

# Prescribing Fire Frequencies in Cape Fynbos in Relation to Plant Demography<sup>1</sup>

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Problems in the ecology and management of South African mediterranean-type ecosystems have been outlined in several recent papers (Bands 1977, Kruger 1977 and these proceedings, Day and others 1979): fire is generally acknowledged as a useful tool in these ecosystems. In this paper I attempt to set out a framework for research on the demography of Mountain Fynbos plants, so that a deductive and a predictive system can be developed for deciding on proper burning frequencies for any given management goal.

Management goals for Mountain Fynbos centre mainly on maintenance of certain dynamic equilibria in the ecosystem, for sustained yield of clean water, and so on. Designing the managed fire regime is largely dependent on our understanding of how a change in regime will determine a new equilibrium in the vegetation. We know, for example, that a change in fire frequency, from about once in 20 yr to about once in 6 yr, can change a dense tall shrubland to a low vegetation dominated by herbaceous plants, eliminating species with slow life cycles (Van Wilgen 1981a, b). On the other hand, if fire is kept out for 40 yr or more, shrub populations decline, seedling recruitment after fire is reduced, and there is an apparent trend toward a sparse shrubland (Bond 1980, Van Wilgen 1981a, b); under favourable conditions, long intervals between fire could result in replacement of fynbos by evergreen rain forest.

Of the elements of fire regime that are regulated by management, fire frequency has the greatest potential for making immediate and marked changes to fynbos. The manager must invariably reconcile conflicting goals. Fire control, for example, is best achieved through frequent burning, which reduces the average biomass in the area. Nature conservation, where species diversity is to be maintained, probably requires intermediate fire frequencies. It is not sufficient to select an arbitrary frequency that will safely achieve one or

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Abstract--Regulating fire frequency in Cape fynbos areas causes marked changes in vegetation. Very frequent fire eliminates seeding shrubs with long youth periods; infrequent fire reduces shrubs because of senescence. Variation between these extremes will cause more subtle compositional changes. Research on plant fecundity schedules and on the dynamics of seed pools is necessary to understand these.

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other of his goals. Therefore, our empirical knowledge of the effects of fire regime must be supplemented through the study of plant demography and hence the dynamic responses of vegetation to fire.

## SPROUTING vs. SEEDING PLANTS

In fynbos as in other mediterranean-type vegetation, fire regime strongly influences the relative abundance of plants that regenerate by sprouting and those that rely on seed. Very frequent fire favours sprouting plants. Survival of fire seems to be high. First, mortality in *Watsonia pyramidata*, a geophyte, is zero or nearly so (Kruger and Bigalke in press). For *Protea nitida*, Haynes (1976) reported mortalities of 1 to 13 per cent in different fires. Second, fires stimulate vegetative reproduction among herbaceous species (Kruger and Bigalke in press) and, possibly, sexual reproduction among shrubs such as *Protea nitida* (Haynes 1976). Although long absence of fire causes a decline in herbaceous sprouters, most sprouters, woody or herbaceous, appear to be very long-lived so that infrequent fires may also favour sprouters over seeders (Bond 1980, Van Wilgen 1981a, b, Kruger and Bigalke in press). Plants of species such as *Watsonia pyramidata* and *Protea nitida* seem to be very long-lived and populations are therefore well able to persist despite long intervals of low recruitment. It is only at very high and very low fire frequencies that sprouters are markedly favoured over seeding shrubs in fynbos. Otherwise, sprouters rarely form dense stands, and most usually are subordinate to seeders. This is unusual in mediterranean-climate ecosystems (Kruger in press) and it would be intriguing to find the reasons. For management, however, the present need is for data that describe the dynamics of sprouter populations.

## DEMOGRAPHY OF SEEDING SHRUBS

### Regeneration

A review shows that seeding shrub populations in mediterranean-type ecosystems are mostly even-aged and that effective population recruitment from seed is generally confined to the period immediately post-fire, and further that this is from propagule stocks of three kinds (a) soil seed-banks (b) canopy-stored seed and (c) continually replenished stocks (Kruger in press). In the first case, populations can survive long intervals between fires in the dormant state after death of adult plants, though the relative decay rates of

the seed-banks must partly determine the composition of the regenerating flora, depending on the length of the fire-free interval. Circumstantial evidence (Kruger 1977) indicates considerable longevity among such seed in fynbos, and the habit would therefore be adaptive in a fire regime marked by variability in the fire recurrence interval. It is apparently present in many fynbos species, including Proteaceae, Aspalathus, and many other large taxa.

Effective reproduction by canopy-stored seed or continually replenished stocks, where dormancy is not marked and seed life after dispersal is short, depends on an extant parent population and hence is ineffective where intervals between fire exceed plant life-spans; Bond (1980) has produced data to support this. Fynbos is often dominated by shrub species that store seed in closed capitula on the plant, until the parent dies, usually after fire. Seed released in unburnt vegetation is subject to very heavy predation (Bond 1980); seed in these species is relatively large, and contains high concentrations of proteins (Van Staden 1978); thus storage in capitula is apparently adaptive in a low-nutrient environment, in that seed tend to be protected against predators and efficient reproduction ensured because seed tend to be released by a reliable cue into the post-fire environment where predation pressure is low and germination conditions favourable. The effectiveness of canopy-stored seed is in some dispute. Seed ripens over seven or more months after flowering, and both Jordaan (1949, 1965) and Van Staden (1978) have claimed or suggested that seed in capitula are short-lived and that there are insufficient viable seed to ensure regeneration if parents are killed during the time of seed ripening (winter and spring). This does not accord with results reported by Lombaard (1971), nor with observations in Williams (1972) and Rourke (1980). Assuming that canopy-stored seed is effective in ensuring regeneration, the habit is adaptive in a predictable fire regime, where recurrence intervals are longer than the youth period but do not exceed the reproductive life-span of parent plants.

Martin (1966) has implied that certain important fynbos taxa, including Ericaceae, are dependent on the annual seed rain for reproduction. He maintained further that, in his study area, no seed store was available on site for post-fire regeneration. This habit will not be adaptive in the fire environment of the fynbos, especially where many species are local, unless species have highly dispersible seed. In view of the generally low capacity for long-range dispersal reported thus far among plants in general (Cook 1980), except among bird-dispersed seed, of which there are few in fynbos (personal observation), it seems necessary first to establish the importance of this trait among fynbos species before management-related research is launched. For a start, careful study is necessary of the floras of the soil seed-bank to determine which species are in fact not represented in the seed-bank.

#### Primary youth periods and fecundity schedules

In the even-aged shrub populations of the fynbos the reproductive potential of a species in a stand of uniform fire history depends on its age. Hence, fire frequencies prescribed for conservation of fynbos are based in the first instance on some estimate of the minimum age at which reproductive potential suffices to replace the parent population; latterly, the question of the period of peak fecundity has become important (e.g. Bond 1980).

The first question of importance relates to the youth period, i.e. time between establishment and age at the beginning of the fecundity period. In fynbos there is interspecific variability in this respect, but relatively little (Kruger and Bigalke in press). Thus, from records for nursery plants of 42 fynbos Protea species quoted by Rourke (1980) we find the following:

<u>Youth period, yr</u>	<u>No. of species</u>
2-4	22
5-7	16
> 7	4

These nursery records are not grossly unrepresentative of field performance, as indicated by Kruger and Bigalke (in press).

Species with differing youth periods sometimes occur in disparate habitats. Thus, Protea rupicola, one of those exceptionally slow to mature, inhabits cliff faces near mountain crests, where fires are infrequent and short primary youth periods are not necessarily adaptive. In management it is important to know the distribution of such species and the behaviour of fire in such habitats; the compartment management system followed in fynbos does not allow fine-grained burns and relies presently on the assumption that if a compartment contains patches of such habitat then prescribed burns will not traverse these patches at excessive frequencies, despite their spreading elsewhere within the compartment.

The present working hypothesis in prescribing fire frequencies is that sympatric species tend to have similar youth periods, and that these are relatively short, i.e. 3-8 yr (Kruger 1979 and unpublished). Prescribed burns at intervals that approach these will begin to eliminate species locally (Van Wilgen 1981a). Where precocious species occur with others that are markedly slow to mature (for example, Protea repens with P. laurifolia) the latter tend to be species where some individuals survive fire, even though they do not sprout (Kruger 1977).

An estimate of the youth period is not sufficient to define the minimum interval between fires. First, the population is seldom uniform with regard to youth period and second, more than one year of flowering would be required to ensure population replacement. Field data for the reproductive

performance for Protea stokoei are as follows (Kruger and Lamb, unpublished):

No. of times an individual has flowered	Per cent of sample 5 yr post-fire	8 yr post-fire
0	85.5	47.9
1	13.3	31.9
2	0.8	17.7
3	0	2.5

A rule of thumb sometimes applied is that in any compartment the species that is slowest to mature should have developed to the point where at least half the individuals have flowered three or more times, before the area is burnt once more. One may simplify and assume that individuals mature at an exponential rate after the age at which the first matures, and that once having flowered, each individual flowers every year after. For Protea stokoei the following function applies approximately:

$$\ln y = 4.6 - t/6,$$

where y is the percentage of the population in the juvenile stage, and t the number of years since the first individual has matured - which occurs at 4 yr, since one year is required after flowering for seed to mature. From this one may calculate that a species such as Protea stokoei requires about 11 years after fire to reach the arbitrary "safe" reproductive condition.

There is variation within the species in the age at which individuals mature and this appears to correlate with habitat factors (see Protea laticolor in Kruger 1979). Thus populations may expand or contract their ranges, depending on the frequency of fire.

This kind of approximation is a necessary but temporary expedient and must be superseded by rules based on knowledge of the fecundity schedules of plants. Data to construct fecundity curves for fynbos species are urgently necessary. Of particular importance are data to show the ages at which peak fecundity is reached, especially in relation to senescence.

#### Plant longevity and senescence

Senescence is used here in Leopold's (1961) sense, for the tendency for mortality in a population to occur toward the end of the maximum life-span of the species. Elsewhere (Kruger in press) I have quoted information that indicates pronounced senescence among fynbos shrubs, and Bond (1980) and Van Wilgen (1981a, 1981b) provide supporting field data and observations. Our experience presently suggests the following features common to seeding fynbos shrubs in the majority of habitats: relatively low seedling to adult ratios in post-fire regeneration (Bond quotes ratios from 12:1 to 18:1 for a burn in a favourable season); low density-dependent mortality, irre-

spective of absolute densities, in young and middle-aged plants; density-independent mortality is usually also low after establishment, barring extreme drought or other catastrophe; most species therefore exhibit senescence, and the age of senescence appears to be species-specific, little affected by environment; among dominant Proteaceae it appears to vary between 30 and about 50 years, according to species. This relatively short life is associated with species whose life-cycles are strongly dependent on the fire cycle, including those that have canopy-stored seed. Among species such as Leucadendron argenteum, Leucospermum conocarpodendron and Protea laurifolia, where individuals tend to survive fire and populations are not even-aged, greater ages are attained and population dynamics are fundamentally different.

Declining density as well as declining reproductive output per individual with onset of senescence severely reduces effective reproductive potential of the local population (e.g. Bond 1980). Therefore, species that do not accumulate seed-banks in the soil are liable to local extinction when fire recurrence intervals approach 30-40 yr.

#### Conclusion

The rather tentative evidence now available indicates that an important proportion of the fynbos flora is adapted to fire frequencies ranging between about once in 10 to once in 40 yr. How does variation within this range affect the relative abundance of species?

The variety of plant forms with different life-history characteristics that may be encountered in any given stand suggests that marked compositional changes are likely, but much more experimental and demographic data are required before this question can be addressed.

#### MODELLING REQUIREMENTS

Both the research scientist and the manager need to synthesize information on relevant aspects of vegetation dynamics in order to explore the implications of varying fire frequency; for this, demographically based models will be necessary. The first requirement is for heuristic models that accommodate the life-cycles typical of fynbos plants. To overcome the problem of diversity in fynbos "archetypal" species will necessarily be used in the models. The practitioner would then need to know the composition in terms of these archetypes of the stand whose dynamics he wishes to model.

Noble and Slatyer (1977, 1980) outline an approach to modelling plant succession that is explicitly intended to accommodate the problems discussed here. They have reduced the particulars of succession to a finite and tractable list of phenomena that essentially define the process. Nevertheless, their approach is based on the as-

sumption that species populations change from one discrete and uniform stage to the next; from juvenile to mature, for example. The models do not allow for dynamics of populations in each stage, for example, for fecundity schedules in the mature stage. As shown, fynbos-fire models must incorporate these dynamics, especially where one considers fire recurrence intervals that approach the thresholds between life-history stages. Their approach is therefore not sufficient for analysis of likely compositional changes in fynbos although it provides the essential framework. It is clear that modelling of stand dynamics after the manner of Botkin and others (1972) and Shugart and Noble (in press) will be necessary.

#### CONCLUSION

This paper has focused on the effects of fire frequency on fynbos vegetation structure and dynamics. We know that fire season, and probably fire intensity, will also have important effects and these must also be accommodated in a synthesis for management. There is also growing evidence for a key role of animals, especially seed and seedling predators. Research by various groups on the demography of selected shrub and herbaceous species and on evidently important plant-animal interactions is currently under way. Nevertheless, the first need is for simulating and predicting fire frequency effects. Successful simulation of vegetation dynamics will also allow progress in simulating fire frequency effects on hydrological and nutrient cycles.

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