amounted to about 900 to 1 300 seed per shrub, of which about 9% was viable. Jordaan (1949) has drawn attention to the significance of the length of the juvenile period in determining whether or not the species would survive a given fire regime. He suggested on the grounds of embryology and phenology that populations were liable to be exterminated if burnt during the period July to December, less so if burnt in April to June, but would regenerate in the period January to March because ripe seed was freely available in that season. Later he showed that *P. repens* had been eliminated in a June burn on Paarlberg. His observation seems to have limited generality, since *P. repens* elsewhere survives winter burns because of bradyspory, but he drew attention to important interactions between fire regime and phenology (Jordaan 1965).

Dominant seed-regenerating shrubs reach ages of about 20 to 50 yr, low shrubs such as *Erica* spp having, on the whole, shorter life spans than tall shrubs. There is little or no establishment of young plants in vigorous stands, but some seed regeneration occurs when adults begin to die out.

The only species of sprouting shrub about which there is some information is *Protea nitida* (Haynes 1976). This species does not have bradysporous capitula, but flowering and seed release occur somewhat irregularly through the seasons with maximum in winter and spring, and germination is usually abundant after fire and rare at other times. Young plants soon develop lignotubers. In the nursery, this occurs within 12 months after germination. These plants seldom reach maturity before being burnt for the first time, upon which they adopt a low, multistemmed habit. This habit is seemingly retained for many years until one of the shoots gains dominance and the plant takes on the form of an erect if crooked shrub, attains maturity and grows in height. At this stage, individuals are able to resprout from epicormic buds in the branches and stem or from the base after even the most intense fires (Haynes 1976).

Animals

Frost (this volume, chapter 13) provides a detailed review of this topic that covers many of the known responses among fynbos animals. It seems that animal responses in fynbos should show peculiarities owing to the following circumstances:-

1 Plant sclerophylly, the widespread occurrence of secondary compounds which apparently reduce palatability, and low nutrient concentrations in plant parts in general, as well as the scarcity of palatable grasses, make for "poor" forage. Herbivores must either accommodate to these conditions, adapt to seasonal "herbivore windows" such as the temporary palatability of expanding leaves, relatively rich in protein and not yet hardened, or search for unusually nutritious resources such as nectar, fruit and seeds. Others may simply avoid the plant assemblage so characterized and immigrate only at certain successional stages when the vegetation is mostly palatable. These features may be intensified by the fine-grained nature of resources in fynbos with its mixture of plant growth forms.

2 The successional changes in fynbos are very marked, proceeding from "bare" ground through a (structurally) grasslandlike stage and mixed herb/shrubland to shrubland. These changes are relatively greater than in grassland or savanna. They would seem therefore to provide opportunity for greater packing of annual species through temporal partitioning of resources than in other ecosystems and responses to firedriven plant succession might be expected to be more diverse. However, richness in annual species does not appear to be particularly great and there are also few endemics (Bigalke 1979).

3 Fynbos fires release more energy, move more slowly and have taller flames and deeper flame fronts than grassland or savanna fires and these features should present special problems of survival to animals.

4 Relatively low fire frequencies in fynbos may favour stratagems that allow low rates of animal survival in situ and show population growth thereafter. In addition, where species are exterminated locally re-establishment through slower immigration than elsewhere would be feasible.

5 Fire seasonality is coupled with hot, dry summers during which many plants are dormant and forage may be scarce.

Survival in situ seems quite feasible in many arthropods. Subterranean forms have not been studied in relation to fire, but Endrody Younga (1978), for example, describes litter and soil insects with Gondwana origins. They must be presumed to have evolved under conditions when fire was rare, and yet have survived in the fire environment of the fynbos. Ants, termites and earthworms generally, though perhaps variably, survive in situ and are active shortly after fire in most places (Martin 1966; Kruger 1980). Specialized life cycles enable some insects to be little affected by fire. For example, various species of scarab beetle, which forage mainly on *Protea* inflorescences, pupate under termitaria of *Amitermes hastatus* (Kruger 1980). Pupation occurs during late summer and autumn, the height of the fire season, and adults emerge not simultaneously but at different times over weeks. These properties would seem to favour survival even if the adults must fly some distance to reach unburnt vegetation.

There are no doubt other examples of survival by particular stages in the life cycle, as well as by use of refuges or by escape. As Tainton and Mentis (this volume,

chapter 6) point out, invertebrates are generally fecund enough for populations to recover rapidly. The means whereby the various species of land snails found in fynbos habitats maintain themselves poses an intriguing problem.

The effects of fire on fynbos amphibians have not been studied but are probably similar to those suggested for grassland species (Tainton and Mentis, this volume, chapter 6). For reptiles too it is likely that refuge habitats are probably important. *Psammobates geometricus* (the geometric tortoise) is an especially interesting case. It is a species of lowland fynbos ecosystems which has a life cycle seasonality and exploits soil insulation in a fashion that suggests adaptation to a fynbos fire regime (J C Greig, personal communication, 1980). Eggs are laid in spring and buried about 100 mm below the soil surface. Incubation lasts about 4 to 6 months and hatchlings emerge in April and May, when exposure to fire is unlikely. Winter and spring are seasons with the best forage and maximum growth rates, and juveniles are well established by the first summer. They reach reproductive maturity at 7 to 8 yr, live till about 30 yr and may attain peak fecundity at about 15 yr. The tortoises avoid the closed habitats of mature vegetation. Thus juveniles are able to grow rapidly in the relatively productive postfire environment and reach reproductive maturity before the probability of fire reaches its maximum. Adults are able to survive some fires, but eggs and hatchlings are seldom if at all exposed.

There would seem to be no reason to expect that birds, by virtue of their mobility, are less able to survive fires in fynbos than in any other vegetation type (Tainton and Mentis, this volume, chapter 6). Though nests are vulnerable, Winterbottom (1963) shows that the incidence of nesting among birds in the winter rainfall region of the southwestern Cape reaches a peak in September (spring) when the wet season has passed and temperatures begin to rise. Although his data may be biased by the inclusion of records from farm and garden birds, it seems that the probability of significant nest loss from fire in fynbos is usually not very great.

Among small mammals, fossorial species are probably least affected by fire as their effective survival has been readily observed (eg Levyns 1929b for rodent moles). Others are likely to survive fire in underground refuges (Delany 1972), under rocks or in unburnt islands of vegetation, although nonburrowing taxa (eg *Otomys* spp, *Rhabdomys pumilio*, *Dendromus mesomelas)* may be especially vulnerable. Willan and Bigalke (1982) report that all of the 11 species listed in Table 7 were found to occur in mesic refuge habitats (Vesey-Fitzgerald 1966; Stewart 1972) unrepresentative of typical fynbos. Trapping on rocky outcrops, usually also regarded as refuge habitats, showed only *Aethomys namaquensis*, *Elephantulus edwardii* (Cape elephant-shrew) and a single specimen of *Mus minutoides* to be present. No dead or injured small mammals were noted after a prescribed burn in the Jakkalsrivier catchment, Lebanon State Forest (Willan and Bigalke 1982).

Mobility probably enables hares, carnivores, bovids and baboons to escape all but very large, intense conflagrations, although anecdotal accounts of small antelope such as Cape grysbok *(Raphicerus melanotis)* burning to death are not uncommon. Dependent young are more likely to perish but in some species (Cape grysbok, grey duiker *(Sylvicapra grimmia))* births may be concentrated in spring (Manson 1974) when fire incidence is low.

Variation in survival rate with variation in fire intensity is expected for at least some species but has not yet been investigated. This brief description of possible patterns of adaptation to the fynbos fire regime indicates an intriguing array of responses well worth investigation.

EFFECTS OF FIRE REGIME ON MICROCLIMATE, SOILS AND HYDROLOGY

Few microclimate studies have been reported for fynbos ecosystems. The immediate, ephemeral effects of fire on microclimate and hence on the ecosystem are seemingly drastic (high temperatures, great turbulence, etc). Apart from the fact that vegetation is razed, the effects are poorly known and perhaps too short-lived to be important in the long run. Nevertheless, cases such as the reported stimulation by ethylene in smoke of flowering of *Xanthorrhoea australis* in Australian heathland (Gill and Ingwerson 1976) suggest that it is important to understand these effects to know the overall ecological role of fire.

Mountain fynbos communities are usually at least 0,75 to 1,0 m tall, with cover normally exceeding 70%. Fire through these stands nearly eliminates or at least severely reduces the vegetal cover. This would immediately change microclimatic lapse rates near the ground and markedly affect wind profiles. Furthermore, the reflective properties of the surface change dramatically. Infiltration capacity of the soil is apparently not changed in many cases (but see below). It is possible to explore the likely effects of fire on the energy balance, evapotranspiration, and wind near the ground by means of established microclimate models, but the likely influences may be summarized as follows:-

1 The uppermost layer of the soil, ca 300 mm deep in sands, deeper in sandy loams, is subject to drying through direct evaporation and when exposed by fire, losses through evaporation are greater and so the surface layers of the soil become drier. However, removal of the vegetative cover drastically reduces losses through transpiration and the subsurface layers may well be moister after fire. The precise nature of the soil profile and the rooting characteristics of the vegetation will determine the net effect on evapotranspiration.

Levyns (1929b) sampled the upper 150 mm of a granitic soil through a full year and found little difference between the moisture contents of soils of burnt and unburnt sites. Wicht (1948b) sampled soils, also granitic, from replicated plots at depths of 0 to 150 and 610 mm at the end of summer.

No statistically significant differences were found between soil moisture of sites burnt 44 days before and that of unburnt sites, although the former were all moister at 610 mm depth. These observations are too few for a proper test of predictions concerning the effect of fire on local soil moisture regimes.

2 Upper soil layers exposed after fire will profoundly influence temperatures of air near the ground, especially since most soils are sands. Surface temperatures will fluctuate more widely, and will be likely to exceed 50°C often in summer. This effect will probably be confined to the upper 50 mm in sands (Geiger 1957). Local variations owing, for example, to variations in soil moisture, aspect differences and different organic matter contents must play a profound role in plant germination and establishment and in determining distribution of plant species, through, among other things, the effect of temperature fluctuations on dormant seed and on relative survival of seedlings. Effects on microorganisms and hence, for example, on mineralization processes would be equally profound.

Levyns (1929b) was apparently the earliest to attempt studies on responses of soil temperatures to burning, without much success. Martin (1966) made a more comprehensive study, but also with limited results. He found little difference in spring between recently burnt and unburnt soils though the former were warmer by about 2°C at 100 mm depth. Differences at 50 mm were small. On a cloudy day in summer, temperatures at 50 mm ranged from 15 to 18°C diurnally and exceeded maximum temperatures of air at 1,2 m (24°C) and of unburnt soil (23°C) by 8 to 9°C.

3 Sands, both in mountain and in coastal fynbos, are sometimes subject to deflation after fire (Walsh 1968; Bond 1979). Wind erosion is apparently not a great problem unless burning is accompanied by grazing with domestic stock, but ecological effects of deflation could be significant. Wind and saltating soil particles will erode or damage young plants, and drift of soil and seed could cause small-scale vegetation patterns.

4 After fire, soil is exposed to raindrops and moved accordingly. This causes patterning through pedestalling, debris dams and large-scale soil transport (Specht et al 1958).

5 At elevations exceeding about 1 500 m and in other frost-prone zones, frost action after fire could become important in determining plant establishment patterns.

6 The effects will be ameliorated gradually as vegetation recovers, but initial microclimatic controls or regeneration will influence the composition of a stand throughout its successional history.

Certain prominent features of the mountain fynbos landscape dominate the effects of fire regime on soils and on the hydrological cycle. First, the steep and rugged topography is in fact relatively old and stable. Frequent rock outcroppings provide local erosional base-levels. Soils derived from the dominant sandstone formations are coarse, structureless and highly permeable and the underlying material coarsely weathered. Deep colluvial and alluvial material is prominent in certain landscapes. Underlying rock is often heavily cracked and jointed. Rainfall intensities are seldom excessive. The highest 15 minute intensity recorded at Jonkershoek in 20 yr was around 60 mm hr^{-1} (Wicht et al 1969) and largest 1 hr storms reported amounted to 50 and 75 mm (Wicht 1943). Consequently, surface runoff as overland flow is exceptional even in the heaviest storms (Versfeld 1981). Most water during storms leaves catchments through rapid lateral drainage (quick seepage) and channel flow, except in zones of saturation near streamlines or below pronounced breaks in the slope. Stream levels respond rapidly and markedly to rainstorms (Wicht 1943) though such stormflow is a small part of annual flow, relative to baseflow (Bosch et al, this volume, chapter 15). Mountain streams usually have very low silt loads, and the major erosional process is apparently in the form of soil slips and subsequent gully erosion during exceptional storms of less than annual frequency (Wicht 1943).

With such physiography and hydrology it is not surprising that the prevailing fire regime has a relatively small effect. Soil structure is apparently not much affected. In a runoff plot study on a sandy loam on granite at Jonkershoek, cover types monitored included a pine stand, a protected fynbos stand and a hoed and a burnt fynbos site. Surface runoff as overland flow collected from these plots was negligible or zero irrespective of treatment, in spite of one of the heaviest storms on record having occurred shortly after hoeing and burning (Versfeld 1981). Clearly, there are many situations where infiltration capacities of soils are greatly in excess of maximum rainfall rates and unlikely to be sufficiently affected by burning so that noticeable reductions in infiltration rates are likely. However, Bond (1980) has reported water repellency in certain fynbos soils, especially humic and organic soils, of the southern Cape, and shown from laboratory studies that the heat from fire is likely to increase repellency, as in chaparral fires of the mountains of southern California (DeBano 1981). The extent of this phenomenon and its importance in erosion and hydrology have yet to be evaluated, but the catastrophic floods and debris flows which follow so many chaparral fires are not a feature of the mountain fynbos.

Field observation indicates also that extremely intense fires which oxidize the organic material of surface soil horizons, drastically modifying physical properties, lead to accelerated erosion after fire, both because soil particles are more mobile and because the site is denuded of vigorous resprouting herbs.

Few studies have been completed of fire's effects on soil chemistry and fertility. Martin (1966) measured pH of soils on burnt and unburnt sites over several months and could find no consistent difference. This contradicts experience elsewhere and merits further investigation. He also looked for responses in

nitrification to burning and could find none. Regarding overall fertility, Schutte (1960) pointed to chlorosis in certain fynbos plants as indicative of deficiencies in the trace elements magnesium, manganese and zinc and used simple field trials to confirm the diagnosis. He suggested that plants in nutrient-deficient environments would be adapted to such conditions, and that an evident deficiency syndrome must therefore be due to soil impoverishment because of "clearing and burning".

The removal of vegetation by fire changes the hydrological regime, but these hydrological effects of fire are not straightforward and require further study. Rycroft (1947) reported increased spateflow rates from a catchment in Jonkershoek after an autumn burn, but this effect had disappeared by the second winter (Banks 1964). Conversely, van der Zel and Kruger (1975) showed in a similar catchment study in Langrivier, Jonkershoek, how streamflow declined with time since burning and ascribed this to steadily increasing evapotranspiration through interception and transpiration losses. Later, van Wyk (1977) analysed results of the same experiment, using additional records, and found a smaller streamflow response (decreases of about 16 mm yr^{-1} of protection on average, as opposed to 20 mm yr^{-1}) that did not persist beyond about the first two decades. Streamflow from catchments nearby, with lower rainfall and shorter vegetation, did not show a declining trend with protection of fynbos against fire. At Zachariashoek, also with low fynbos communities, burning the vegetation produced slight increases in streamflow that were not detectable beyond the first winter after fire (van Wyk 1982).

Van Wyk (1982) has studied aspects of the mineral nutrient balance of fynbos catchments near Zachariashoek, Paarl, and the effects of fire on it by monitoring atmospheric inputs and losses in streams. Concentrations of nitrogen and phosphorus were too low for detection by the analytic techniques used (thresholds for NH_4-N, NO_3-N, and PO_4 were 0,1, 0,05 and 0,02 mg l^{-1}, respectively) and it seems that quantities of these compounds moving through the ecosystem in water are negligible, even after fire. Ion export, estimated from water conductivity records, rose by 8% of preburn levels (on an annual basis) after fire. The increased rate of outflow persisted only for about 10 months. Most net losses occurred in the first two spates after the fire, when ionic concentrations increased briefly to averages double the preburn levels. All ions normally detectable (Na^+, K^+, Ca^{++}, Mg^{++}, $SO_4^=$ and $CO_3^=$) increased in concentration during these spates, but estimated net mass losses were negligible compared to normal inputs and outputs. Suspended sediments behaved similarly, and net yields were 0,2 kg ha^{-1} and about 1,0 kg ha^{-1} for the two burnt catchments. Mineral losses in this form were therefore also negligible. Van Wyk also reported preliminary results for a burning experiment in a nearby catchment with different fynbos communities (more phreatic vegetation, higher average biomass). Here, increases in ionic concentration were greater though also short-lived. The pH in these "black waters" increased from about 3,5 to about 4,5 immediately after burning, but the effect did not persist.

PRESCRIBED BURNING IN CONSERVATION AND MANAGEMENT OF FYNBOS ECOSYSTEMS

Fire is applied by managers in almost all natural or near-natural fynbos vegetation. The objectives vary. On the lowlands as in the mountains, patch-burning is often used to provide seasonal grazing, as described above, and this practice was previously widespread as shown by air photographic records. Timing of burns varies according to local custom as dictated, apparently, by local climatic conditions. Thus in the southwest burns are applied in early spring, with favourable weather at the change of the season. Stock is also brought onto the land at this time, but the animals would of course first graze the burns of the previous and earlier springs, and later that of the current spring. In the south, for example around Bredasdorp, the practice has been to burn in late summer, around February, as winds are then steady, bergwinds few, and relative humidities high. Stock is brought onto the burns for about 2 spring seasons, and not thereafter. Burns are repeated on a cycle of about 6 yr.

Fire has been and is also applied to increase or regulate the yield of veld products. Thus in the Cedarberg and southwards veld from which *Agathosma betulina* and *A. crenulata* are harvested is burnt by farmers in late summer or autumn, on about a 6 to 8 yr cycle, after the last of two or three biennial harvests. Experience has shown that such burns are required to rejuvenate the sprouting shoots and maintain yields, while also favouring recruitment from seed (Bands 1980). In the south, especially on coastal lowlands where flowers and florists' material are harvested from for example short-lived *Helichrysum* spp and Restionaceae, there is a tendency among some producers to burn on short rotations to increase yields.

Burning fynbos for fire control and safety of humans, livestock and property is seldom an explicitly stated goal among private landowners and seems to have been implicitly accepted as important.

Prescribed burning also has a place in conservation areas. It is instructive to examine the policies and practices applied on State forests, since these are the largest conservation areas in mountain fynbos ecosystems. These areas are managed with several objects in view including the following:-

1 Maintenance of maximum yields of silt-free water.

2 Nature conservation, principally the maintenance of species diversity and the control and eradication of invasive plants.

3 Provision of outdoor recreation opportunities compatible with 1 and 2.

4 Control of wildfires by creating a mosaic of veld of different ages and hence discontinuous fuels of low average flammability.

Ecological and managerial considerations led to a management policy that includes prescribed burning and in 1970 replaced a policy of complete protection against fire (Garnett 1973; Bands 1977). This policy includes the following:-

1 "Dry" catchment areas, high peaks, forest kloofs and "...areas in which springs occur..." will not be burnt.

2 Burning will be applied at a frequency of about once in 12 yr, although the frequency would be adjusted according to the conditions and management objectives specific to a certain area.

3 Burns shall be applied in late summer, in simulation of a "natural" regime, but burns at safer times will be used where necessary because in the initial stages of implementing the policy much of the country would be covered in old vegetation and burning conditions would be hazardous.

The framework for management is provided by a compartment system where each reserve is subdivided into natural units of some 500 to 1 500 ha, each of which receives a uniform treatment. Weed control is sought principally by a judicious combination of clearing and burning (Fenn 1980).

Wicht (1945) and Wicht and Kruger (1973) have reviewed the history of controversy surrounding the ecological role of fire and use of prescribed burning in fynbos, and Bands (1977) and Kruger (1977b, 1979a) set out the rationale of the policy and the elements of practice. Policies have now been laid down for several mountain fynbos ecosystems, and the practice that emerges has the following features. Firstly, weed control takes priority where necessary, and management is adjusted accordingly (Fenn 1980). Secondly, burning cycles prescribed range from 9 to 15 yr, depending on how planners interpret vegetation dynamics. In several cases, a "natural" fire regime has been prescribed especially in the case of dry north slopes in karoo mountains. Here, burns may be used initially to create a compartment mosaic of different veld ages but thereafter individual compartments would be allowed to burn if a fire does occur and on condition that the vegetation is older than a stated minimum age and contains no invasive plant species, with the proviso that the fire is to be contained within compartment boundaries. Thirdly, burns are proscribed for the period from the end of April until the end of August. Field managers are encouraged to burn in late summer and autumn.

Management of reserves of this kind is constrained by various factors, including legal requirements and developments outside the reserves. The Forest Act makes the landowner responsible for reasonable precautions against spread of fire to adjoining properties, for example. Specific management objectives within the reserve are often an expression of imperfect scientific knowledge that must be incorporated in policy and practice by the planner. Parallel objectives, pursued simultaneously on the same site, often contain a greater or lesser measure of conflict and the need for fire control in nature conservation is an example. Certain options are also closed. Thus, presence of invasive plants dictates the controlled use of fire. Consequently, the final prescription of a fire regime is the best possible compromise using current methods selected from limited options and criticisms of policy must take this into account to be effective.

Focusing for the present on policies for State forests, it would seem that criticism to date has not yet contributed to constructive evaluation of the problem of determining appropriate prescriptions. Thus Moll et al (1980) propose much longer (40 yr) burning cycles than are presently employed, on the grounds that shrub species with relatively long primary youth periods will not survive the cycles presently favoured, but fail to accommodate the alternative mechanisms and conditions that allow persistence of such species and neglect to consider the effects of senescence like those reported by Bond (1980). We feel that the problems that require attention for development of appropriate polices are as follows:-

1 The constraints outlined above and goals of individual owners (eg production of *Helichrysum* flowers) tend to favour shorter rather than longer burning cycles. Methods of simulating the consequences of such shifts and hence of selecting among alternatives are urgently required.

2 Field managers have legal obligations and tend to burn in safe seasons, for example in spring in the southwest (van Wilgen 1981a). The means to proper fire management, including fire hazard and behaviour prediction systems, are required to enable safe burning operations in the desirable season.

3 Successional depletion of plant populations through senescence and decay of seedbanks are processes poorly understood yet central to considerations affecting choice of fire frequency.

4 Fire intensity is an important but poorly understood factor governing the nature of the postfire community. Management will tend to favour low to moderate intensities and this may have important consequences which must be urgently identified.

5 Some evidence of the importance of variance in the regime experienced by the community at any given site indicates that this aspect requires evaluation for possible incorporation in management systems.

6 The likely depletion of nutrient pools and enhancement of erosion rates by relatively frequent burning could severely constrain management options, especially where water conservation is a primary aim, and this question must be urgently resolved.

7 Effects of compartment size, frequency, season and intensity of burn on faunal composition and dynamics require investigation, particularly in relation to the roles that animals play either as pollinators or dispersers of plants.

8 No attention has been given to the effects of burning regimes on recreational use of fynbos reserves.

CONCLUSION

The view of fire in fynbos presented here focuses largely on its role as an agent in community succession. This perhaps reflects the immediate need to understand pyric succession to manage fynbos ecosystems, and its importance as a very pervasive process in the fynbos landscape. The demographic and morphological responses to fire and consequences of changes in fire regime have been touched on but this is clearly an area where much work is necessary for an understanding of the likely long-term effects of man's influence in this environment. It seems particularly relevant to study the population biology of representative fynbos organisms in relation to burning. The rich array of life strategies evident in the biota promises to reward further study.

Aside from pioneering work by forest hydrologists there has been little study of fire in the ecosystem context and it is clearly imperative to expand our knowledge of the influence of fire regime on the hydrological cycle and nutrient balance. This would require carefully targeted studies of ecosystem processes and the ecophysiology of nutrient transfer between the plant and soil as they are affected by burning. A central question here is how fire regime could play a role in releasing nutrients accumulated in standing biomass and litter to the active pools, and how this reflects on possible adaptations of plants to a fire environment under nutrient-poor conditions. Furthermore, the ecological role of fire in the longer term and on a geographic scale requires closer attention. Thus, major patterns of vegetation such as those of rain forest, eucalypt forest and shrublands in Australia and Tasmania have been linked with patterns in fire regime and this view must clearly be tested in the fynbos environment, for example as a possible explanation of the relationships between fynbos and forest.

In spite of the major gaps in our knowledge it seems that a coherent account of certain features of the ecological role of fire can be presented. Firstly, fire regime should be viewed as a stochastic process, varying temporally and spatially within certain wide limits (Martin 1966). It is partly this variability that permits the existence of so large a number of species in the fynbos biome, diverse in form, phenology and life history. Secondly, the process of pyric succession itself allows coexistence of plant and animal species by preventing final dominance of the plant community by one or a few species and by allowing dynamic local migrations. If these relationships between fire regime and species' biology can be explicitly elucidated much of the knowledge required for rational management of fynbos will be made available. However, a knowledge of fire behaviour in relation to climate, weather and vegetation type is an essential prerequisite for management. Without this understanding field practitioners using fire or seeking to control fire regimes will not achieve their goals economically. This is a priority requirement, because without fire control and management, protection of fynbos ecosystems against deleterious effects such as invasive weeds is impossible.

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Appendix 3.1 Description of soil profile for the unburnt control site at Jakkalsrivier (Plot 2b)

CLASSIFICATION. SA: Cartref form, Grovedale series, slightly podzolised phase.
FAO: Intergrade Lithosol/Gleyic Luvisol
USDA: Ochric Haplaquept

SLOPE: 31% linear, colluvial midslope.

SLOPE AZIMUTH: 216°

GEOLOGY: Table Mountain Group, Peninsula Formation.

PROFILE DESCRIPTION:

O_1 10 mm, absent in places, very loose

O_2 5 mm, F-layer, no sign of H-layer

A 0-100 mm Greyish brown (2,5Y 5/2) moist to light grey (5Y 7/1) dry, coarse sandy loam; clear bleached sand grains; apedal single grain; loose, common fine to medium irregular roots; rapid permeability with a gradual even transition. Few or no stones or rocks.

E 100-700 mm Pale brown (10YR 6/3) moist, light grey (10YR 7/2) dry, coarse gravel; apedal single grain; many fine to coarse angular and subangular quartzite fragments. Rooting is common to 350 mm and rare lower down. Permeability is very rapid. Gradual irregular boundary. Few or no stones or rocks to 320 mm, 85% by volume below that.

B/C_w 700 mm + B horizon development is limited to the joint planes of the quartzite. There are signs of weak podzol B formation within the more porous rocks and weathering fragments (negative NaF test). Rocks about 95% by volume. Few roots.

Drainage is rapid in this soil, but it may be saturated for short periods.

Appendix 3.2 Description of the soil profile for the site of permanent quadrat no. 1 at Jakkalsrivier (Plot 1g-1)

CLASSIFICATION
SA: Clovelly form (Mossdale series?)
FAO Ochric Ferralsol
USDA: Ustochrept

SLOPE: 35%, convex, colluvial midslope.

SLOPE AZIMUTH: 236°

GEOLOGY: Table Mountain Group, Peninsula Formation. Soil developed on a colluvial fan deposit of shale and tillite.

PROFILE DESCRIPTION:

O_1 10 mm, L layer

O_2 5 mm, F layer, absent over large areas

A 0-150 mm Very dark greyish brown (10YR 3/2) moist brown (10YR 5/3) dry, medium sandy loam; apedal single grain; loose, very friable; few medium very soft faunal casts; rare quartz grit; many fine random roots; many fine/medium irregular voids; moderate permeability and a clear smooth transition. Stones and rocks occupy about 2% by volume.

B_{21S} 150-300/350 mm Strong brown (7,5YR 5/6) moist, reddish yellow (7,5YR 7-6/6) dry medium sandy loam; apedal single grain; very friable; rapid permeability; rare medium soft faunal casts, faint darker brown irregular clay-humate cutans; many quartz pebbles and grits rounded to highly angular; rare small indurated iron concretions; many fine and medium irregular voids; common fine roots; clear smooth transition. Stones and rocks occupy about 1% by volume.

B_{22} 300/350-490/500 mm Gritline of coarse angular sands and highly rounded quartzite pebbles; same colour and texture as the B21 but very rapid permeability. Many roots. This marks the break with older fan material lower down the profile which consists of weathered quartzite fragments to a depth of 700 mm. Stones and rocks occupy up to 5% by volume.

This soil is very well drained and contains more clay than its neighbours perhaps as a result of colluviation from the Cedarberg shales higher upslope.

Appendix 3.3 Description of soil profile for the site of permanent quadrat no. 2 at Jakkalsrivier (Plot 1g-2)

CLASSIFICATION: SA: Lamotte form. Chamond series, wet phase.
FAO: Gleyic Podzoluvisol
USDA Typic Haplaquod

SLOPE: 20% - concave, colluvial toeslope (riparian site)

SLOPE AZIMUTH: 238°

PARENT MATERIAL: Colluvial deposits from Table Mountain Group.

PROFILE DESCRIPTION:

O_1 5 mm, L layer

O_2 Absent

A 0-300 mm Very dark grey (5Y 3/1) moist, dark grey (5Y 4/1) dry, medium loamy sand; apedal single grain; soft and friable (moist); slightly hydrophobic; many fine and medium roots throughout; common fine/medium irregular mottles; gradual transition. No stones or rocks.

E 300-700 mm Very dark grey (5YR 3/1) moist, grey (5YR 5/1) dry, medium sand; apedal, single grain; slightly hard, friable; rapid permeability; common fine and medium distinct mottles; common humic dark grey stains; common fine roots; few large irregular channels in lower part; slightly wavy abrupt boundary. No stones or rocks.

B_{hs} 700 mm + Dark brown (7,5Yr 3/2-4) moist, medium loam; apedal massive, brittle; moderate permeability; many large distinct ferrihumic dark reddish brown irregular nodules; common black organic stains on root channels; common fine and medium root mat at the top of spodic B forming a horizontal contact; lower boundary not recorded. The B horizon acts as a pan and clearly prevents rooting and may help to perch water in the winter. No stones or rocks.

Appendix 3.4 Description of soil profile for the site of permanent quadrat No. 3 at Jakkalsrivier (Plot 1g-3)

CLASSIFICATION: SA: Cartref form, Grovedale series, shallow humic phase (almost Mispah)
FAO: Gleyic Luvisol, humic lithosolic phase
USDA Humic Haplaquept

SLOPE: 65%, linear, lower midslope

SLOPE AZIMUTH: 92°

GEOLOGY: Table Mountain Group, Peninsula Formation. Soil is influenced by colluvial deposits from the same parent material.

PROFILE DESCRIPTION:

O_1 Absent.

O_2 10 mm mixed with mineral soil F-layer.

A 0-100 mm Very dark grey (N3/0), dark grey (N4/0) dry, coarse sand; apedal single grain; loose, friable; slightly hydrophobic; rare small, rounded-subangular quartzite pebbles and grit; many fine/medium roots throughout; clear, slightly irregular boundary. Stones and rocks about 2% by volume.

E 100-150 mm Grey (10YR 5/1) moist, light grey (10YR 6/1) dry, coarse sand; apedal, bound by roots; very friable; moderately permeable; many fine roots; irregular sharp boundary. Stones and rocks about 2% by volume.

B/Cw 150-340 mm Minimal development of B-horizon properties in the coarse jointed sandstone and quartzite. Many fine roots. Stones and rocks about 65% by volume.

C 340 mm + Drift material. Roots present.

This profile does not represent the 'average' conditions for the plot which is a deeper soil similar to that of the control plot except for the humic topsoil and the slight indications of podzolisation.

Appendix 3.5 Chemical data for soil profiles at Jakkalsrivier. See Appendix 3.7 for methods of analysis.

	"Control" Plot 2-b		"Mesic" Plot 1g-1			"Phreatic" (Plot 1g-2)			"Dry" (Plot 1g-3)	
	A	E	A	B_1	B_2	A	E	B	A	E
Mineral nutrients										
(all in mg/kg)										
Total N	252	56	826	476	196	1260	420	672	756	196
Total P	30	23	75	55	50	58	55	43	25	18
"Available" P	4	3	3	2	2	9	5	11	8	2
Potassium	8	3	26	12	9	29	9	11	30	4
Calcium	70	12	94	35	19	64	20	22	174	29
Magnesium	21	4	34	21	14	41	12	9	101	14
Sodium	10	5	28	16	12	36	13	15	28	6
Zinc	0,36	0,50	0,15	0,39	0,14	0,92	0,20	0,79	0,53	0,13
Copper	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Boron	0,90	0,60	1,00	0,80	0,64	1,00	0,70	0,60	1,10	0,70
Molybdenum	0,30	0,35	0,34	0,30	0,50	0,35	0,33	0,30	0,31	0,63
pH water (a)	4,61	5,17	5,40	5,32	5,03	4,54	4,68	4,75	4,21	4,79
pH KCL(a)	3,37	3,98	4,40	4,49	4,47	3,65	3,81	3,97	3,02	3,44
Cation exchange capacity (meq/100 g)	0,19	0,15	1,83	0,26	0,16	0,53	0,21	0,33	2,01	0,12
Resistance, ohms	2600	7200	1800	3100	3500	1100	2600	3400	1240	3900
Organic matter,%[a]	1,80	0,20	4,87	1,19	0,56	5,72	1,81	3,63	6,82	0,95
Organic carbon,%[a]	1,04	0,11	2,82	0,69	0,33	3,32	1,05	2,16	3,96	0,55

[a] mean for two readings.

Appendix 3.6. Physical analysis of soil profiles at Jakkalsrivier. See appendix 3.7 for methods of analysis.

	Plot 2B		Plot 1g-1			Plot 1g-2			Plot 1g-3	
	A	E	A	B_1	B_2	A	E	B	A	E
Textural analysis										
Clay %[a]	0,0	1,0	11,0	4,0	3,0	8,0	4,0	10,5	2,0	1,0
Silt %[a]	14,5	16,5	27,0	26,5	15,0	21,0	20,5	20,5	11,0	10,0
Sand %[a]										
- coarse	26,0	24,0	6,0	31,5	46,0	1,0	2,5	3,0	22,5	29,5
- medium	32,5	34,5	19,0	15,5	24,0	29,0	29,0	26,5	41,5	41,5
- fine	22,0	20,0	29,0	18,5	10,0	38,0	39,0	35,5	20,0	14,5
- very fine	5,0	5,0	8,0	4,0	1,5	4,0	5,0	5,0	3,5	3,0
Textural class	LmSacg	LmSacg	SaLmfg	LmSacg/ SaLmcg	LmSacg	SaLmfg	LmSafg/	SaLmfg	Sacg	Sa
Bulk density, $g.ml^{-1}$	1,03	1,3	0,91	1,0	1,0	0,95	1,35	1,24	1,03	1,2

[a] Mean of two values.

Appendix 3.7 Details of soil analytic methods

1. Chemical analysis

1.1 Total Nitrogen

Digestion by Kjeldahl method preceded by treatment with salicylic acid and sodium thiosulphate to include nitrate nitrogen. Determination by distillation with NaOH, collection of distillate in boric acid and titration with standard alkali. See Black (1965), pp. 1162-1164.

1.2 Total Phosphorus

Digestion with $HClO_4$ followed by colorimetric determination by the molybdenum blue method.

1.3 Available Zinc, Copper, and Manganese

Extraction with 1N HCl in ratio 1:10. Determination by atomic absorption spectroscopy. See Black (1965), pp. 1057-1097.

1.4 Available Boron

Extraction of hot-water-soluble boron by refluxing with $BaCl_2$ solution. Determination by (colorimetric) cucurmin method.

1.5 Available Molybdenum

Extraction with ammonium oxalate in ratio 1:10. See Black (1965). Determination is colorimetric with Rhodamine B (Tucker and Bowling 19xx).

1.6 Available Phosphorus

Extraction with Bray No. 1 solution in ratio 1:7,5. Determination by molybdenum blue method using ANSA as reductant. See Anonymous (ND).

1.7 Available cations (K, Ca, Mg, Na)

Extraction with 1 M ammonium acetate at pH7 in ratio 1:10. Determination by atomic absorption spectroscopy using lanthanum chloride as releasing agent for Ca and Mg, and lithium nitrate as suppressant for K and Na. See Anonymous (ND).

1.8 pH Water

Measured with glass electrode in soil water suspension ratio 1:2,5 after 1 hour.

1.9 Resistance

In saturated soil paste in standard cup.

1.10 Cation exchange capacity

By leaching with 0,5 M $CuSO_4$ then with KCl solution and determining Cu in the KCl solution by atomic absorption spectroscopy. See Anonymous (ND).

Appendix 4.1. List of vascular plant species recorded in the succession studies as Jakkalsrivier, classified according to growth from and vital attributes. Nomenclature follows Gibbs Russell et al. (1984, 1985). Species types are according to Noble and Slatyer (1980), and fire response types according to Bell et al. (1984). Species classified as "delta" species in the Noble-Slatyer system are here identified by means of a lower-case "d". The value 999 stands for infinity. UNK in the column for fire response type stands for "unknown".

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire response type
Agathosma bifida (Jacq.) Bartling & Wendl.	Rutaceae	narrow-scl shrub	UI	21	100	100	100	OVS
Agathelpis angustifolia Choisy	Selaginaceae	narrow-ortho shrub	SI	18	8	30	8	PFE
Agathelpis dubia: = Agathelpis angustifolia								
Amphithalea sp. indet.	Fabaceae	broad-orthoph shrub	SI	.	.	.	.	OS
Anemone capensis: = Anemone tenuifolia								
Anemone tenuifolia (L.F.) DC	Ranunculaceae	evergr. geophyte	UI	9	100	100	100	ALS
Anthospermum prostratum Sonder	Rubiaceae	narrow-ortho shrub	SI	28	30	35	30	OS
Argyrolobium filiforme Ecklon & Zeyher	Fabaceae	narrow-scl shrub	UI	3	100	200	2	ALS
Argyrolobium lanceolatum Ecklon & Zeyher	Fabaceae	broad-orhoph shrub	.	.	.	.	.	.
Argyrolobium lunaris: = Argyrolobium lanceolatum								
Aristea racemosa Baker	Iridaceae	evergr. geophyte	UI	5	100	100	1	ALS
Aristea spiralis L.f.) Ker Gawler	Iridacea	evergr. geophyte	UI	3	100	100	1	ALS
Aspalathus globosa Andrews	Fabaceae	narrow-scl shrub	SI	22	4	100	4	PFE
Aspalathus millefolia R. Dahlgren	Fabaceae	narrow-scl shrub	UI	3	100	200	3	ALS
Asteraceae sp#2	Asteraceae	forb	SI	.	.	.	.	UNK
Athrixia heterophylla (Thunb.) Less	Asteraceae	narrow-scl shrub	UI	8	100	100	3	ALS
Berzelia abrotanoides (L.) Brongn.	Bruniaceae	narrow-scl shrub	VI	36	100	100	100	ALS
Berzelia lanuginosa (L.) Sonder	Bruniaceae	narrow-scl shrub	CI	54	50	50	50	OS
Berzelia squarrosa (Thunb.) Sonder	Bruniaceae	narrow-scl shrub	CI	54	50	50	50	OS
Blaeria dumosa Wendl.	Ericaceae	narrow-scl shrub	SI	66	30	30	32	OS
Bobartia gladiata (L.f.) Ker Gawler	Iridaceae	evergr. geophyte	UI	7	100	100	2	ALS

Species	Family	Growth form	Noble-Slatyer type	Age at matur-(months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire response type
Brunia alopecuroides Thunb.	Bruniaceae	narrow-scl shrub	CI	54	50	50	50	OS
Brunia nodiflora L.	Bruniaceae	narrow-scl shrub	VI	50	100	100	100	ALS
Caesia sp. indet.	Asphodelaceae	evergr. geophyte	UI	.	.	.	.	ALS
Calopsis membranacea (Pillans) Linder	Restionaceae	resioid herb	UI	10	100	100	100	ALS
Carpobrotus pillansii L. Bolus	Mesembre-anthemaceae	succulent forb	DR	36	20	20	20	OS
Carpacoce spermacocea (Reichb.) Sonder	Rubiaceae	forb	SI	28	20	20	20	OS
Carpacoce vaginellatta T.M. Salter	Rubiaceae	narrow-scl shrub	UI	12	100	100	2	ALS
Cassytha ciliotata Nees	Lauraceae	parasitic vine	DI	50	50	999	100	OS
Castalis nudicaulis (L.) T. Norlindh	Asteraceae	forb	UI	15	20	20	2	ALS
Centella difformis (Ecklon & Zeyher) Adamson	Apiaceae	forb	SI	30	10	35	20	PFE
Centella eriantha (Rich.) Drude	Apiaceae	forb	SI	34	20	35	20	OS
Chamarea capensis (Thunb.) Ecklon & Zeyher	Apiaceae	deciduous geophype	UI	12	100	100	3	ALS
Chironia decumbens Levyns	Gentianaceae	forb	SI	.	.	.	.	PFE
Chironia jasminoides L.	Gentianaceae	broad-orthoph shrub	SI	30	12	40	30	PFE
Chondropetalum deustum Rottb.	Restionaceae	restioid herb	UI	21	100	100	100	ALS
Chondropetalum hookerianum (Masters) Pillans	Restionaceae	restioid herb	SI	36	50	50	50	OS
Chondropetalum mucronatum (Nees) Pillans	Restionaceae	restioid herb	SI	.	.	.	.	OS
Chrysithrix capensis L.	Cyperaceae	sedge	UI	15	100	100	100	ALS
Chrysithrix junciformis Nees	Cyperaceae	sedge	UI	15	100	100	100	ALS
Cliffortia atrata Weim	Rosaceae	narrow-scl shrub	SI	66	30	50	50	OS
Cliffortia eriocephalina Cham.	Rosaceae	narrow-scl shrub	VI	24	100	100	100	ALS
Cliffortia graminea L.f.	Rosaceae	narrow-ortho shrub	UI	18	100	100	100	ALS
Clutia alaternoides	Euphorbiaceae	semi-succulent shr	VI	24	100	100	100	ALS
Clutia polifolia Jacq.	Euphoriaceae	semi-succulent shr	SI	28	15	65	15	PFE
Clutia polygoniodes L.	Euphoruaceae	semi-succulent shr	UI	7	100	100	100	ALS

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire response type
Corymbium congestum E. Meyer ex. DC.	Asteraceae	evrgr. geophyte	UI	7	100	100	1	ALS
Corymbium glabrum L.	Asteraceae	evrgr. geophyte	UI	4	100	100	1	ALS
Corymbium latifolium	Asteraceae	evrgr. geophyte	UI	.	.	.	.	ALS
Corymbium scabrum L.	Asteraceae	evrgr. geophyte	UI	4	100	100	1	ALS
Cyphia digitata (Thunb.) Willd.	Campanulaceae	deciduous geophyte	UI	8	100	100	100	ALS
Dilatris viscosa L.f.	Haemodoraceae	evrgr. geophyte	UI	.	.	.	.	ALS
Disa cornuta (L.) Swartz	Orchidaceae	deciduous geophyte	dI	6	100	100	2	ALS
Drosera aliceae Raym.-Hamet	Proseraceae	evrgr. geophyte	dI	18	100	100	100	ALS
Drosera hilaris cham & Schlechtd	Droseraceae	evrgr. geophyte	dI	18	50	50	50	ALS
Drosera ramentacea Burchell ex DC.	Droseraceae	evrgr. geophyte	dI	18	50	50	50	ALS
Ehrharta bulbosa J.E. Smith	Poaceae	grass	UI	.	.	.	.	ALS
Ehrharta ottonis Kunth ex Nees	Poaceae	grass	UI	.	.	.	.	ALS
Ehrharta ramosa (Thunb.) Thunb.	Poaceae	grass	UI	18	20	30	1	FSS
Erhartha rehmannii Stapf	Poaceae	grass	SI	12	4	50	2	PFE
Ehrharta setacea Mees ex Trin	Poaceae	grass	UI	.	.	.	.	ALS
Elegia asperiflora (Nees) Kunth	Restionaceae	restioid herb	UI	20	100	100	100	ALS
Elegia juncea L.	Restionaceae	restioid herb	UI	18	100	100	100	ALS
Elegia racemosa (Poir.) Pers.	Restionaceae	restioid herb	UI	9	100	100	100	ALS
Elegia spathacea Masters	Restiomaceae	restioid herb	UI	9	100	100	100	ALS
Elegia thyrsifera (Rottb.) Pers.	Restionaceae	restioid herb	UI	20	100	100	100	ALS
Ephischoenus adnatus Levyns	Cyperaceae	sedge	UI	18	100	100	100	ALS
Epischoenus quadrangularis (Boeckeler) C.B. Clarke	Cyperaceae	sedge	UI	18	100	100	100	ALS
Epischoenus villosus Levyns	Cyperaceae	sedge	UI	.	.	.	.	ALS
Erica coccinea L.	Ericaceae	narrow-scl shrub	UI	.	.	.	.	ALS
Erica corifolia L.	Ericaceae	narrow-scl shrub	SI	66	30	32	30	OS
Erica fascicularis L.f.	Ericaceae	narrow-scl shrub	SI	54	30	32	30	OS
Erica hispidula L.	Ericaceae	narrow-scl shrub	DR	66	999	999	30	OS
Erica imbricata L.	Ericaceae	narrow-scl shrub	SI	.	.	.	.	OS
Erica longifolia Aiton	Ericaceae	narrow-scl shrub	SI	54	30	32	30	OS
Erica massoni L.f.	Ericaceae	harrow-scl shrub	SI	.	.	.	.	OS
Erica parviflora L.	Ericaceae	narrow-scl shrub	SI	54	30	32	30	OS
Erica plukenetii L.	Ericaceae	narrow-scl shrub	SI	66	30	32	30	OS
Erica pulchella Houtt.	Ericaceae	narrow-scl shrub	SI	.	.	.	.	OS

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire respon type
Edmondia pinifolia (Lam.) Hilliard	Asteraceae	narrow-scl shrub	SI	8	100	100	100	ALS
Edmondia sesamoides (L.) Hilliard	Asteraceae	narrow-scl shrub	DI	.	.	.	.	PFE
Erica sessiliflora L.f.	Ericaceae	narrow-scl shrub	CI	66	50	50	50	OS
Euryops abrotanifolius (L.) DC	Asteraceae	narrow-scl shrub	UI	.	.	.	.	Als
Festuca scabra Vahl	Poaceae	grass	UI	8	20	40	2	FSS
Ficinia sp. cf F. bergiana Kunth	Cyperaceae	sedge	UI	12	50	50	50	ALS
Ficinia capillifolia (Schrader) C.B. Clarke	Cyperaceae	sedge	UI	6	100	100	100	ALS
Ficinia deusta (Bergius) Levyns	Cyperaceae	sedge	UI	.	.	.	.	ALS
Ficinia filiformis (Lam.) Schrader	Cyperaceae	sedge	UI	8	100	100	100	ALS
Ficinia monticola Kunth	Cyperaceae	sedge	UI	3	100	100	100	ALS
Ficinia tenuifolia Kunth	Cyperaceae	sedge	UI	.	.	.	.	ALS
Ficinia zeyheri Boeckeler	Cyperaceae	sedge	UI	.	.	.	.	ALS
Geissorhiza ovata (Burm.f.) Aschers. &. Graebn	Iridaceae	deciduous geophyte	UI	3	100	100	100	ALS
Geissorhiza parva Baker	Iridaceae	deciduous geophyte	UI	4	100	100	100	ALS
Gerbera asplenifolia: = Gerbera linnaei								
Gerbera linnaei Cass.	Asteraceae	evrgr. geophyte	UI	.	.	.	.	ALS
Gerbera tomentosa DC	Asteraceae	evrgr. geophyte	UI	5	100	100	100	ALS
Gladiolus debilis Ker Gawler	Iridaceae	deciduous geophyte	UI	6	100	100	100	ALS
Gladiolus sp. indet	Iridaceae	deciduous geophyte	UI	.	.	.	.	ALS
Gnidia anomala Meissner	Thymelaeaceae	broad-orthoph shrub	SI	.	.	.	.	OS
Gnidia humilis Meissner	Thymelaeaceae	broad-orthoph shrub	SI	32	30	80	30	OS
Gnidia juniperifolia LAM.	Thymelaeaceae	narrow-scl shrub	SI	32	30	80	30	OS
Grubbia tomentosa (Thunb.) Harms	Grubbiaceae	broad-scl shrub	UI	.	.	.	.	ALS
Haplocarpha lanata (Thunb.) Less.	Asteraceae	evrgr. geophyte	UI	1	100	100	100	ALS
Heliophila crithmifolia Willd.	Brassicaceae	annual	SI	6	1	50	1	MFE
Helichrysum felinum (Thunb.) Less.	Asteraceae	forb		.	.	.	.	
Helichrysum litorale Bolus	Asteraceae	forb	DI	20	8	30	8	PFE
Helichrysum pinifolium : Edmondia pinifilia								

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire resp type
Helichrysum sesamoides L.: Edmondia sesamoides								
Helichrysum spiralepis Hilliard & B.L. Burtt	Asteraceae	narrow-scl shrub	DI	22	10	20	10	PFE
Helichrysum vestitum (L.)	Asteraceae	broad-ortoph shrub	DI	36	6	50	6	PFE
Helichrysum zeyheri Less.	Asteraceae	broad-orthoph shrub	SI	.	.	.	.	PFE
Helichrysum sp.	Asteraceae	.	.	.	.	.	.	.
Helichrysum sp. (yellow)	Asteraceae	narrow-scl shrub	SI	18	.	.	.	.
Hermas capitata L.f.	Apiaceae	evrgr. geophyte	UI	12	100	100	100	ALS
Hermas quinquedentata L.f.	Apaiceae	evrgr. geophyte	UI	.	.	.	.	ALS
Holothrix villosa Lindley	Orchidaceae	deciduous geophyte	dI	8	100	100	100	ALS
Homeria sp.?	Iridaceae	deciduous geophyte	UI	6	100	100	100	ALS
Hypodiscus albo-aristatus (Nees) Masters	Restionaceae	restioid herb	UI	8	100	100	100	ALS
Hypodiscus aristatus (Thunb.) Krauss	Restionaceae	restioid herb	UI	20	100	100	100	ALS
Hypocalyptus oxalidifolius (Sims) Baillon	Fabaceae	broad-scl shrub	SI	18	4	100	4	PFE
Hypochoerus radicata L.	Asteraceae	deciduous geophyte		.	.	.	.	PFE
Indigofera glomerata E. Meyer	Fabaceae	broad-scl shrub	SI	30	12	100	20	PFE
Indigofera gracilis Vogel	Fabaceae	narrow-scl shrub	SI	18	20	100	20	OS
Ischyrolepis capensis (L.) Linder	Restionaceae	restioid herb	UI	.	.	.	.	ALS
Ischyrolepis tenuissima (Kunth) Linder	Restionaceae	restioid herb	UI	18	100	100	100	ALS
Lachenalia sp.	Hyacinthaceae	deciduous geophyte	UI	6	100	100	100	ALS
Lachnospermum umbellatum (D.Don) Pillans	Asteraceae	narrow-scl shrub	UI	17	100	100	100	ALS
Lebeckia carnosa (E. Mey.) Druce	Fabaceae	semi-succulent shr	SI	12	3	100	3	PFE
Lebeckia wrightii (Harvey) H. Bolus	Fabaceae	semi-succulent shr	SI	12	3	100	3	PFE
Lebeckia sp.	Fabaceae	semi-succulent shr	SI	.	.	.	.	PFE
Leontonyx spathulatus : = Helichrysum litorale								
Leontonyx squarrosus: = Helichrysum spiralepis								
Leptocarpus distichus : = Resio distichus								
Leptocarpus membranaceus : = Calopsis membranacea								
Leucadendron laureolum (lam.) Fourcade	Proteaceae	broad-scl shrub	CI	54	50	50	50	OS

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fir resp typ
Leucadendron salicifolium (Salisb.) I.J. Wiliiams	Proteaceae	broad-scl shrub	CI	54	50	50	50	OS
Leucadendron spissifolium (Salisb. ex Knight) I.J. Williams	Proteaceae	broad-scl shrub	UI	.	.	.	.	ALS
Leucadendron xanthoconus (Knutze) K. Schum.	Proteaceae	broad-scl shrub	CI	54	50	50	50	OS
Lightfootia sp. cf. L. parvifolia (Berg) Adamson	Lobeliaceae	forb	UI	17	10	.	10	UNK
Lightfootia subulata L. Hent	Lobeliaceae	narrow-scl shrub	SI	22	4	50	4	PFE
Lobelia coronopifolia L.	Lobeliaceae	forb	UI	.	.	.	.	ALS
Lobelia jasionoides (A.DC.) E.Wimm.	Lobeliaceae	forb	UI	18	50	50	50	FSS
Lobelia linearis Thunb.	Lobeliaceae	forb	UI	4	50	50	50	ALS
Lobelia pinifolia L.	Lobeliaceae	narrow-scl shrub	SI	36	50	50	50	OS
Mairea crenata (Thunb.) Nees	Asteraceae	evrgr. geophyte	dI	6	100	999	100	ALS
Mairea sp.	Asteraceae	evrgr. geophyte	UI	.	.	.	.	ALS
Merxmuellera rufa (Nees) Conert	Poaceae	grass	UI	4	100	100	100	ALS
Merxmuellera stricta (Schrader) Conert	Poaceae	grass	UI	.	.	.	.	ALS
Metalasia muricata (L.) D.Don	Asteraceae	narrow-scl shrub	DI	28	30	40	30	OS
Mimetes cucullatus (L.) R.Br.	Proteaceae	broad-scl shrub	UI	12	100	100	100	ALS
Moraea ramossima (L.f.) Druce	Iridaceae	deciduous geophyte	UI	6	100	100	100	MFE
Muraltia concava Levyns	Polygalaceae	broad-scl shrub	SI	.	.	.	.	PFE
Muraltia sp.	Polygalaceae	narrow-scl shrub	SI	.	.	.	.	PFE
Myrica kraussiana Buchinger ex Meisn.	Myricaceae	broad-scl shrub	UI	12	100	100	100	ALS
Nebelia fragarioides (Willd.) Kuntze	Bruniaceae	narrow-scl shrub	CI	54	50	32	50	OS
Nebelia paleacea (Bergius) Sweet	Bruniaceae	narrow-scl shrub	VI	38	100	100	100	ALS
Orchidaceae sp.		deciduous geophyte	dI	6	100	100	100	ALS
Osmitopsis afra (L.) Bremer	Asteraceae	narrow-ortho shrub	UI	12	100	100	100	ALS
Othonna quinquedentata Thunb.	Asteraceae	semi-succulent shr	DI	17	8	10	8	PFE
Oxalis commutata Sond.	Oxalidaceae	deciduous geophyte	UI	7	100	100	100	ALS
Oxalis strigosa Salter	Oxalidaceae	deciduous geophyte	UI	.	.	.	.	ALS
Oxalis truncatula Jacq	Oxalidaceae	deciduous geophyte	UI	7	100	100	100	ALS
Penaea mucronata L.	Penaeaceae	broad-scl shrub	UI	6	100	100	100	ALS

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fir res typ
Pentameris macrocalycina (Steudel) Schweickerdt	Poaceae	grass	UI	4	100	100	100	ALS
Pentaschistis colorata (Steudel) Stapf	Poaceae	grass	UI	4	100	100	100	ALS
Pentaschistis heptamera (Nees) Stapf	Poaceae	grass	UI	.	.	.	.	ALS
Pentaschistis malouinensis (Steud.) Clayton	Poaceae	grass	UI	20	50	50	50	ALS
Pentaschistis sp. cf P. viscidula (Nees) Stapf Thunb.	Poaceae	grass	UI	18	50	50	50	ALS
Peucedanum ferulaceum Thunb.	Apiaceae	evrgr. geophyte	UI	6	100	100	100	ALS
Philippia leeana Klotzsch	Ericaceae	narrow-scl shrub	SI	66	30	32	100	OS
Phylica gracilis D.Dieter	Rhamnaceae	narrow-scl shrub	SI	45	30	80	30	OS
Phylica lasiocarpa Sond	Rhamnaceae	narrow-scl shrub	UI	6	100	100	100	ALS
Podalyria biflora (Retz.) Lam.	Fabaceae	broad-scl shrub	UI	12	100	200	100	ALS
Polygala bracteolata L.	Polygalaceae	narrow-ortho shrub	SI	18	20	30	20	OS
Polyarrhena reflexa (L.) Cass.	Asteraceae	narrow-scl shrub	SI	38	20	35	30	OS
Protea cynaroides (L.) L.	Proteaceae	broad-scl shrub	UI	18	100	100	100	ALS
Protea lacticolor Salisb.	Proteaceae	broad-scl shrub	CI	.	.	.	.	OS
Protea neriifolia R.Br.	Proteaceae	broad-scl shrub	CI	72	50	50	50	OS
Protea scabra R.Br.	Proteaceae	broad-scl shrub	UI	.	.	.	.	ALS
Pseudopentameris macrantha (Schrader) Conert	Poaceaceae	grass	UI	12	100	100	100	ALS
Psoralea aphylla L.	Fabaceae	narrow-ortho shrub	UI	14	80	150	80	ALS
Psoralea restioides Ecklon & zeyher	Fabaceae	narrow-ortho shrub	SI	.	.	.	.	OS
Pterygodium catholicum (L.) Swartz	Orchidaceae	deciduous geophyte	dI	8	100	100	100	ALS
Restio ambiguus Masters	Restionaceae	restioid herb	UI	.	.	.	.	ALS
Restio bifidus Thunb.	Restionaceae	restioid herb	UI	.	.	.	.	ALS
Restio cuspidata : = Ischyrolepis capensis								
Restio dispar Masters	Restionaceae	restioid herb	UI	18	100	100	100	ALS
Restio distichus Rottb.	Restionaceae	restioid herb	UI	18	100	100	100	ALS
Restio egregius Hochst.	Restionaceae	restioid herb	UI	.	.	.	.	ALS
Restio perplexus Kunth	Restionaceae	restioid herb	UI	18	50	50	50	ALS
Restio purpurascens Nees ex Mast.	Restionaceae	restioid herb	UI	18	100	100	100	ALS

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fi re ty
Restio tenuissimus : = Ischyrolepis tenuissima								
Restio triticeus Rottb.	Restionaceae	restioid herb	UI	18	100	100	100	AL
Roella incurva A.DC.	Campanulaceae	forb	SI	18	10	40	10	PF
Roella psammophila Schltr.	Campanulaceae	narrow-scl shrub	S	.	.	.	.	PF
Schizeae pectinata (L.) Swartz	Schizaeaceae	evrgr. geophyte	dI	12	100	100	100	AL
Sebeae exacoides (L.) Schinz	Gentianaceae	deciduous geophyte	dI	3	100	100	100	AL
Selago verbenacea L.f.	Selaginaceae	forb	SI	6	3	50	3	PF
Selago sp. cf S. paniculata	Selaginaceae	narrow-ortho shrub	UI	.	.	.	.	AL
Senecia cymbalariifolius (L.) Less.	Asteraceae	deciduous geophyte	UI	4	100	100	100	AL
Senecio sp. cf S paniculatus Bergius	Asteraceae	forb	DI	17	20	25	20	OS
Senecio pinifolius (L.) Lam.	Asteraceae	narrow-scl shrub	UI	12	100	100	100	AL
Senecia pubigerus L.	Asteraceae	narrow-scl shrub	DI	15	4	999	4	PF
Senecio rigidus L.	Asteraceae	forb	DI	12	2	999	2	PF
Senecio umbellatus L.	Asteraceae	forb	DI	17	20	30	20	OS
Senecio sp.	Asteraceae	forb	DI	.	.	.	.	UN
Siphocodon spartioides Turcz.	Campanulaceae	forb	UI	.	.	.	.	AL
Spiloxene monophylla (Schltr) Garside	Hypoxidaceae	deciduous geophyte	UI	17	100	100	100	AL
Staberoha cernua (L.f.) Durand & Schinz	Restionaceae	restioid herb	UI	18	100	100	100	AL
Stilbe mucronata N.E. Br.	Stilbaceae	narrow-scl shrub	UI	.	.	.	.	AL
Stoebe cinerea Thunb.	Asteraceae	narrow-scl shrub	DI	36	12	25	12	PF
Stoebe incana Thunb.	Asteraceae	narrow-scl shrub	DI	36	12	25	12	PF
Struthiola myrsinites Lam.	Thymelaeaceae	narrow-scl shrub	SI	48	20	20	12	OS
Sympieza articulata (Thunb.) N.E. Br.	Ericaceae	narrow-scl shrub	SI	66	30	32	30	OS
Tetraria brevicaulis C.B. Cl.	Cyperaceae	sedge	SI	45	12	30	20	PF
Tetraria bromoides (Lam.) Pheiffer	Cyperaceae	sedge	UI	18	100	100	100	AL
Tetraria compar (L.) Lestib.	Cyperaceae	sedge	UI	7	50	50	50	AL
Tetraria crassa Levyns	Cyperaceae	sedge	UI	7	50	50	50	AL
Tetraria cuspidata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	9	50	50	50	AL
Tetraria exilis Levyns	Cyperaceae	sedge	UI	8	100	100	100	AL
Tetraria fasciata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	8	100	100	100	AL

Species	Family	Growth form	Noble-Slatyer type	Age at matur- (months)	Long-evity (yr)	Time to extinction (yr)	Maximum age flowering (yr)	Fire response type
Tetraria fimbriolata (Nees) C.B. Clarke	Cyperaceae	sedge	UI	9	100	100	100	ALS
Tetraria flexuosa (Thunb.) C.B. Clarke	Cyperaceae	sedge	UI	8	100	100	100	ALS
Tetraria thermalis (L.) C.B. Clarke	Cyperaceae	sedge	UI	12	100	100	100	ALS
Tetraria triangularis (Boeckeler) C.B. Clarke	Cyperaceae	sedge	UI	12	100	100	100	ALS
Thamnochortus dichotomus : = Thamnochortus lucens								
Thamnochortus gracilis Masters	Restionaceae	restioid herb	UI	8	100	100	100	ALS
Thamnochortus lucens (Poir) Linder	Restionaceae	restioid herb	UI	8	100	100	100	ALS
Thamnochortus pulcher Pillans	Restionaceae	restioid herb	UI	.	.	.	.	ALS
Thamnochortus sporadicus	Restionaceae	restioid herb	UI	8	100	100	100	ALS
Thereianthus bracteolatus (Lam.)	Iridaceae	deciduous geophyte	UI	15	100	100	100	ALS
Thesium carinatum A. DC. G.J. Lewis	Santalaceae	hemi-parasitic sub-shrub	SI	32	12	62	20	PFE
Thesium euphorbiodes L.	Santalaceae	hemi-parasitic sub-shrub	SI	32	12	62	15	PFE
Thesium euphrasioides A. DC	Santalaceae	hemi-parasitic sub-shrub	SI	32	12	62	20	PFE
Thesium sedifolium A. DC ex Levuyns	Santalaceae	hemi-parasitic sub-shrub	SI	33	12	62	20	PFE
Tritoniopsis sp	Iridaceae	deciduous geophyte	UI	12	100	100	100	ALS
Ursinia caledonica (E. Phillips) Prassler	Asteraceae	narrow-ortho shrub	UI	.	.	.	.	ALS
Ursinia crithmoides: = Ursinia paleacea								
Ursinia paleacea (L.) Moench	Asteraceae	narrow-ortho shrub	SI	14	8	40	8	PFE
Ursinia dentata (L.) Poiret	Asteraceae	narrow-ortho shrub	UI	.	.	.	.	ALS
Ursinia digitata	Asteraceae	narrow-ortho shrub	UI	.	.	.	.	ALS
Villarsia capensis (Houtt.) Merrill	Gentianaceae	evrgr. geophyte	UI	.	.	.	.	ALS
Wachendorfia paniculata Burm	Haemodoraceae	deciduous geophyte	UI	.	.	.	.	ALS
Watsonia pyramidata (Andrews) Stapf	Iridaceae	deciduous geophyte	UI	9	120	120	120	ALS
Watsonia schlechteri L. Bolus	Iridaceae	deciduous geophyte	UI	9	100	100	100	ALS
Willdenowia humilis Nees ex Masters	Restionaceae	restioid herb	UI	20	100	100	100	ALS
Willdenowia sulcata Masters	Restionaceae	restioid herb	UI	20	100	100	100	ALS

Appendix 4.2. List of plant Species recorderd in permanent quadrats at Zachariaschoek and classified by attributes according to the system of Noble and Slatyer (1981) and Pate and Dell (1984).

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Acrostemon glandulosus Rach	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Acrosanthes teretifolia Ecklon & Zeyher	Aizoaceae	narrow-orthophyllous shrub	SI	PFE
Adenogramma glomerata (L.f.)	Aizoaceae	annual	SI	MFE
Agathelpis angustifolia Choisy	Selaginaceae	narrow-sclerophyllous shrub	SI	OS
Agathelpis dubia: = A. angustifolia				
Agathosma acuminata: = A. ovalifolia				
Agathosma bifida (Jacq.) Bartling & Wendl.	Rutaceae	narrow-sclerophyllous shrub	UI	OVS
Agathosma ovalifolia Pillans	Rutaceae	narrow-sclerophyllous shrub	SI	OS
Agathosma virgata (Lam.) Bartling & Wendl.	Rutaceae	narrow-sclerophyllous shrub	UI	ALS
Albuca cooperi Baker	Hyacinthaceae	deciduous geophyte	UI	ALS
Albuca sp. indet.	Hyacinthaceae	deciduous geophyte	UI	ALS
Anapalina nervosa (Thunb.) G.J. Lewis	Iridaceae	deciduous geophyte	UI	ALS
Anapalina sp. indet.	Iridaceae	deciduous geophyte	UI	ALS
Anthospermum aethiopicum L.	Rubiaceae	narrow-orthophyllous shrub	SI	OS
Anthospermum ciliare L.	Rubiaceae	narrow-orthophyllous shrub	SI	OS
Anthospermum prostratum Sonder	Rubiaceae	narrow-orthophyllous shrub	SI	OS
Arctotis angustifolia L.	Asteraceae	forb	SI	OS
Argyrolobium filiforme (Thunb.) Ecklon & Zeyher	Fabaceae	narrow-orthophyllous shrub	dI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Argyrolobium lanceolatum Ecklon & Zeyher	Fabaceae	narrow-orthophyllous shrub	UI	ALS
Argyrolobium lunaris:= lanceolatum	Fabaceae	narrow-orthophyllous shrub	UI	ALS
Aristea africana (L.) Hoffm.	Iridaceae	evergreen geophyte	UI	ALS
Aristea confusa Goldbl.	Iridaceae	evergreen geophyte	UI	ALS
Aristea dichotoma (Thunb.) Ker Gawler	Iridaceae	evergreen geophyte	UI	ALS
Aristea major Andrews	Iridaceae	evergreen geophyte	UI	ALS
Aristea racemosa Baker	Iridaceae	evergreen geophyte	UI	ALS
Aristea spiralis (L.f.) Kew Gawler	Iridaceae	evergreen geophyte	UI	ALS
Askidiosperma paniculatum (Masters) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Aspalathus arida E. Meyer	Fabaceae	narrow-sclerophyllous shrub	SI	PFE
Aspalathus carnosa Bergius	Fabaceae	semi-succulent shrub	UI	ALS
Aspalathus ciliaris L.	Fabaceae	narrow-sclerophyllous shrub	UI	ALS
Aspalathus crenata (L.) R. Dahlgren	Fabaceae	narrow-sclerophyllous shrub	UI	ALS
Aspalathus divaricata Thunb.	Fabaceae	narrow-sclerophyllous shrub	SI	PFE
Aspalathus juniperina Thunb.	Fabaceae	narrow-sclerophyllous shrub	SI	PFE
Aspalathus linearis (Burn. f.) R. Dahlgren	Fabaceae	narrow-sclerophyllous shrub	UI	ALS
Asteraceae sp. (F.J. Kruger 1497)	Asteraceae	narrow-sclerophyllous shrub	UNK	UNK
Berkheya herbacea (L.f.) Druce	Asteraceae	deciduous geophyte	UI	ALS
Bobartia gladiata (L.f.) Kew Gawler	Iridaceae	evergreen geophyte	UI	ALS
Bobartia indica L.	Iridaceae	evergreen geophyte	UI	ALS
Brunia nodiflora L.	Bruniaceae	narrow-sclerophyllous shrub	VI	ALS
Bulbine alooides (L.) Willd.	Asphodelaceae	deciduous geophyte	UI	ALS
Bulbine favosa (Thunb.) Roemer & Schultes	Asphodelaceae	deciduous geophyte	UI	ALS
Bulbine sp. indet.	Asphodelaceae	deciduous geophyte	UI	ALS
Bulbinella triquetra (L.f.) Kunth	Asphodelaceae	deciduous geophyte	UI	ALS
Bulbinella sp. indet.	Asphodelaceae	deciduous geophyte	UI	ALS
Caesia contorta (L.f.) Durand & Schinz	Asphodelaceae	evergreen geophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Calopsis viminea (Rottb.) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Cannomois virgata (Rottb.) Steud.	Restionaceae	restioid hemicryptophyte	UI	ALS
Carpacoce vaginellata T.M. Salter	Rubiaceae	narrow-sclerophyllous shrub	UI	ALS
Cassytha ciliolata Nees	Lauraceae	parasitic twiner	DI	OS
Castalis nudicaulis (L.) Norlindh	Asteraceae	forb	UI	ALS
Centella glabrata L.	Apiaceae	forb	UI	ALS
Centella virgata (L.f) Drude	Apiaceae	forb	SI	PFE
Chironia sp. indet.	Gentianaceae	forb	SI	PFE
Chondropetalum paniculatum: =Askidiosperma paniculatum				
Chrysithrix capensis L.	Cyperaceae	sedge	UI	ALS
Cliffortia ruscifolia L.	Rosaceae	broad-sclerophyllous shrub	SI	OS
Clutia alaternoides L.	Euphorbiaceae	semi-succulent shrub	UI	ALS
Clutia polygonoides L.	Euphorbiaceae	semi-succulent shrub	UI	ALS
Coleonema juniperinum Sonder	Rutaceae	narrow-sclerophyllous shrub	UI	ALS
Corymbium africanum L.	Asteraceae	evergreen geophyte	UI	ALS
Corymbium glabrum L.	Asteraceae	evergreen geophyte	UI	ALS
Corymbium villosum Less.	Asteraceae	evergreen geophyte	UI	ALS
Cotula sp. indet.	Asteraceae	annual	ST	NEU
Crassula capensis (L.) Baillon	Crassulaceae	deciduous geophyte	UI	ALS
Crassula fascicularis (Lam.)	Crassulaceae	annual	SI	PFE
Crassula filiformis (Ecklon & Zeyher) Dietr.	Crassulaceae	annual	SI	MFE
Crassula nudicaulis L. var. nudicaulis	Crassulaceae	succulent forb	UI	ALS
Crassula obvallata: = C. nudicaulis				
Crassula orbicularis L.	Crassulaceae	succulent forb	UI	ALS
Cryptadenia uniflora (L.) Meisner	Thymelaeaceae	narrow-sclerophyllous shrub	UI	ALS
Cyclopia falcata (Harvey) Kies	Fabaceae	broad-sclerophyllous shrub	UI	ALS
Cymbopogon marginatus (Steudel)	Poaceae	grass	UI	ALS
Cyphia capitata	Lobeliaceae	deciduous geophyte	UI	ALS
Dilatris ixioides Lam.	Haemodoraceae	evergreen geophyte	UI	ALS
Diosma hirsuta L.	Rutaceae	narrow-sclerophyllous shrub	UI	ALS
Disparago ericoides Gaertner	Asteraceae	narrow-sclerophyllous shrub	dI	ALS
Drosera cistiflora L.	Droseraceae	deciduous geophyte	dI	ALS
Ehrharta bulbosa J.E. Smith	Poaceae	grass	UI	ALS
Ehrharta calycina J.E. Smith	Poaceae	grass	SI	OS
Ehrharta longifolia Schrader	Poaceae	grass	UI	ALS
Ehrharta ottonis Kunth ex Nees	Poaceae	grass	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Elegia juncea L.	Restionaceae	restioid hemicryptophyte	UI	ALS
Elegia filacea Masters	Restionaceae	restioid hemicryptophyte	SI	OS
Elegia parviflora: = Elegia filacea				
Elegia vaginulata Masters	Restionaceae	restioid hemicryptophyte	UI	AlS
Elytropappus glandulosus Less.	Asteraceae	narrow-sclerophyllous shrub	DI	OS
Engisyphon exscapus = Geisorrhiza confusa				
Eragrostis capensis (Thunb.)Trin.	Poaceae	grass	UI	FSS
Erepsia anceps (Haw.) Schwart.	Mesembre-anthemaceae	succulent semi-shrub	SI	PFE
Erica articularis L.	Ericaceae	narrow-sclerophyllous shrub	UI	ALS
Erica calycina L.	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Erica cerinthoides L.	Ericaceae	narrow-sclerophyllous shrub	UI	ALS
Erica coccinea L.	Ericaceae	narrow-sclerophyllous shrub	UI	ALS
Erica corifolia L.	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Erica grandiflora L. f.	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Erica nudiflora L.	Ericaceae	narrow-sclerophyllous shrub	UI	FSS
Erica plukenetii L.	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Erica sessiliflora L.	Ericaceae	narrow-sclerophyllous shrub	CI	OS
Erica taxifolia Ait.	Ericaceae	narrow-sclerophyllous shrub	SI	OS
Euphorbia genistoides A. Berger	Euphorbiaceae	forb	UI	ALS
Euphorbia silenifolia (Haw.) Sweet	Euphorbiaceae	deciduous geophyte	UI	ALS
Euryops abrotanifolius (L.) D.C.	Asteraceae	narrow-orthophyllous shrub	SI	OS
Felicia sp. indet.	Asteraceae	annual	SI	NEU
Festuca scabra Vahl	Poaceae	grass	UI	ALS
Ficinia bulbosa (L.) Nees	Cyperaceae	sedge	UI	ALS
Ficinia deusta (Bergius) Levyns	Cyperaceae	sedge	UI	ALS
Ficinia ecklonea Steudel	Cyperaceae	sedge	UI	ALS
Ficinia filiformis (Lam.) Schrader	Cyperaceae	sedge	UI	ALS
Ficinia levynsiae Arnold & Gordon-Grey	Cyperaceae	sedge	UI	ALS
Ficinia nigrescens (Schrader) Raynal	Cyperaceae	sedge	UI	ALS
Ficinia zeyheri Boeckeler	Cyperaceae	sedge	UI	ALS
Gazania serrata	Asteraceae	evergreen geophyte	UI	ALS
Geissorhiza confusa Goldbl.	Iridaceae	deciduous geophyte	UI	ALS
Geissorhiza sp. indet.	Iridaceae	deciduous geophyte	UI	ALS
Gerbera asplenifolia Spreng	Asteraceae	evergreen geophyte	UI	ALS
Gerbera crocea (L.) Kuntze	Asteraceae	evergreen geophyte	UI	ALS
Gerbera tomentosa DC.	Asteraceae	evergreen geophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Gladiolus debilis Ker Gawler	Iridaceae	deciduous geophyte	UI	ALS
Gnidia anomala Meissner	Thymelaeaceae	broad-orthophyllous shrub	SI	PFE
Gnidia inconspicua Meissner	Thymelaeaceae	broad-orthophyllous shrub	SI	OS
Gnidia juniperifolia Lam.	Thymelaeaceae	broad-orthophyllous shrub	SI	PFE
Gnidia sdlg	Thymelaeaceae	broad-orthophyllous shrub	SI	OS
Haplocarpha lanata (Thunb.) Less.	Asteraceae	deciduous geophyte	UI	ALS
Heeria argentea (Thunb.) Meisn.	Anacardiaceae	broad-sclerophyllous shrub	VI	ALS
Helichrysum indicum (L.) Grierson	Asteraceae	annual	SI	NEU
Helichrysum litorale H. Bolus	Asteraceae	forb	DI	PFE
Helichrysum rotundifolium (Thunb.) Less.	Asteraceae	Forb		
Helichrysum rutiland (L.) D. Don.	Asteraceae	broad-orthophyllous shrub	UNK	UNK
Helichrysum tomentosulum (Klott) Meisn.	Asteraceae	broad-orthophyllous shrub	UI	ALS
Helichrysum vestitum (L.) Schrank.	Asteraceae	broad-orthophyllous shrub	DI	PFE
Heliophila meyeri Sonder	Brassicaceae	annual	SI	MFE
Heliophila scoparia Burchell ex DC.	Brassicaceae	narrow-sclerophyllous shrub	UI	ALS
Heliophila sp. (Kruger 1795)	Brassicaceae	forb	SI	OS
Helipterum canescens (L.) DC.	Asteraceae	narrow-orthophyllous shrub	DI	PFE
Helipterum gnaphaloides (L.) DC.	Asteraceae	narrow-orthophyllous shrub	DI	PFE
Hermas quercifolia Ecklon & Zeyher	Apiaceae	evergreen geophyte	UI	ALS
Hermannia rudis N.E. Br.	Sterculiaceae	broad-orthophyllous shrub	SI	OS
Hesperantha sp. indet.	Iridaceae	deciduous geophyte	UI	ALS
Holothrix sp. indet.	Orchidaceae	deciduous geophyte	dI	ALS
Homeria sp. indet.	Iridaceae	deciduous geophyte	UI	ALS
Hypochoeris radicata L.	Asteraceae	deciduous geophyte	UI	ALS
Hypodiscus albo-aristatus (Nees) Masters	Restionaceae	restioid hemicryptophyte	UI	ALS
Hypodiscus argenteus (Thunb.) Masters	Restionaceae	restioid hemicryptophyte	UI	ALS
Hypodiscus aristatus (Thunb.) Nees	Restionaceae	restioid hemicryptophyte	UI	ALS
Hypodiscus striatus (Kunth) Masters	Restionaceae	restioid hemicryptophyte	UI	ALS
Hypodiscus willdenowia (Nees)	Restionaceae	restioid hemictyptophyte	UI	ALS
Indigofera filicaulis Ecklon & Zeyher	Fabaceae	narrow-sclerophyllous	SI	PFE
Ischyrolepsis capensis (L.) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Ischyrolepis curviramis (Kunth) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Ischyrolepis gaudichaudiana (Kunth) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Ischyrolepis sieberi (Kunth) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Ischyrolepis tenuissima (Kunth) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Lachenalia orchioides (L.) Ait.	Hyacinthaceae	deciduous geophyte	UI	ALS
Lachenalia sp. indet.	Hyacinthaceae	deciduous geophyte	UI	ALS
Lapeirousia corymbosa (L.) Ker Gawler	Iridaceae	deciduous geophyte	UI	ALS
Lebeckia carnosa (E. Mey.) Druce	Fabaceae	semi-succulent shrub	SI	PFE
Leontonyx spathulatus = Helichrysum litorale				
Leptocarpus distichus (=Restio distichus Rottb.?)	Restionaceae	restioid hemicryptophyte	UI	ALS
Leptocarpus vimineus: = Calopsis viminea				
Leucadendron salignum Bergius	Proteaceae	broad-sclerophyllous shrub	UI	ALS
Leucadendron spissifolium (Salisb ex Knight) I.J. Williams	Proteaceae	broad-sclerophyllous shrub	UI	ALS
Lightfootia subulata l'Herit.	Campanulaceae	forb	SI	PFE
Linum thunbergii Ecklon & Zeyher	Linaceae	forb	SI	OS
Lobelia coronopifolia L.	Lobeliaceae	forb	UI	ALS
Mairea burchellii DC.	Asteraceae	evergreen geophyte	UI	ALS
Mairea lasiocarpa DC.	Asteraceae	narrow-sclerophyllous shrub	UI	ALS
Merxmuellera rufa (Nees) Conert	Poaceae	grass	UI	ALS
Metalasia cephalotes (Thunb.) Less.	Asteraceae	narrow-sclerophyllous shrub	UI	ALS
Metalasia muricata (L.) D. Don	Asteraceae	narrow-sclerophyllous shrub	DI	OS
Moraea viscaria (L.f.) Ker Gawler	Iridaceae	deciduous geophyte	UI	ALS
Moraea sp. indet.	Iridaceae	deciduous geiphyte	UI	ALS
Muraltia heisteria (L.) DC.	Polygalaceae	narrow-sclerophyllous shrub	SI	OS
Nebelia paleacea (Bergius) Sweet	Bruniaceae	narrow-sclerophyllous shrub	UI	ALS
Holothrix sp. indet.	Orchidaceae	deciduous geophyte	dI	ALS
Ornithogalum sp. indet.	Hyacinthaceae	deciduous geophyte	dI	ALS
Osteospermum junceum Bergius	Asteraceae	broad-orthophyllous shrub	UI	ALS
Othonna heterophylla L.f.	Asteraceae	deciduous geophyte	UI	ALS
Othonna quinquedentata Thunb.	Asteraceae	broad-orthophyllous shrub	DI	OS
Oxalis purpurea L.	Oxalidaceae	deciduous geophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Oxalis strigosa Salter	Oxalidaceae	deciduous geophyte	UI	ALS
Pelargonium longifolium (Burn. f.) Jacq.	Geraniaceae	deciduous geiphyte	UI	ALS
Pelargonium myrrhifolium (L.) L'Herit.	Geraniaceae	deciduous geophyte	UI	ALS
Pelargonium sp. indet.	Geraniaceae	forb		
Penaea,mucronata L.	Penaeaceae	broad-sclerophyllous shrub	UI	ALS
Pentameris macrocalycina (Steudel) Schweick	Poaceae	grass	UI	ALS
Pentaschistis aristidoides (Thunb.) Stapf	Poaceae	grass	SI	MFE
Pentaschistis colorata (Steudel) Stapf	Poaceae	grass	UI	ALS
Pentaschistis curvifolia (Schrader) Stapf	Poaceae	grass	UI	ALS
Pentaschistis eriostoma (Nees) Stapf	Poaceae	grass	UI	ALS
Pentaschistis filiformis (Nees)	Poaceae	grass	SI	PFE
Pentaschistis malouinensis (Stend.) Clayton				
Pentaschistis pallens	Poaceae	grass	UI	ALS
Pentaschistis steudelii:= P. malouinensis				
Pentaschistis thunbergii (Kunth) Stapf	Poaceae	grass	UI	PFE
Pentaschistis viscidula (Nees) Stapf	Poaceae	grass	UI	ALS
Petalacte coronata (L.) D. Don	Asteraceae	forb	UI	ALS
Peucedanum ferulaceum Thunb.	Apiaceae	evergreen geophyte	UI	ALS
Phaenocoma prolifera (L.) D. Don	Asteraceae	narrow-sclerophyllous shrub	DI	OS
Philippia leeana Klotzsch	Ericaceae	narrow-sclerophyllous shrub	DI	OS
Phylica callosa L.f.	Rhamnaceae	narrow-sclerophyllous shrub	SI	OS
Phylica imberbis Bergius	Rhamnaceae	narrow-sclerophyllous shrub	UI	ALS
Phylica stipularis L.	Rhamnaceae	narrow-sclerophyllous shrub	UI	ALS
Phylica thunbergiana Sonder	Rhamnaceae	narrow-sclerophyllous shrub	SI	OS
Pinus pinaster Aiton	Pinaceae	coniferous tree	DT	OS
Plagiochloa uniolae (L.f.) Adamson & Sprague	Poaceae	grass	UI	FSS
Podalyria sp. indet.	Fabaceae	broad-sclerophyllous shrub	UI	ALS
Priestleya stokoei L. Bolus	Fabaceae	broad-sclerophyllous shrub	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Printzia aromatica (L.) Less.	Asteraceae	forb	UI	ALS
Prismatocarpus diffusus (L.f.) A. DC.	Campanulaceae	narrow-sclerophyllous shrub	UI	ALS
Prismatocarpus fruticosus L'Herit.	Campanulaceae	narrow-sclerophyllous shrub	SI	PFE
Protea acaulos (L.) Reichard	Proteaceae	broad-sclerophyllous shrub	UI	ALS
Protea amplexicaulis (Salisb.) R. Br.	Proteaceae	broad-sclerophyllous shrub	SI	OS
Protea laurifolia Thunb.	Proteaceae	broad-sclerophyllous shrub	CI	OS
Protea repens (L.) L.	Proteaceae	broad-sclerophyllous shrub	CI	OS
Protea scorzonerifolia (Salisb. ex Knight) Rycroft	Proteaceae	broad-sclerophyllous shrub	UI	ALS
Psoralea rotundifolia L.	Fabaceae	broad-sclerophyllous shrub	UI	ALS
Pterygodium catholicum (L.) Swartz	Orchidaceae	deciduous geophyte	dI	ALS
Rafnia capensis (L.) Druce	Fabaceae	broad-sclerophyllous shrub	UI	ALS
Rafnia perfoliata E. Meyer	Fabaceae	broad-sclerophyllous shrub	SI	PFE
Restio curviramis: = Ischyrolepis curviramis				
Restio cuspidatus: = Ischyropepis capensis				
Restio filiformis Poir.	Restionaceae	restioid hemicryptophyte	UI	ALS
Restio gaudichaudianus: = Ischyrolepis gaudichaudiana				
Restio sieberi: = Ischyrolepis sieberi				
Restio tenuissimus: = Ischyrolepis tenuissima				
Restio triticeus Rottb.	Restionaceae	restoid hemicryptophyte	UI	ALS
Rhus africana = Rhus scytophylla				
Rhus rosmarinifolia Vahl	Anacardiaceae	narrow-orthophyllous shrub	UI	ALS
Rhus scytophylla Ecklon & Zeyher	Anacardiaceae	broad-sclerophyllous shrub	UI	ALS
Rhus tomentosa L.	Anacardiaceae	broad-sclerophyllous shrub	dT	ALS
Roella ciliata L.	Campanulaceae	forb	SI	PFE
Roella psammophila Schltro	Campanulaceae	forb	SE	PFE
Scabiosa columbaria L.	Dipsacaceae	deciduous geophyte	UI	ALS
Schizaea pectinata	Schizaeaceae	evergreen geophyte	dI	ALS
Schizodium sp.	Orchidaceae	deciduous geophyte	dI	ALS
Scirpus digitatus	Cyperaceae	sedge	UI	ALS
Scirpus ecklonii: = Ficinia ecklonea				
Selago paniculatus	Selaginaceae	forb	UI	ALS
Selago spuria L.	Selaginaceae	forb	SI	PFE
Senecio cymbalariifolius (L.) Less.	Asteraceae	deciduous geophyte	UI	ALS
Senecio erubescens Aiton	Asteraceae	forb	UI	ALS
Senecio grandiflorus Bergius	Asteraceae	forb	DI	PFE
Senecio paniculatus Bergius	Asteraceae	forb	DI	PFE

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Senecio pinifolius (L.) Lam.	Asteraceae	narrow-orthophyllous shrub	UI	ALS
Senecio pubigerus L.	Asteraceae	forb	DI	PFE
Senecio umbellatus L.	Asteraceae	forb	DI	PFE
Senecio sp. indet.	Asteraceae	annual	SI	NEU
Serruria rosea E. Phillips	Proteaceae	narrow-sclerophyllous shrub	SI	OS
Serruria subsericea Hutch.	Proteaceae	narrow-sclerophyllous shrub	SI	OS
Staavia radiata (L.) Dahl.	Bruniaceae	narrow-sclerophyllous shrub	UI	ALS
Staberoha cernua (L.f.) Durand & Schinz	Restionaceae	restioid hemicryptophyte	UI	ALS
Stoebe aethiopica L.	Asteraceae	narrow-sclerophyllous shrub	SI	OS
Stoebe cinerea Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe ericoides	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe fusca Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe incana Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe plumosa (L.) Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	OS
Stoebe spiralis Less.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Struthiola ciliata (L.) Lam.	Thymelaeaceae	narrow-sclerophyllous shrub	SI	OS
Tetraria compar (L.) Lestib.	Cyperaceae	sedge	UI	ALS
Tetraria crinifolia (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria cuspidata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria exilis Levyns	Cyperaceae	sedge	UI	ALS
Tetraria fasciata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria fimbriolata (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria involucrata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria nigrovaginata (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria ustulata (L.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Thamnochortus dichotomus: = Thamnochortus lucens				
Thamnochortus fruticosus Berg.	Restionaceae	restioid hemicryptophyte	UI	ALS
Thamnochortus lucens (Poir.) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Thamnochortus sporadicus Pill.	Restionaceae	restioid hemicryptophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Senecio pinifolius (L.) Lam.	Asteraceae	narrow-orthophyllous shrub	UI	ALS
Senecio pubigerus L.	Asteraceae	forb	DI	PFE
Senecio umbellatus L.	Asteraceae	forb	DI	PFE
Senecio sp. indet.	Asteraceae	annual	SI	NEU
Serruria rosea E. Phillips	Proteaceae	narrow-sclerophyllous shrub	SI	OS
Serruria subsericea Hutch.	Proteaceae	narrow-sclerophyllous shrub	SI	OS
Staavia radiata (L.) Dahl.	Bruniaceae	narrow-sclerophyllous shrub	UI	ALS
Staberoha cernua (L.f.) Durand & Schinz	Restionaceae	restioid hemicryptophyte	UI	ALS
Stoebe aethiopica L.	Asteraceae	narrow-sclerophyllous shrub	SI	OS
Stoebe cinerea Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe ericoides	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe fusca Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe incana Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Stoebe plumosa (L.) Thunb.	Asteraceae	narrow-sclerophyllous shrub	DI	OS
Stoebe spiralis Less.	Asteraceae	narrow-sclerophyllous shrub	DI	PFE
Struthiola ciliata (L.) Lam.	Thymelaeaceae	narrow-sclerophyllous shrub	SI	OS
Tetraria compar (L.) Lestib.	Cyperaceae	sedge	UI	ALS
Tetraria crinifolia (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria cuspidata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria exilis Levyns	Cyperaceae	sedge	UI	ALS
Tetraria fasciata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria fimbriolata (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria involucrata (Rottb.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria nigrovaginata (Nees) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Tetraria ustulata (L.) C.B. Clarke	Cyperaceae	sedge	UI	ALS
Thamnochortus dichotomus: = Thamnochortus lucens				
Thamnochortus fruticosus Berg.	Restionaceae	restioid hemicryptophyte	UI	ALS
Thamnochortus lucens (Poir.) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Thamnochortus sporadicus Pill.	Restionaceae	restioid hemicryptophyte	UI	ALS

Species	Family	Growth form	Noble-Slatyer category	Fire-response category
Thereianthus spicatus (L.) G.J. Lewis	Iridaceae	deciduous geophyte	UI	ALS
Thesium capitatum L.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium capituliflorum Sonder	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium carinatum A. DC.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium densiflorum A. DC.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium euphorbioides L.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium euphrasioides A. DC.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium imbricatum Thunb.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium nigromontanum Sonder	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium nudicaule A.W. Hill	Santalaceae	hemi-parasitic sub-shrub	UI	ALS
Thesium spicatum L.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium strictum Bergius	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thesium virgatum Lam.	Santalaceae	hemi-parasitic sub-shrub	SI	PFE
Thunbergiella filiformis (Lam.) Wolff	Apiaceae	deciduous geophyte	UI	ALS
Trachyandra hirsuta (Thunb.) Kunth	Asphodelaceae	deciduous geophyte	UI	ALS
Trachyandra hirsutiflora (Adamson) Oberm.	Asphodelaceae	deciduous geophyte	UI	ALS
Trachyandra muricata (L.F.) Kunth	Asphodelaceae	deciduous geophyte	UI	ALS
Tritonia crispa (L.f.) Ker Gawler	Iridaceae	deciduous geophyte	UI	ALS
Tritoniopsis parviflora (Jacq.) G. Lewis	Iridaceae	deciduous geophyte	UI	ALS
Ursinia paleacea (L.) Moench (= U. crithmoides)	Asteraceae	semi-succulent shrub	SI	PFE
Ursinia scariosa (Aiton Poiret	Asteraceae	forb	SI	PFE
Wachendorfia paniculata L.	Haemodoraceae	deciduous geophyte	UI	ALS
Wahlenbergia exilis A. DC.	Campanulaceae	annual	SI	MFE
Watsonia pyramidata (Andrews) Klatt	Iridaceae	deciduous geophyte	UI	ALS
Willdenowia glomerata (Thunb.) Linder	Restionaceae	restioid hemicryptophyte	UI	ALS
Willdenowia lucaeana: = Willdenowia glomerata				
Zygophyllum fulvum L.	Zygophyllaceae	semi-succulent shrub	UI	ALS