SOME EFFECTS OF FIRE FREQUENCY ON FYNBOS AT JONKERSHOEK, STELLENBOSCH, SOUTH AFRICA

by

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CONTENTS

ABSTRACT

A short literature review on fynbos ecology, with special reference to fire, is presented as an introduction to the thesis.

Three post-fire ages of fynbos were studied at the Jonkershoek Forest Reserve, with the aim of determining the effects of fire frequency on the vegetation. The three frequencies investigated were short (about six year) rotation burning, normal rotation burning (about 15 to 20 years) and protection from fire for 37 years.

Aerial plant biomass was determined for the three post-fire ages of vegetation. Total (live plus dead) biomass amounted to 6,5 tonnes $\cdot ha^{-1}$ for four year old vegetation, 50 tonnes ha^{-1} for 21 year old vegetation and 75 tonnes ha^{-1} for 37 year old vegetation. Live biomass apparently increases to an age of roughly 30 years, whereafter it declines, whereas the total mass of dead plus live material showed an increase right up to 37 years of age.

A total of 100 releves were enumerated using the Braun-Blanquet method. Results showed that short rotation burning resulted in a reduction in plant cover, height and biomass, as well as in the elimination of longer lived seed regenerating shrubs. Species diversity was high and shorter grami-

noid and herb species dominated the vegetation. Twenty year old vegetation had a high cover and mean plant height, but species diversity was low and undergrowth species were of much reduced importance.

In very old vegetation, larger shrubs were reduced in importance due to high mortality; as a result undergrowth species showed some signs of recovery, and species diversity increased. Some germination was noted, and certain tree species also appeared.

The results are used to support an argument for a variable burning rotation of 15 to 25 years for the Jonkershoek area. Certain limited areas, which may be seral to forest, should be protected from fire.

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PREAMBLE:

This study was undertaken to investigate the effects of fire frequency on the fynbos vegetation at Jonkershoek. It was designed as a short-term investigation, the results of which would also be suitable for use in a thesis for degree purposes. In the past work undertaken for post graduate (mostly M.Sc. and Ph.D.) studies has been presented in the form of an unpublished thesis. It would seem that a thesis is often regarded, by the author at least, as an endpoint and that the contents are in many cases never published. The main reason for this is that a thesis is not written in a form suitable for publication, and that considerable work would be required to make it suitable. Nevertheless, the publication of results of such studies is desirable for the wider dissemination of information, as theses are not always readily available or even well known. To overcome this problem, it was suggested to me that I write the results of the investigation as papers suitable for publication, and that these be used as the basis for a thesis.

The results of this study have been presented in two papers: one deals with the biomass of the different areas studied, while the other deals with floristic and structural differences between these areas. The thesis itself is divided into four parts. Part I is a general introduction, and consists mainly of a literature review which deals with fynbos and

the effects of fire. I have attempted to extract relevant information and to use this both to introduce and to justify the study. Parts II and III are the papers in which methods, results and some discussion are presented. There is of necessity some degree of repetition in the introductions and descriptions of the study area in these papers, as well as in the references, but each paper is a complete entity, and can be submitted as is for publication. Part IV is a general conclusion which leads on from the introduction and draws on the results of the study as a whole. References given in Parts I and IV are included at the back of the thesis.

This layout is similar to that used by Milton (1980) and I have followed her manner of presentation.

PART I

GENERAL INTRODUCTION

PART I: GENERAL INTRODUCTION

1.1 THE CAPE REGION AND ITS FLORA

The Cape Region occupies a small area at the extreme south-west of the southern African subcontinent. The exact geographic limits of the region vary according to various authors (e.g. Bolus 1905, Pole-Evans 1936, Weimarck 1941, Taylor 1978 and Goldblatt 1978). Goldblatt delineated the region as an area which includes the fynbos veld type as defined by Acocks (1953), and extends from Nieuwoudtville in the north, following the eastern slopes of the Cedarberg, and thence east from Karoopoort along the north slope of the Witteberg, Swartberg, Baviaans Kloof and Groot Winterhoek Mountains, ending at Port Elizabeth. All territory south and west of this line to the coast forms the Cape Floral Region.

The region essentially covers the Cape folded mountain belt, the mountains occurring for the most part in sub-parallel ranges with an average height of 1000 to 1500 m, individual peaks reaching over 2000 m. In the south these ranges strike from east to west while in the west the strike is more nearly north-north west. The two series of folds meet near Ceres where the axes of folds strike east-north-east (Haughton 1969).

The major ranges are comprised of Table Mountain sandstones and the minor ones of smaller sandstone folds or the Witteberg quartzites of the Cape System, while the Cape Granites commonly form the foothills and lower slopes in the western part. In the intervening valleys and parts of the coast belt Bokkeveld shales, sandstones of the Cape System and the Malmesbury shales of the Archaean Complex form the underlying rock. The coastal lowlands consist of sands, conglomerate and limestones of Tertiary to Recent origin (Taylor 1978).

The soils on mountain slopes are mainly weathered from sandstones in situ and are generally acid, leached and of low fertility. The soil in the valleys derived from Bokkeveld shales is clayey, more fertile and of good texture especially where it is mixed with some sand from the mountain slopes (Wellington 1955). Soils derived from granite are mostly sandy loams (Taylor 1978) and are also generally of higher nutrient status than those derived from sandstone.

The climate of the region is mainly of a mediterranean type (cf. di Castri and Mooney 1975) and rainfall is usually from 300 to 2500 mm or more per annum (Taylor 1978). In the western part more than 50 per cent of the rainfall is in winter (Marloth 1929) and the resulting summer drought is alleviated by the moisture bearing clouds of the south-east wind (Marloth 1904; 1907; Stewart 1904). Travelling eastward from Swellendam the rainfall becomes more evenly distributed throughout the year (Taylor 1978).

During the winter snow falls regularly on the higher mountains, especially in the west, though in the lowlands frost is rare except in some deep valleys of the interior (Taylor, 1978).

The Cape flora is one of the most distinctive in the world, having been given kingdom status by most plant geographers (Good 1964 ; Takhtajian 1969). It is the smallest of the six Floral Kingdoms of the world, representing only 4% (89 000 km^2) of the total land surface of southern Africa, that is South Africa, Lesotho, Swaziland, Namibia and Botswana. Within this region there occur 8 550 species, of which 73%, or 6 252 species, are endemic. These 8 550 species are in 957 genera, of which 198 genera are endemic. Seven families, namely the Bruniaceae, Peneaceae, Grubbiaceae, Roridulaceae, Retziaceae, Stilbaceae and Geissolomataceae are also endemic to the Cape Region (Goldblatt 1978).

Acocks (1953) recognizes seven veld types within the Cape Region (Taylor, 1978). Three of these types, namely the Knysna forest (type 4), Karroid Broken Veld (type 26) and Strandveld (type 34) occupy minor areas of the Cape Region.

The four important types, in terms of area, are Coastal Renosterbosveld (type 46), Coastal Macchia (type 47), Mac-

chia (Fynbos) (type 69) and False Macchia (type 70).

Fynbos is an indigenous word probably used for the first time in the literature by Bews (1916) and now replacing older ambiguous terms such as Sclerophyllous Bush (Schimper 1903, Pole Evans 1936, Adamson 1938), Sclerophyllous Scrub (Riley and Young 1966), Maqui (Warming 1909), Macchia (Phillips 1931, Acocks 1953, Roberts 1966) and Heath (Martin 1965). The word implies both the fine leaved form of many of the shrubs and the bushy nature of the vegetation (Taylor, 1978).

Fynbos (type 69) is the characteristic element of the distinctive Cape flora (Taylor 1978; Goldblatt 1978). The distribution of fynbos follows a geological rather than climatic pattern, with most fynbos and certainly all fynbos in marginal areas, restricted to sandstones of the Cape System. The pattern of winter rainfall does not follow, except very generally, the distribution of Cape Sandstones, with winter rainfall extending somewhat inland and far to the north of the Cape Region. Moreover, in the eastern portion of the Cape Region at least half of the precipitation falls in the summer months (Adamson 1938; Coetzee and Werger 1975). Fynbos vegetation would appear to be linked to the peculiar soils, under climates of rather irregular but year-round rain (Goldblatt 1978).

Floristically, fynbos can be defined by one or two striking salient features: the lack of single species dominance, and/or the conspicuous presence of members of the family Restionaceae (Taylor 1972). Physiognomically, fynbos is characterised by three elements: restioid, ericoid and proteoid. These elements comprise plants that resemble typical members of the Restionaceae, Ericaeae and Proteaceae respectively in growth form but do not necessarily belong to these families. The Restionaceae and some Cyperaceae give the vegetation its most characteristic physiognomic feature - the restioid element (Taylor 1978). At Jonkershoek and elsewhere, Bobartia indica L. (Iridaceae) could be considered as a member of the restioid element due to its abundance and tufted habit. The only other constant physiognomic feature, the small narrow often rolled leaves of some of the shrubs, is the ericoid element. Typical Cape plants representing the ericoid element belong to families such as Ericaceae (Erica), Rutaceae (Agathosma), Bruniaceae (Brunia), Polygalaceae (Muraltia), Thymeliaceae (Struthiola), and to many species in genera like Aspalathus (Fabaceae), Cliffortia (Rosaceae), Phylica (Rhamnaceae) and a number of Asteraceae including Metalasia and Stoebe. Taller bushes with moderate sized hard leaves with a dull surface, comprising the proteoid element, belong mainly to the family Proteaceae e.g. Leucadendron, Leucospermum, Mimetes and often Protea itself. In certain habitats this element may be absent (Taylor 1978).

The Department of Forestry is by far the largest single controller of mountain land under natural vegetation in the Republic. In the Western Cape it owns approximately 267 000 hectares of unafforested mountain land, much of which constitutes important catchment areas (Kruger 1974). With the incorporation of private land into proclaimed mountain catchment areas, this figure will be more than doubled. Most of this area belongs to the fynbos veld type.

The catchment areas are managed by means of prescribed rotational burning. This study is aimed at assessing some effects of differing rotations of burn on the vegetation at the Jonkershoek Research Station.

1.2 THE ROLE OF FIRE IN FYNBOS

Fire has occurred in fynbos for a long time. Fires of human origin have occurred at least for 2 000 and possibly even as much as 250 000 years (Kruger 1976, Klein 1977), but natural fires occur too and may be a phenomenon as old as fynbos. At present, fires occur in fynbos communities at intervals of between 6 and 20 years, but may occur more often or less frequently under human influence. Current information is set out below.

1.2.1 History of ideas on burning in fynbos

We know from the chronicles of early Portugese navigators

that fynbos was burnt long before Van Riebeeck landed at the Cape (see Taylor 1973). Cape farmers learnt the practice of veld burning from the Hottentots in the early days. From the outset, the Government was against this practice, and a law passed in 1687 imposed severe penalties for veld burning. Despite these laws veld burning went on (Botha 1924). It was at the beginning of the 20th century that the battle against veld fires was tackled in earnest (Levyns 1924, Marloth 1924, Pillans 1924). Marloth (1924) postulated that veld burning would lead to "the extinction of many species and perhaps even genera of plants". He mentions hundreds of species of plants in herbaria which had been collected by older botanists "more than a hundred years ago and have not been seen again since". Pillans (1924) mentions that the average extent of tall shrub-formation and forest had been greatly reduced in the Cape Peninsula due to continual burning. In a study of regeneration following fire on Table Mountain Adamson (1935) noted that certain broadleafed and shade loving hemicryptophytes had disappeared and five species in total had failed to reappear after 6 years. Jordaan (1949) found that Protea repens (L.) L. requires an eight year period between burns to attain maturity and form seed. Burning on a rotation of less than eight years will eliminate the species because regeneration following fire is by seed. He suggested that the same must be true for many other species. He also suggested that burning at certain times of the year would be

dangerous for certain species, and later substantiated this with evidence of the disappearance of certain plants following a winter fire (Jordaan 1965). In contrast, van der Merwe (1966) found that all species regenerated after fifteen years following a February burn in Swartboschkloof. Dr CL Wicht was one of the first to seriously consider burning as a natural phenomenon in the vegetation, and to suggest it as a management tool (Wicht 1945). His publication admitted that at that stage data on the precise effects of burning were not available, and emphasized the need for such data.

Le Roux (1966) mentions areas of fynbos which had become totally moribund ("doods") due to protection from fire and that game and birds were no longer to be found there. There is a lack of information on the subject in South Africa, but Specht et al (1958) found that on a nutrient-poor sand soil site in Australia, a longer protection from fire led to a reduction in the number of species in a stand (after burning, 36 species, after 25 years, 20 species and after 50 years, only 10 species). They suggest that this is due to the cessation of transfer of mineral nutrients to the above-ground parts after a certain stage because these are needed in the roots and underground organs. Above-ground growth stops and the vegetation becomes moribund.

Martin (1966), in concluding a study on the effects of burning in the Grahamstown area, made the following points:

(a) Repeated burning of heath at relatively short intervals leads to a predominance of geoxylic shrubs and grasses and the total elimination of Erica demissa Kl. ex Benth. and E.chamissonis Kl. ex Benth., resulting in the establishment of a "grass-heath" complex.

(b) On the other hand, prolonged absence of fire must result in some herbaceous species and possibly some shrubs becoming rare or disappearing. Irregular occurrence of fires appears to be essential to the maintenance of a diversified flora.

(c) Controlled burning of heath at average intervals greater than 8-10 years, but not necessarily in excess of 20 years, seems to be consonant with the maintenance of all components of the present flora.

The following points indicating further that fire is necessary in fynbos, and that complete protection will lead to extinction of species are made by Taylor (1972).

(a) Many component species need fire for their reproduction and survival (as examples Orothamnus zeyheri Pappe and Serruria florida Knight).

(b) Some species put out toxins from their roots that alter the soil environment adversely. Their effects seem to be cumulative and hence are most felt in old stands. These toxins are probably destroyed by fire.

More recent experimental evidence shows that these toxins are not likely to be root secretions. Christensen and Muller (1975) show that leaf secretions and leachates accumulate in chaparral litter and soil and inhibit germination. However, although Taylor has mentioned these toxins, there does not appear to be any documented evidence of this phenomenon in the fynbos.

The first point, namely that certain species are totally dependent on fire for regeneration, has been supported by Kruger (1976). Examples are fire lilies (Cyrtanthus species) which flower only in the first year after fire and remain dormant until the next burn; certain Aspalathus species whose seeds germinate freely after a burn to produce a population of vigorous plants which grow rapidly and produce seed in the third or fourth year after burning, dying thereafter to survive in the community as dormant seed; and finally Proteaceae, which return from dormant seed, grow slowly and seed after 6 to 8 years and then die off from an age of 30 years or so if further fires do not occur. Fires occurring before a species has reached the mature phase will tend to eliminate that species.

Further, the probability of occurrence of fire increases as the community develops due to slow decomposition and rapid accumulation of dead plant material with senescence.

Evidence also suggests that areas which have not been burnt for some time (20-25 years) regenerate better than areas that are continually burnt (McLachlan and Moll 1976). In contrast Bond (1980) presents evidence to show that a burn in 50 year old fynbos in the Southern Cape resulted in very poor regneration of seed regenerating species. He suggests that this is due to degradation of the seed pool with advancing age and scenescence of the vegetation.

There is acceptance today that fire in fynbos is a natural phenomenon. Fires caused by lightning and falling rocks are commonplace, and there is no reason to believe this was not so from prehistoric times (Bands 1977). Moll et al (1980) have postulated that the lack of tree vegetation in the fynbos may be due to an increase in fire frequency since the advent of pasturalists about 2000 years B.P.; this is based on the assumption that there may be an "empty" tree niche in the fynbos (Campbell et al 1979), but this has not been substantiated.

The Department of Forestry had adopted a policy of protection of mountain areas from fire since being entrusted with the land through the Forest Act of 1913, and in the case of the Cedarberg since 1876 (Bands 1977). This policy proved largely unsuccessful (Kruger 1974) and uncontrolled fires burnt large areas of fynbos vegetation.

The accumulation of evidence indicating that complete fire protection of mountain fynbos was not only impracticable and costly, but also undesirable as a conservation measure, ultimately resulted in the Department of Forestry adopting prescribed burning as a catchment management and ecosystem conservation tool. In a memorandum drawn up in 1968 the policies of the Department were revised, and the principle of using prescribed burning as a mangement tool was accepted (Wicht and Kruger 1973). Rotation and practical execution of the policy would vary from place to place and research into these questions was to be tackled in earnest. In a preliminary report on the management of the Marloth Nature Reserve (Swellendam), a burning rotation of 8 years was proposed to allow species to mature and set seed while at the same time preventing the community from reaching an overmature stage (Departmental report, unpublished 1970). This allowed for planning but flexibility was emphasized should later assessment of this rotation show a need for change to a longer rotation. Rotations for other areas, for example the Kogelberg, were set at twelve years (Kruger & Lamb 1979). Present policy calls for burning on a twelve year rotation, with burning in late summer (Bands 1977). However, flexibility is still stressed and Kruger and Lamb (loc.cit.) have given the following guideline: the rotation should be long enough to permit at least fifty per cent of any seed-regenerating plant species population in a compartment (area to be

burnt) to have flowered and set mature seed for three successive seasons. It is not reasonable to wait for the whole population to reach maturity, because there are always suppressed or inherently slow members of the population which do not reach maturity. Kruger and Lamb (loc.cit.) recommend that the burning rotation at Kogelberg be lengthened from 12 to 15 years on the basis of data they collected there.

1.2.2 Species survival following fire

Most fynbos species survive as individuals through vegetative regeneration (Wicht 1945; van der Merwe 1966; Taylor 1969). Sixty-seven per cent of species in Swartboschkloof, for example had the capacity for vegetative regeneration. No quantitative data on relative survival rates of sprouting species have been published.

Wicht (1945) has listed four ways in which plants survive fire. These are:

(a) Geophytes - plants which have a regrowth from underground organs.

(b) Plants which are killed by fire but regenerate from seed.

(c) Plants that sprout from rootsocks.

(d) Well insulated plants (with thick bark) that grow again

from dormant buds.

Most woody species, especially the dominant shrubs, rely on seed for survival of fire.

Species surviving in the form of seed, show various adaptive strategies (Kruger et al 1977) :

(a) Bradyspory or serotiny. In a number of shrub species, seed is retained on the plant in a protective organ for at least one season after maturation. This is typical of many species of Protea and Leucadendron and of Bruniaceae. The strategy is best developed in Leucadendron species where seed is retained in hard, woody "cones" and may be held on the live plant for up to eight years.

When adult plants are killed by fire, the serotinous organs open as tissues dry and seed is then released into a safe environment.

There is no evidence that heat is required for seed release as in, for example, Banksia (Coaldrake 1951).

(b) Protected seed. Some Proteaceae, such as Leucospermum species, release seed annually on ripening. These have

a hard impervious seed-coat, and remain dormant (Brown et al 1971). They apparently survive fire on or in the soil and germinate readily after fire.

(c) Abundant seed. Many dwarf and low shrubs shed copious small seeds annually, and these are typically members of the Ericaceae and Asteraceae. Seed are not protected in any notable way, but show symptoms of dormancy. It seems that a sufficient proportion of the extremely abundant supply will survive fire to re-establish the population. Levyns' work on Elytropappus glandulosus Less. provides an example of this kind (Levyns 1956). Martin (1966) contends, however, that Erica chamissonis K. ex Benth. regenerates from wind-borne seed from sources outside the burnt area.

1.2.3 Initial regeneration and establishment

Vegetative plants begin to sprout within fourteen days following fire (Adamson 1935, Wicht 1948), and germination occurs during the first season following fire, usually in winter. The rapidity of a plant species response to a fire depends on the timing of a fire in relation to the phenology of the relevant species. For example, Watsonia pyramidata (Andr.) Stapf at Jonkershoek, suffers no growth check if burnt early in the growing season (April or May); the tops of leaves are

scorched or burnt off, but continue to grow from intercalary meristems (Kruger 1978). Restionaceae, Cyperaceae and Poaceae behave similarly.

On the whole, reproductive regeneration occurs during the first season after a fire. It appears that germination starts in winter (July to August) and cotyledons emerge by late winter or early spring (August to September). On moist sites germination may occur out of season (Kruger 1972). There is some evidence from casual observation that germination may, in some cases (such as Erica hispidula L. at Jakkalsrivier near Grabouw) be delayed for several seasons until a suitable microclimate has developed (FJ Kruger pers.comm.).

Wicht (1948) has analysed the early response of fynbos communities in detail. The effects of burns in January to April were tested in a statistically designed experiment and he reported results recorded in the succeeding winter and spring. Sprouting of graminoid plants began within a week after the burns, and shrubs sprouted within three weeks, in spite of hot dry conditions. At the onset of rains in April, sprouting accelerated, germination began, and geophytes began to develop foliage. "The experiment provided no evidence at this stage that germination of seeds and development of geophytes were either promoted or retarded by fire ".

Unfortunately, Wicht did not publish any further results of his experiment. The effects of burns in every month of the year were to be tested, with adequate replication. To permit this small plots (4 m^2) were used; this was a severe disadvantage. Natural burns, for example, were not possible and fuel had to be added.

1.2.4 Development of the community

Taylor (1969), has described the development of a fynbos community from general observation, and is worth quoting in full:

"Floristically, the community is richest two to five years after fire when annuals, geophytes, sprouting perennials and seed-regenerating shrubs all occur together. In subsequent stages the last-named predominate while the other three classes become moribund and eventually die out. Converseley, stratification is simplest in the early stage and becomes more complex with advancing age. After some twenty years of protection from fire all the layers become moribund; the emergents and canopy shrubs slowly die out, littering the ground with dead twigs and leaves which decompose slowly, suppressing even the sprouting element of the lower layer ... On more level, less rocky ground (at Cape Point), fynbos may be self-perpetuating by regeneration of the early stages in openings caused by the death of shrubs in the mature community".

This account is largely supported by those of Adamson (1935), Wicht (1945), Hall (1959) and Kruger (1972).

Adamson (1935) analysed the succession of life-forms and species after fire, and his results may be summarised as follows:

(a) After fire there was an increase in geophytes and a small increase in annuals. Chamaephytes showed a progressive increase.

(b) The number of species showed a progressive increase, and was larger than the original number after six years.

(c) Immediately after the fire there was an increase in the ratio of nanophyllous to leptophyllous nanophanerophytes owing to the fact that many of the former sprout freely from the base after burning while the latter regenerate only from seed.

(d) Grass-like hemicryptophytes increased and relatively broad-leaved hemicryptophytes decreased in percentage after burning, giving a more xerophytic aspect to the vegetation.

In the Kamiesberg, a zone of arid fynbos, Adamson (1938) found that a large number of annuals and small plants became temporarily prominent after fire, the actual species varying with season of the fire and the distribution of rain following

it. Burning in the early summer resulted in a great spread of Wahlenbergia namaquana Sond., Pelargonium sp., Pentaschistis patula (Nees) Stapf, Anchusa capensis Thunb. and others. There was no large increase in geophytes, and regeneration of bushes commenced at once from either persistent basal parts or from seed.

Wicht's experiment (Wicht 1948) contributes some detailed information on the early stages of community development. Further contributions were made by Kruger (1972). It was found that rapid growth followed burns. Both canopy and basal cover reached 70 to 90 per cent of original levels within 25 to 30 months after fire. Sprouting graminoid and restioid species contributed most of the cover at this stage. In a subsequent contribution (Kruger 1977.) he reported on early growth of fynbos communities. The data indicated that phreatic communities grow at a rate of about 3 400 kg $ha^{-1}yr^{-1}$ in the first five years, whereas low shrub communities on dry sites had rates of increment as low as 1 000 kg $ha^{-1}yr^{-1}$ over the same period. A rate of 2 500 kg $ha^{-1}yr^{-1}$ appeared a reasonable average. Young stands are dominated by hemicryptophytes, which comprise about 2 000 to 6 000 kg ha^{-1} or about 60 to 75 per cent of the biomass in stands of about four years of age. This element persists and is

still significant by the age of sixteen years, although it declines relative to shrub biomass. Kruger et al (1977) classified pyric succession in fynbos communities into five phases, given below:

(a) Immediate post-fire phase. The first twelve months after fire are crucial in fynbos conservation since only during this interval do various species appear in the sexual phase (annuals, and "fire lilies"), and does sufficient germination occur. Sprouting species, especially hemicryptophytes, reappear rapidly and soon provide an effective cover. Some are already able to flower and set seed.

(b) Youth phase. During the intervals betwen two and four or five years after fire the graminoid herbs reach maximum biomass (up to 8000 kg ha^{-1}) and usually dominate communities. Canopy cover approaches pre-burn levels. Remaining sprouting species attain reproductive maturity. Opportunistic shrub species (Aspalathus spp., Euryops abrotanifolius (L.) DC. mature and die. Longer lived shrubs begin to emerge from the canopy. The veld becomes inflammable at about 4 years, as dead shoots and leaves of hemicryptophytes

accumulate.

(c) Maturing phase. In the subesequent interval, up to about 10 years after fire, all species reach reproductive maturity. Tall shrubs emerge and adopt the ascending branch habit.

(d) Mature phase. Tall shrubs attain maximum height and full rounded form, with maximum flowering activity. Seed-regenerating low shrubs (e.g. Erica spp.) begin to die; litter accumulates and lower herbaceous strata are reduced in importance; no germination occurs.

(e) 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 reproduction may occur. There is further accumulation of dead plant material. On special, limited sites which are both fertile and have moist soils, immigration of forest precursors may occur.

1.2.5 Effects of fire regime

Following Gill (1975), the components of a fire regime are given as the variables (a) fire intensity, (b) frequency of fire and (c) season of fire occurrence. The vegetation as it stands is a product of the fire regime.

Data on fire behaviour and intensity in fynbos are few, and Kruger (in Day et al 1979), suggests that fynbos fires are

not exceptionally intense. Evidence from elsewhere indicates that fire intensity may have a pronounced role in governing species survival, regeneration and subsequent community development. Van Wilgen and Kruger (1978) found that fynbos communities underwent little change when subjected to six year rotational burns at Kasteelkloof in the Paarl district, although there was a reduction in the importance of seed regenerating species. Other experiments on burning rotations have not yet been reported.

The present policy of burning on a twelve year rotation is a compromise between requirements of fuel control and high quality water production on one hand and conservation of natural communities and sound soils on the other; the former considerations tend to support relatively frequent burns while the latter support the opposite. The twelve year rotation is based mainly on considerations described by Jordaan (1949, 1965) and will permit all plant species to reach reproductive maturity in most cases, without allowing excessive fuel accumulation (Garnett 1973).

There is almost no information upon which to base prescriptions with respect to season of the burn. Jordaan (1949, 1965) has described certain hypotheses from the study of the life-cycle and phenology of Protea repens, and from field studies after a winter burn on Paarl Mountain. He concluded and

showed in that instance that burns from April to June were unfavourable, and burns in July to December unsafe for Protea repens, and that other Proteaceae could respond similarly. This he maintains was due to the fact that seed in current inflorescences was not mature during the periods in question. Nevertheless his tentative hypotheses may be questioned. Field observations at Jonkershoek indicate successful regeneration of P.repens after sufficient seed was held in serotinous inflorescences to ensure adequate supplies. (FJ Kruger, pers. comm.).

Nevertheless, Jordaan's work has emphasised the importance of life-cycle and seasonality studies in relation to the effect of the season of a burn.

Kruger (1972) was not able to find significant effects of burns in different seasons on overall community composition in the study at Jakkalsrivier. There was a lower biomass on autumn than on spring burns six months after the autumn and one year after the spring treatments. This difference was chiefly the difference between biomass of restioid and graminoid components which grow mainly in late winter and spring. These components would have grown for two seasons on the spring burns, and one on the other.

Of geophytes, Watsonia pyramidata showed a pronounced response

in that at least ten times as many ramets flowered after autumn burns as did after spring burns (Kruger 1978).

1.3 STRUCTURE OF FYNBOS COMMUNITIES

Structure of vegetation is the three-dimensional arrangement of individual species in time and space. It is variable in both time and space, and has two major components. Pattern is horizontal dispersion of species and species populations, while stratification is the vertical distribution of species and species populations (Gimingham 1972). Stratification reflects niche differentiation in a plant community, but the structural component of niche differentiation is normally analysed by a study of life-form.

Few data are available on the structure of fynbos communities. The high species diversity of fynbos communities is often noted (Wicht 1945 ; Acocks 1953; Boucher 1972; Werger et al 1972) and this is probably reflected in peculiar features of community pattern.

There is a broad gradient in stratification, with many-layered communities occurring on sites at lower elevations, while simple low communities occur at upper exposed sites (Adamson 1931). Adamson (1938), Rycroft (1950) and Van der Merwe (1966) present quantitative data on the life-form composition of medium and tall scrub fynbos communities.

Adamson (1931) described a fynbos community approaching climax on Table Mountain (Cape Town). The community was stratified; the uppermost stratum, composed of Protea lepidocarpodendron (L.) L. was by no means continuous. The bushes were scattered and only occasionally formed groups. Between and below them was a lower stratum of shrubs and monocotyledons, with smaller plants forming an incomplete herb layer. His analysis of life forms is shown in Table 1.

TABLE 1: LIFE-FORM COMPOSITION OF A TABLE MOUNTAIN FYNBOS COMMUNITY (Adamson 1931).

LIFE FORM	SPECIES PER CENT	AERIAL COVER PER CENT
Microphanerophyta microphylla	1	14,2
Nanophanerophyta nanophylla	7	0,4
" leptophylla	15	9,0
" with compound leaves	2	0,4
Chamaephyta microphylla	1	-
" nanophylla	6	0,2
" leptophylla	12	0,5
" with compound leaves	1	-
Hemicryptophyta with assimilating stems	9	6,9
" with "grass habit"	10	0,9
Others	35	2,5

In a later publication Adamson (1938) calls the vegetation type in which we are interested "sclerophyll bush" and gives the

following description:

"The climax community is a relatively dense and complex one, made up of bushes or occasionally of small trees. In its fully developed form it has three layers. The uppermost consists of larger bushes 1,5 to 2,5 m high, most of which have flat leaves of moderate size, but hard and with a dull surface. Proteaceous shrubs are abundant in this upper layer. Of these Protea, Leucospermum and Leucadendron are abundant, together with Maytenus, Heeria and a number of others. The uppermost layer is rarely continuous. Below is a dense layer of small shrubs with thin and more flexible stems and typically small heath-like leaves. A large variety of plants takes part in the building of this stratum.

Shrubby members of Compositae, Ericaceae, Rutaceae and many others are abundant. Below and between these bushes are smaller woody plants, herbs and geophytes in considerable numbers. Restionaceae are often very abundant in the lower strata. Annuals are usually few in number".

Rycroft (1950), working in Biesievlei, Jonkershoek, found that hemicryptophytes had the highest mean species density, and were closely followed by geophytes. The following was the order of mean species density per quadrat:

Hemicryptophytes	2,845
Geophytes	2,270
Nanophanerophytes	1,600
Chamaephytes	1,260
Therophytes	0,240

Microphanerophytes, Helophytes and Hydrophytes were very poorly represented and therefore not considered.

A comparison of life form data from fynbos communities with a normal spectrum (Mc Dougall 1951) has been made by Rycroft (1950) for Biesievlei and by van der Merwe (1966) for Swartboschkloof. Data are presented in Table 2.

TABLE 2: BIOLOGICAL SPECTRA OF TWO FYNBOS COMMUNITIES

Life form	Normal spectrum %	Biesievlei %	Swartbosch-kloof %
Stem succulents	1	0,3	0
Epiphytes	3	0	0,7
Mega-and Mesophanerophytes	6	0	0
Microphanerophytes	17	6,4	6,0
Nanophanerophytes	20	23,5	27,0
Chamaephytes	9	23,2	30,8
Hemicryptophytes	27	14,1	15,8
Geophytes	3	22,1	15,2
Helo- and Hydrophytes	1	2,3	0,2
Therophytes	13	8,1	3,6

Comparing fynbos to a normal spectrum, it is evident that the former has a high percentage of geophytes and chamaephytes, a lack of succulents, a low percentage of microphanerophytes and therophytes. Nanophanerophytes are slightly higher.

1.4 FUNCTIONAL FEATURES OF CAPE FYNBOS AND ALLIED COMMUNITIES

There is very little published information on Cape Fynbos.

The fynbos environment is very low in nutrients, which is similar to Australian heathland vegetation, but not like Californian chapparal, European Mediterranean vegetation and Chilean mattaral. Specht et al (1958) have indicated that the Australian substrate is very infertile, and that nutrients steadily accumulate in the underground organs of plants, often at the expense of aerial organs. Translocation of many nutrients (N, P, K, Ca, Cu, Zn & Mn) to aerial organs may be greatly reduced, that of some elements almost to zero. This must contribute greatly to the decreasing growth rate of the aerial organs. Those plants with a greater nutrient requirement, are eliminated earlier in the pyric succession under nutritional stress. Gradually only those species suvive in which the concentration of nutrient elements is low. Over 50% of the nutrients in the aerial organs of these species are bound in fruits and dead leaves so that even these species must suffer nutrient stress. Degradation of the stand must inevitably occur, to be followed by regene-

ration on the release of the nutrients.

1.5 FIRE AND FYNBOS CONSERVATION

A multiple use management policy is applied on State Forests, but with the primary aim of ensuring maximum sustained yields of clean water. Other aims are nature conservation, provision of recreation opportunity, and fire control. The remaining mountain fynbos areas, mainly in private hands, are subject to a variety of uses of which seasonal rough pasturage is probably the most important, harvesting of veld products (such as Agathosma betulina (Berg.) Pillans and A.crenulata (L.) Pillans)(buchu) for essential oils, and various species of cut flowers) the next, and recreation the least important (Kruger et al 1977).

A history of ideas on veld management by means of burning has already been presented. Veld management of fynbos areas has always been based on various veld burning or fire protection practices, culminating in the present policy of prescribed burning on a flexible rotation of about 12 years. The question of whether shorter rotations are detrimental, and if so to what extent, has remained unanswered, as well as the effects of long-term protection from fire. Catchment and conservation areas, especially those close to large towns and cities (for example the Cape Peninsula) are often subject to unplanned burns, and the question of their effect is a pressing

one. Furthermore, short rotation burning will be prescribed in some cases, e.g. for weed control. On the other hand, critics often propose intervals of longer than 12 years between burns. It has therefore become necessary to expand our knowledge of the effects of short rotation burning and of deferred burning. This study investigates the floristic and structural differences between three adjacent vegetation stands managed on short (about six year) rotations, normal (15 to 20 year)rotations, and protection from fire repectively.

PART II

FIRST PAPER: AERIAL PLANT BIOMASS OF BYNBOS COMMUNITIES AT JONKERSHOEK, STELLENBOSCH

AERIAL PLANT BIOMASS OF FYNBOS COMMUNITIES AT JONKERSHOEK, STELLENBOSCH

by

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ABSTRACT

Fynbos communities of three different post-fire ages were sampled in the Jonkershoek Valley to determine aerial plant biomass. This was done by a combination of clip plots, for the shorter vegetation and regression analysis for the larger shrubs or trees. The biomass was divided into fuel and non-fuel components, using a particle diameter of 6 millimeters as a dividing point.

Biomass of four year old fynbos amounts to about 6 500 kg ha^{-1}, all of which may be considered to be fuel. At 21 years of age biomass amounted to 49 681 kg ha^{-1}, of which 35 422 kg ha^{-1} was live. The fuel component (dead plus live) at this age was 26 621 kg ha^{-1}. At 37 years total biomass was 75 629 kg ha^{-1}. Of this 22 639 was live and 43 108 was fuel (dead plus live). These figures represent the highest yet reported for the fynbos as well as for vegetation from other mediterranean-type climate zones. Live biomass apparently increases to an age of roughly 30 years, whereafter it declines, whereas the total mass of dead plus live material increases right up to 37 years of age. The buildup of fuel in older stands of fynbos usually results in very intense fires, which apparently have an adverse effect on the vegetation. Although the further development of fynbos communities protected from fire is not known, it does not seem likely that forest will develop.

INTRODUCTION

There has been an increased interest in recent years in the aerial plant biomass of fynbos* communities. Biomass figures aid in the determination of primary productivity as well as in the prediction of fire intensities and behaviour (see, for example, Specht 1969b, Countryman and Philpot 1970, Kruger 1977). The fynbos vegetation of the south-western Cape Province has been subjected to periodic fires for some time (Kruger 1979), and is apparently adapted to survive such fires (Van der Merwe 1966). Inherent productivity in fynbos allows sufficient fuel for spreading fires to accumulate only by about the fourth year after a previous fire, but most fynbos vegetation must be somewhat older to burn readily (Kruger 1979). A subsequent fire usually takes place within 20 years and hence communities with a post-burn age of greater than 30 years are rare. Such fires may be caused either through human action or natural phenomena such as lightning or falling rocks (Kruger 1979). Preliminary data on the aerial plant biomass in fynbos communities, have been reported by Kruger (1977) and Rutherford (1978). The former gives biomass figures for three locations with post burn ages from one year and nine months to 17 years, whilst the latter gives data from two sites of about 14 years post-fire age.

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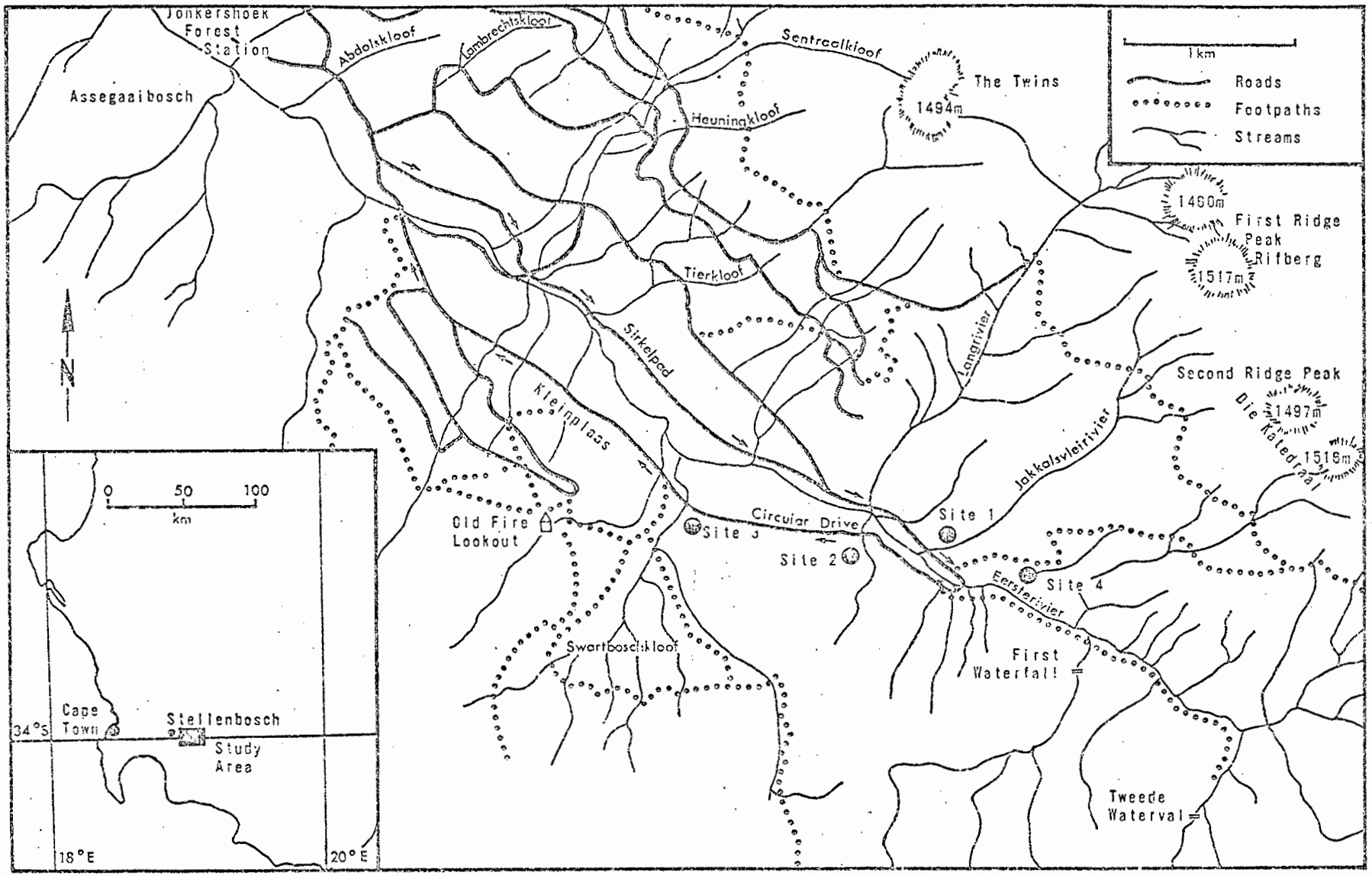
*As described by Acocks (1953) and including his types 69 (Macchia or Fynbos) 70 (False Macchia) and 47 (Coastal Macchia).

Four sites at the Jonkershoek Forestry Research Station (33°57'S and 18°55'E) were sampled and aerial plant biomass determined. The sites represent essentially the same community at three post-fire ages. Two of these sites were in firebreaks that had been subjected to frequent burning (burnt in 1942, 1948, 1954, 1960, 1968 and 1975) and were four years of age when sampled. A further site was in 21 year old vegetation previously burnt in 1942 and 1958. The last site had a post burn age of 37 years. The sites were selected so as to compare the effects of rotation of burn on fynbos community structure. The older sites were each paired with a site in the firebreak which had a similar elevation, aspect and soil type. Further investigations into the effects of rotation of burn on the plant community composition and structure were carried out and a report on the results of this study is in preparation.

THE STUDY AREA

The Jonkershoek ecosystem has been described by Wicht et al (1969). The area is situated roughly 8 km from Stellenbosch and 48 km from Cape Town (see Figure 1) and forms the source catchment of the Eerste River. Sandstones of the Table Mountain Series (Cape System) rest on the Cape Granite and form the upper parts of the mountains enclosing the valley on three sides. Due to faulting there is a difference in altitude of the base of the Table Mountain Series on the

Figure 1: Map of the Jonkershoek Forestry Research Station showing its position and major features. The position of the four biomass sample sites are shown.


Jonkershoek Forest Station
Assegaaibosch
Abdolskloof
Lambrechtskloof
Sentraalkloof
The Twins
1494m
Heuningkloof
1 km
Roads
Footpaths
Streams
1460m
First Ridge Peak
Rifberg
1517m
Tierkloof
Sirkelpad
Langrivier
Second Ridge Peak
1497m
Die Katedraal
1518m
Kleinplass
Jakkalsvleirivier
Old Fire Lookout
Site 3
Circular Drive
Site 1
Site 2
Site 4
Eersterivier
Swartboschkloof
First Waterfall
Tweede Waterval
0 50 100
km
Cape Town
Stellenbosch
Study Area
34°S
18°E
20°E
N

N.E. and S.W. sides of the valley, which are from 426 m to 610 m respectively. The soils of the Jonkershoek valley are young and mostly of mixed origin, with horizons not clearly defined (Wicht et al 1969). Stony soil derived from quartzitic colluvial material from the Table Mountain Series covers the major proportion of the area. Where granite provides the parent rocks, there is an admixture of quartzitic material from the sandstones above. The climate is of the Mediterranean type, described by Köppen (1931) as humid-mesothermal, with a dry summer and the average temperature of the warmest month below 22°C (Csb). Rainfall on the sample site averages 1 700 mm yr^{-1}, of which 1 000 mm (59%) falls between the months of May and August. The principal climatic features are illustrated in Figure 2 by means of a Walter diagram (Walter 1963).

METHODS

The methods used, can be divided into two categories; sampling on young sites with homogenous vegetation of relatively low biomass and sampling on older sites of a somewhat less homogenous nature and considerably higher biomass. I shall deal with each method separately.

Sampling of four year old vegetation (Sites 1 and 2)

Four year old vegetation (depicted in Figure 3) is of a

Figure 3: Four year old vegetation in the firebreak dominated by graminoid and restioid plants. The shrub in the foreground is Protea nitida.

structurally homogenous nature, when compared to older fynbos, and is dominated by graminoid and restioid plants, with shrubs being of little importance. The homogenous nature of the vegetation at this stage, as well as its relatively low biomass, makes sampling by means of clip-plots relatively easy.

Two plots, 50 by 50 meters in extent, were positioned in the firebreaks on opposite sides of the Eerste River. The sites were selected for structural homogeneity of vegetation, as well as to match a plot in the older vegetation with regard to altitude, aspect and soil type. In the latter resrespect, Site 1 was paired with Site 4, and Site 2 with Site 3. Salient features of each site are summarized in Table 1.

Statified random sampling following the ranked set sampling procedure of Halls and Dell (1966) was used. Biomass was determined by clipping aerial plant parts from 24 two-metre-square (1x2 m) quadrats on each site. Plants were clipped as close to the soil surface as possible, using seccateurs. Litter was collected by raking the soil surface with the fingers. Dead plants were included as litter. Clipped material was segregated into growthform categories during the clipping routine. The plant material was placed into brown paper bags and transported to a nearby laboratory at the end of each day, where they were stored until they could be placed in

TABLE 1: PRINCIPAL FEATURES OF EACH SAMPLE SITE

Site Number	Altitude (meters)	Aspect (slope, azimuth, degrees)	Slope (degrees)	Geology	Vegetation age (years)
1	470	235	14	Cape granite	4
2	455	20	20	TMS	4
3	425	31	28	TMS	21
4	425	241	26	Cape granite	37

drying ovens.

The categories used for the separation of clipped material are the same as used by Kruger (1977) and are detailed below:

(i) Shrubs: Microphanerophytes and nanophanerophytes of families such as Proteaceae, Bruniaceae, Ericaceae and Fabaceae.

(ii) Sub-shrubs: Sub-ligneous nanophanerophytes and chamaephytes of genera such as Stoebe and Metalasia (Asteraceae).

(iii) Graminoid: Hemicryptophytes typical of Poaceae and Cyperaceae.

(iv) Restioid: Leafless hemicryptophytes of the family Restionaceae and, sometimes, Cyperaceae described as assimilating stem type hemicryptophytes by Adamson (1931).

(v) Herbs (forbs): Non-ligneous elements not included in above categories, and including ferns.

All samples were oven-dried at 105°C for 24 hours and massed.

Sampling of 21 year old vegetation (Site 3)

The 21 year old vegetation, depicted in Figure 4, is dominated by large shrubs belonging to the genus Protea (Proteaceae) mainly Protea neriifolia and Protea repens. These shrubs are large, sometimes over four meters tall, and form

Figure 4: Twenty-one year old vegetation in Swartbosch-kloof. The vegetation is dominated by Protea neriifolia and P.repens.

an almost closed canopy. The understorey contains other smaller shrubs and sub-shrubs, restioid, graminoid and herb components as described earlier although these form a relatively small part of the total biomass of the vegetation.

A plot of 50 by 50 m was positioned within the vegetation and 24 two-meter square quadrats were laid out at random within the plot, as described previously. All plant material with the exception of live Protea repens and P.nerrifolia was clipped from these quadrats in order to estimate the biomass of the understorey vegetation. The material was divided into the categories listed below:

(i) Shrubs and sub-shrubs
(ii) Graminoid
(iii) Restioid
(iv) Herbs
(v) Litter

In order to provide an estimate of the fuel available, the classes (i) and (v) above were subdivided into particles with diameters less than, and those greater than six millimeters. This was measured by means of calipers. Branches were cut off where their diameters became less than six millimeters. It is arbitrarily assumed that particles with a diameter of greater than six millimeters will not burn, and that all graminoid, restioid and herb-type plants could be counted as

fuel. Methods are otherwise as previously described.

Estimation of the biomass of the two dominant shrub species on the plot was done by means of regression analysis. Twenty-two Protea neriifolia and 23 P.repens shrubs were harvested from outside the sample plot after measuring their diameters at 20 cm above ground level. Shrubs were selected so as to cover a representative range of diameters. The shrubs were divided into "fuel" components (leaves, cones and branches with diameters less than six millimeters) and larger parts with diameters greater than six millimeters. Each component was massed and subsampled for moisture content. The subsamples were oven-dried at 105°C for 24 hours (or, in the case of large stumps, until constant mass was reached) and the mean moisture content of the subsamples was used to estimate oven-dry mass of the original material. Linear, power and exponential regressions were fitted (Daniel and Wood 1971) and these lines were tested for goodness of fit using Furnivals Index (Furnival 1969). In all cases power curves provided the best fit. The following equations were obtained to describe the biomass of Protea neriifolia shrubs based on their diameters at 20 cm.

(i) Diameter at 20 cm in cm (x) vs total dry mass in kg (y).

$$\ln y = -2,2340 + 2,2593 \ln x \quad \text{---------- (1)}$$

Correlation = 0,9542

(ii) Diameter at 20 cm in cm (x) vs dry mass large branches in kg (y).

$\ln y = -2,2321 + 2,1221 \ln x$ ---------- (2)

Correlation = 0,9297.

A similar allometric model for Protea repens is given below.

(iii) Diameter at 20 cm in cm (x) vs total dry mass in kg (y).

$\ln y = -2,6971 + 2,4596 \ln x$ ---------- (3)

Correlation = 0,9591.

(iv) Diameter at 20 cm in cm (x) vs dry mass large branches in kg (y).

$\ln y = -2,8932 + 2,3648 \ln x$ ---------- (4)

Correlation = 0,9161.

The diameter of each Protea nerrifolia shrub in the 50 x 50 sample plot, was measured at 20cm above ground level. The total dry mass and dry mass of large branches of Protea neriifolia was obtained by summing mass values calculated using equations (1) and (2) above. The "fuel" component was estimated by subtraction.

The same procedure was followed for Protea repens, with biomass of different components obtained using equations (3) and (4) above.

Sampling of 37 year old vegetation (Site 4)

In this case the vegetation had reached a scenescent stage. The community was previously dominated by Protea neriifolia, together with Brunia nodiflora (Bruniaceae) and Widdringtonia nodiflora (Cupressaceae). Of these, Widdringtonia had remained healthy and apparently vigourous, while Brunia had reached a stage where much of the plant consisted of dead material. Protea neriifolia had died in great numbers; surviving plants often had only one or two live branches; the rest were dead and dry. The vegetation is depicted in Figures 5 and 6. A sampling approach similar to that used for 21 year old vegetation was adopted, and a regression biomass model for Widdringtonia was constructed. This was not possible for Protea, however, because plants had very irregular shapes due to branches dying and breaking off; in any case, the majority of shrubs were completely dead. Therefore all plant material, excluding live Widdringtonia, was clipped from 24 two meter square quadrats within one 50 x 50 meter plot. Again methods were the same as for the first two plots except that seccateurs proved inadequate and pruning saws were used to cut large branches overhanging the sample plots. Care was taken to ensure that all overhanging vegetation was accurately sampled. Vegetation was subdivided into classes in the same way as for 21 year old vegetation.

Figure 5: Thirty-seven year old vegetation in Langrivier. The large trees in the background are Widdringtonia nodiflora. A dying Protea neriifolia is visible in the middle distance, and Brunia nodiflora can be seen in the foreground.

Figure 6: Close up view of a dead Protea neriifolia shrub showing the heavy build-up of dry fuel material.

Twenty Widdringtonia trees were harvested from outside the sample plot, after measuring their diameters at 20 cm above ground level. Again, trees were selected so as to cover a representative range of diameters. The trees were divided into cones, large (greater than six millimeters in diameter) branches and "fuel" components. The material was subsampled for moisture content as previously described for the determination of dry masses. The data were used to determine an allometric biomass model in the same way as for the Protea shrubs. The model is given below:

(i) Diameter at 20 cm in cm (x) vs total dry mass in grams (y).

$$\ln y = 4{,}0848 + 2{,}3366 \ln x \quad \text{---------- (5)}$$

Correlation = 0,9857

(ii) Diameter at 20 cm in cm (x) vs dry mass fuel in g (y).

$$\ln y = 3{,}7117 + 1{,}9377 \ln x \quad \text{---------- (6)}$$

Correlation = 0,9702.

(iii) Diameter at 20 cm in cm (x) vs dry mass cones in g (y).

$$\ln y = -1{,}0768 + 3{,}4153 \ln x \quad \text{---------- (7)}$$

Correlation = 0,8873.

Diameters at 20 cm of all live Widdringtonia nodiflora trees on the site were measured and the equations (5), (6) and (7) above were used to calculate masses of the different

components. The large branch and stem component was estimated by subtraction.

RESULTS AND DISCUSSION

Biomass data for the 24 clipped plots on each site are presented in Table 2. On Site 3 a total of 105 Protea neriifolia bushes and 241 Protea repens bushes were measured, and on Site 4 a total of 247 Widdringtonia trees were measured. Table 3 presents a breakdown of data from Table 2 as well as figures obtained from regressions for the three large shrubs.

It is unfortunate that a standard deviation for the two sites which included estimations by regressions cannot be computed to allow statistical testing for differences between age classes. The figures presented in Table 2 show that the standard deviations for clipped plots in the older vegetation are very high, due to structural heterogeniety of the vegetation sampled. Data from clipped plots and regressions were added so that estimation of standard deviation for the total cannot be obtained. However, as far as total live biomass was concerned, the estimates for large shrubs from regressions contributed most of the live biomass component (82,5 percent for site 3 and 71,6 percent for site 4). These estimates are considered to be good because of the high correlations obtained for the regression equations.

TABLE 2: BIOMASS STATISTICS FOR CLIPPED PLOTS

Site Number	Sample Size	Aerial plant biomass (total live)($kg.ha^{-1}$)+	STATISTICS FOR TOTAL LIVE BIOMASS Standard deviation	Confidence Interval p = 0,95	Coefficient of variation (%)	Litter $kg\ ha^{-1}$	STATISTICS FOR LITTER MASS Standard deviation	Confidence Interval p = 0,95	Coefficient of variation (%)
1	24	6599	790	± 344	11,97	535	372	± 157	70,86
2	24	5897	908	± 384	15,40	235	113	± 48	34,77
3*	24	4091	2519	±1064	61,57	14259	7737	±3260	54,26
4*	24	6334	5500	±2323	86,83	53260	14903	±6279	27,98

*Data incomplete, biomass from regressions on shrub species to be added. See Table 2.

+A breakdown of this total biomass, is given in Table 2.

TABLE 3: TOTAL AERIAL PLANT BIOMASS STATISTICS FROM FOUR SITES (SEE TEXT FOR EXPLANATION)

COMPONENT	Total mass (kg. ha $^{-1}$)				Mass of fuel component (kg. ha^{-1})	
	Site 1	Site 2	Site 3	Site 4	Site 3	Site 4
Protea neriifolia	0*	0*	9065	0+	2641	0+
Protea repens	0*	0*	22266	0+	7581	0+
Widdringtonia	0*	0*	0*	16017	0*	4292
Shrubs	925	521	944	5564	712	3047
Sub-shrubs	1	5	209	1	3	1
Restioid	1755	1671	632	258	632	258
Graminoid	3070	2869	488	155	488	155
Herbs	848	831	1818	357	1818	357
Total live	6599	5897	35422	22639	12476	34999
Total live plus litter	7124	6222	49681	75629	26621	43108

*Absent or nearly absent

+Included in shrubs

The estimates for litter (shown in Table 2) are comparable. Estimates for litter on sites 1 and 2 do not differ significantly, whereas those from sites 3 and 4 are significantly different from each other and from sites 1 and 2 at a 1% level of significance.

Figure 7 shows the approximate relationship between total live biomass, litter mass and post-burn age of vegetation. The lines join the points given in Table 1. It would appear as though total live biomass increases with age to a point, whereafter it again declines. Dead material (litter mass) continues to rise with age of vegetation. This rise becomes more marked once the live biomass starts to decline, due to the large number of dying proteaceous (and other) shrubs. The mass of fuel (shown in Table 3) also increases with age. At four years of age most communities are dominated by graminoid and restioid plants with particle diameters less than six millimeters (Kruger 1977). For this reason, the total biomass of the four year old vegetation could be considered to be fuel.

At 20 years of age much of the biomass of large shrubs is live, uncured and held aloft. Under extreme fire weather conditions, a fire would crown and much of the "fuel" component of the large shrubs would burn. In fires burning under cooler and moister conditions, such as experienced

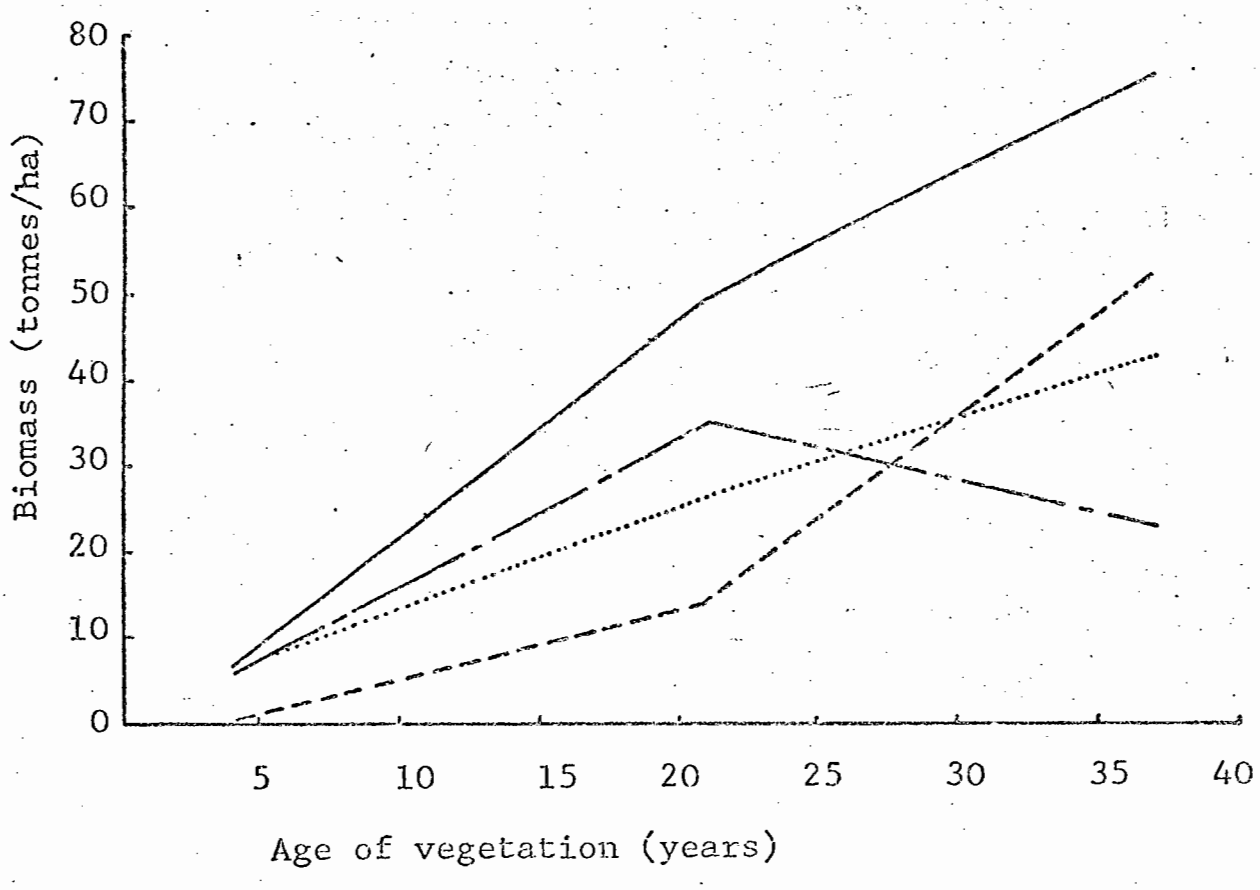


Figure 7: Comparison of approximate biomass and litter values from three post fire ages of fynbos at Jonkershoek. Lines represent total live plus litter mass (————), live biomass (——··——), litter mass (– – – –) and fuel mass (·····).

in many prescribed burns in fynbos, it could be expected that much of this uncured fuel component would not be consumed. In vegetation older than 30 years, this biomass has become dead and cured, and much has broken off and fallen to the ground. Under normal summer weather conditions a fire in such vegetation could be expected to be intense, and would probably burn much of the coarser litter as well as fine material. Under severe weather conditions a fire in such vegetation would probably consume all the litter and much of the live vegetation. The ability of the vegetation to withstand such severe burns is little understood. McLachlan and Moll (1976) have made the tentative observation that areas of fynbos which had not burnt for some time (20-25 years) recovered better than areas which were continually burnt. Data from older stands has recently become available. Bond (1980) has reported poor regeneration after a burn in very old (approximately 50 years) vegetation dominated by Protea punctata on the lower southern slopes of the Swartberg mountain range. Observations after a fire in 40 year old fynbos in the Cedarberg mountain range, showed unusually high mortality in certain species which normally survive fires by means of vegetative regeneration. Thirty-two percent of all Heeria argentea trees tallied along a pathway were found to be dead (FJ Kruger, pers.comm.). These results are almost certainly due, in part at least, to very intense fires resul-

ting from heavy fuel loads.

CONCLUSION

Kruger (1977) has compared biomass of fynbos communities with that of plant communities in mediterranean type ecosystems elsewhere. The maximum biomass reported elsewhere was 49 700 kg ha^{-1} at 13 years for garrigue (France) and 49 100 kg ha^{-1} at 37 years for chaparral (California) of which 21 800 kg ha^{-1} was standing dead sticks (Specht 1969a, 1969b). The maximum biomass reported for fynbos, from a 17 year old scleorophyll scrub community at Jonkershoek was 25 700 kg ha^{-1}. The figures given here represent the highest yet reported.

Jonkershoek is not entirely representative of the fynbos communities elsewhere, mainly because of soil differences, and slightly higher rainfall. Most fynbos soils are derived from sandstones alone, whereas soils from the sites at Jonkershoek are partly derived from granite. Kruger (1977) points out, however, that soil moisture availability overrides the effect of soil fertility when considering growth rates in fynbos.

As far as the rotation of burning is concerned, some tentative conclusions may be made. Burning on short rotations drastically reduces the biomass, due to the elimination of most of the seed-reproducing shrub component (see, for exam-

ple Jordaan 1949, van Wilgen and Kruger 1980). Secondly, protection of communities from fire for periods longer than 30 years resulted in a decline in total live biomass, and a considerable increase in the amount of litter and fuel available. There is evidence from elsewhere that communities of similar age on sandstone soils have not reached the same extent of degeneration (EJ Moll, pers. comm.). This may indicate that such communities are on a longer cycle, but it can be expected that they would follow a similar course to those at Jonkershoek. What happens if communities are protected from fire for much longer periods can only be speculated upon. There is some growth of forest precursors on the moister sites, for example Kiggelaria africana, Rapanea melanophleos and Olea africana, but it is doubtful whether a true forest could develop on these sites due to shallow rocky soils and summer drought. Hopefully, some of the older communities at Jonkershoek will be protected from fire for some time to come, thus allowing further observations on the effects of exclusion of fire.

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PART III

SECOND PAPER: THE EFFECT OF FIRE FREQUENCY ON FYNBOS PLANT COMMUNITY STRUCTURE AT JONKERSHOEK, STELLENBOSCH

THE EFFECT OF FIRE FREQUENCY ON FYNBOS PLANT COMMUNITY COMPOSITION AND STRUCTURE AT JONKERSHOEK, STELLENBOSCH

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ABSTRACT

Fynbos vegetation previously subjected to three differing fire regimes was investigated by means of the enumeration of 100 releves using the Braun-Blanquet method. The three treatments (fire regimes) investigated, were short (about six year) rotation burning, normal rotation burning (about 15-20 years) and protection from fire for 37 years.

Short rotation burning resulted in a reduction in plant cover, height, and biomass, as well as in the elimination of longer lived seed regenerating shrubs. Species diversity was high and shorter graminoid and herb species dominated the vegetation. Twenty year old vegetation had a high cover and mean plant height, but species diversity was low and undergrowth species were of much reduced importance.

In very old vegetation larger shrubs were reduced in importance due to high mortality; as a result undergrowth species showed some signs of recovery, and species diversity increased. Some germination was noted, and certain tree species also appeared. The development of true forest does not seem likely due to shallow soils and summer drought. Healthy fynbos vegetation would probably be maintained by burning on a 15 to 25 year rotation.

INTRODUCTION

Fynbos is a sclerophyllous vegetation type characteristic of the south western Cape Province of South Africa (see Acocks 1953). This vegetation has been subjected to periodic fires, of both human or natural origin, for some time. Such fires could occur at all times of the year under suitable weather conditions, although most occur in the summer months. Kruger (1977, 1979a) suggests that fire frequency would have ranged between about once in six to once in 40 years, varying more or less at random between these limits, but this hypothesis is challenged by Moll et al (1980), who suggests somewhat longer periods between fires. Burning of fynbos has been condemned from early times (Botha 1924) and the battle against fires was tackled in earnest in the early 20th century (Levyns 1924, Marloth 1924, Pillans 1924). Burning as a natural phenomenon was first seriously considered by Dr CL Wicht, who admitted that data on the effects of burning were not available and emphasized the need for such data (Wicht 1945). The present day fynbos vegetation is apparently adapted to survive fires (van der Merwe 1966) and there is acceptance today that fire in fynbos is a natural phenomenon. Fires caused by lightning and falling rocks are commonplace, and there is no reason to believe that this was not so from prehistoric times (Bands 1977).

Information on the effects of fire frequency on the vegetation is scant. Jordaan (1949) found that Protea repens (L.) L. requires an eight year period between burns to attain maturity and form seed. Because regeneration is only from seed following a fire, burning frequencies of less than eight years will tend to eliminate the species. On the other hand, Le Roux (1966) mentions areas of fynbos which had become totally moribund due to long protection from fire, resulting in the absence of game and birds found in more frequently burnt fynbos areas. Specht et al (1958) have made interesting observations on analogous vegetation on nutrient poor sandy soils in Australia. Long protection from fire led to a reduction in the number of species in a stand (after burning, 36 species, after 25 years, 20 species, and after 50 years only 10 species). They suggest that this is due to the cessation of transfer of mineral nutrients to above-ground parts after a certain stage, because these are needed in the roots and underground organs. This results in the cessation of above-ground growth, and the vegetation becomes moribund. More recently it has become apparent that component species of fynbos need fire for their reproduction and survival (as examples Orothamus zeyheri Pappe and Serriria florida Knight) (Taylor 1972). Post fire succession in fynbos has been described by Kruger (1979b). The initial recovery is rapid, and regeneration and germination of seeds for all or most species occurs within 12 months following a

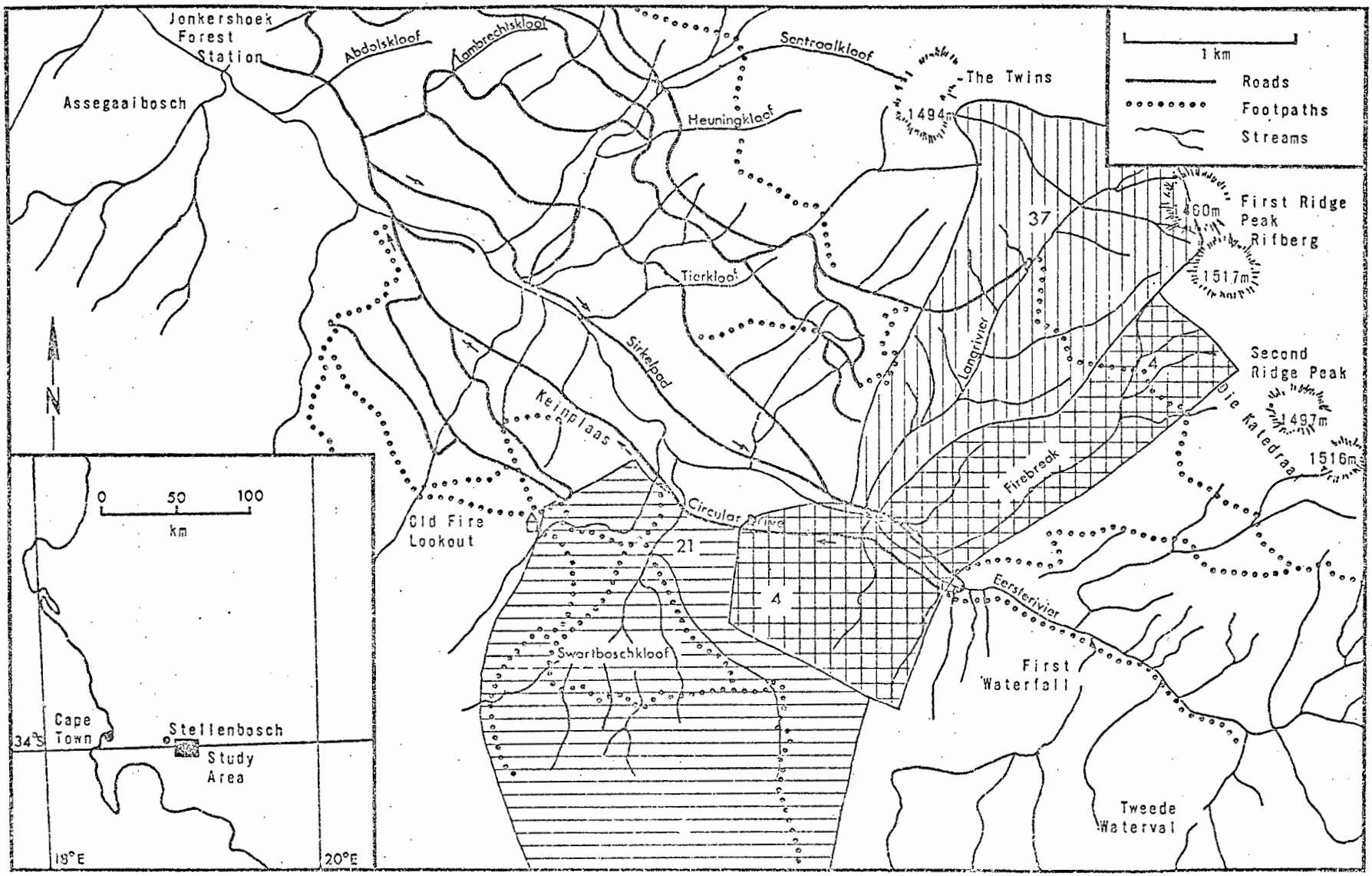
fire. All plant species attain reproductive maturity within 10 years. Should a fire occur before a seed reproducing species has attained maturity, that species will be eliminated from the community. The mature phase lasts up to 30 years post fire age, after which the vegetation becomes senescant, with high mortality among dominant shrubs and accumulation of dead material and litter (van Wilgen 1980). Experimental burning of fynbos at six year intervals was found to have much less effect on the overall composition of the vegetation than may have been expected, although there was some reduction in the importance of seed regenerating species (van Wilgen and Kruger 1980).

The object of the present study was to compare adjacent stands of vegetation representing essentially the same community managed under three different burning frequencies. Data on the structural and floristic differences between such stands is necessary as a basis for determining a burning regime suitable for the sound management of fynbos.

THE STUDY AREA

The area chosen for the study falls within the Jonkershoek State Forest, and lies roughly 8 km from the town of Stellenbosch (see Figure 1). The Jonkershoek ecosystem has been described by Wicht et al (1969). The climate is of the Mediterranean type and rainfall on the study area aver-

Figure 1: Map of the Jonkershoek Forestry Research Station showing its position and major features. The various post-fire ages of vegetation studied are depicted by means of shading, with numbers referring to post-fire age in years.


Jonkershoek
Forest
Station
Assegaaibosch
Abdolskloof
Lambrechtskloof
Sentraalkloof
The Twins
1494m
Heuningkloof
1 km
Roads
Footpaths
Streams
First Ridge
Peak
Rifberg
1460m
1517m
37
Tierkloof
Sirkelpad
Langrivier
Second
Ridge Peak
1497m
1516m
Die Katedraal
Kelnplaas
Firebreak
Old Fire
Lookout
Circular Drive
21
4
Eersterivier
Swartboschkloof
First
Waterfall
Tweede
Waterval
0 50 100
km
Cape
Town
Stellenbosch
Study
Area
34°S
18°E
20°E

ages 1700 mm yr^{-1}, of which 1000 mm (59%) falls between the months of May and August.

The areas was chosen because of the variety of post-burn ages of fynbos communities that occurred in close proximity to each other, thus providing a good opportunity for comparison of the effects of fire frequency on the vegetation. The Eerste River runs down the centre of the Jonkershoek valley. The study area is situated on the foothills on either side of the river. The Langrivier experimental catchment on the south facing aspect has been protected from fire since 1942, making it one of the longest protected areas in the fynbos (37 years old at the time of the survey in late 1979). The Swartboschkloof area, across the valley on the north facing aspect has been burnt on a 15 to 20 year rotation, and burnt out completely in 1927, 1942 and 1958 (van der Merwe 1966), making it 21 years old at the time of survey. Adjacent to the two areas is a firebreak which has been frequently burnt. Department of Forestry records indicate that the area burnt out entirely in 1942, 1948, 1954, 1960, 1968 and 1975, and was four years old at the time of survey.

Major geological and aspect differences exist between the 21 and 37 year old stands and their adjacent parts of the firebreak on either side of the river. Sandstones of the

Table Mountain series (Cape System) rest on the Cape Granite and form the upper parts of the mountains enclosing the Jonkershoek valley on three sides. Due to faulting there is a difference in altitude of the base of the sandstones on the NE and SW sides of the valley, which are from 426 to 610 m respectively (Wicht et al 1969). Swartboschkloof (21 years old) and its adjacent firebreak are underlain by standstone, while the opposite side of the valley is in turn underlain by granite. Swartboschkloof, with an equatorial aspect, will also have a higher potential evapotranspiration resulting in more xeric plant communities than would be the case with the polar aspect associated with Langrivier (Holland and Steyn 1975). This polar aspect was also sampled over a much larger altitudinal range than was the equatorial aspect (370 to 960 m and 370 to 525 m respectively).

The mature vegetation of the area is a closed shrubland dominated by Protea neriifolia and P. repens with some P.nitida. Differences in the plant communities are apparent on the two diametrically opposed aspects. On south facing (polar aspect) slopes Protea repens is of lesser importance and Widdringtonia nodiflora, a small cuppressoid tree, is prominent. Brunia nodiflora, a fynbos endemic shrub, is dominant over large areas and relatively moisture dependent shrubs such as Myrsine africana are found. Understorey communities on both aspects are dominated by, among others,

members of the Restionaceae, Cyperaceae, Ericaceae and Fabaceae. Bobartia indica, a tufted member of the Iradaceae with terete leaves is prominent throughout. In younger vegetation the large shrubs are absent and restioid and graminoid plants are prominent; these diminish in importance as the shrub canopy closes. In old vegetation, mortality of large shrubs causes the canopy to re-open and understorey plants become somewhat more important. Examples of the various ages of vegetation sampled are depicted in Figures 2, 3 and 4.

METHODS

Features of the vegetation were enumerated from 100 quadrats placed so as to cover a spectrum of altitude, aspect and soil types present in the area. Similar "environmental types" were sampled in different stands, using the assumption that areas with similar environmental conditions should support similar vegetation under the same burning regime. This would theoretically separate the effects of fire regime on the vegetation from the controlling influences of the physical environment. Twenty of these quadrats were placed on the north facing aspect, with 10 each in the 21 year old and four year old vegetation respectively. The remaining 80 plots were divided equally among the 37 year old and four year old vegetation on the south slopes, and spread evenly along the altitudinal gradient. Quadrats were each 50 m^2 (5x10m) in

Figure 2: Four year old vegetation in a frequently burnt fire break. The vegetation is dominated by shorter hemicrytophytes, with larger shrubs being represented by Protea nitida, a species which survives fire by means of sprouting from epicormic buds. The two meter board shown here is divided into 20 cm intervals.

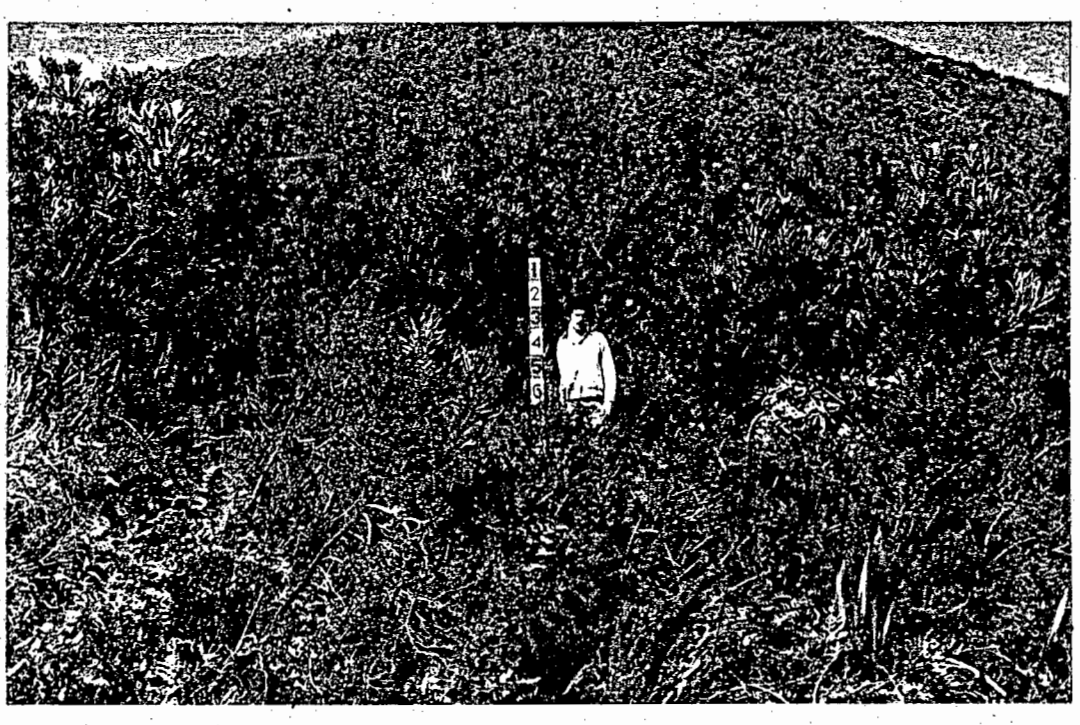


Figure 3: Twenty-one year old vegetation dominated by large seed-reproducing shrubs of the genus Protea. The shrub canopy is closed over most of the area as can be seen behind the observer.

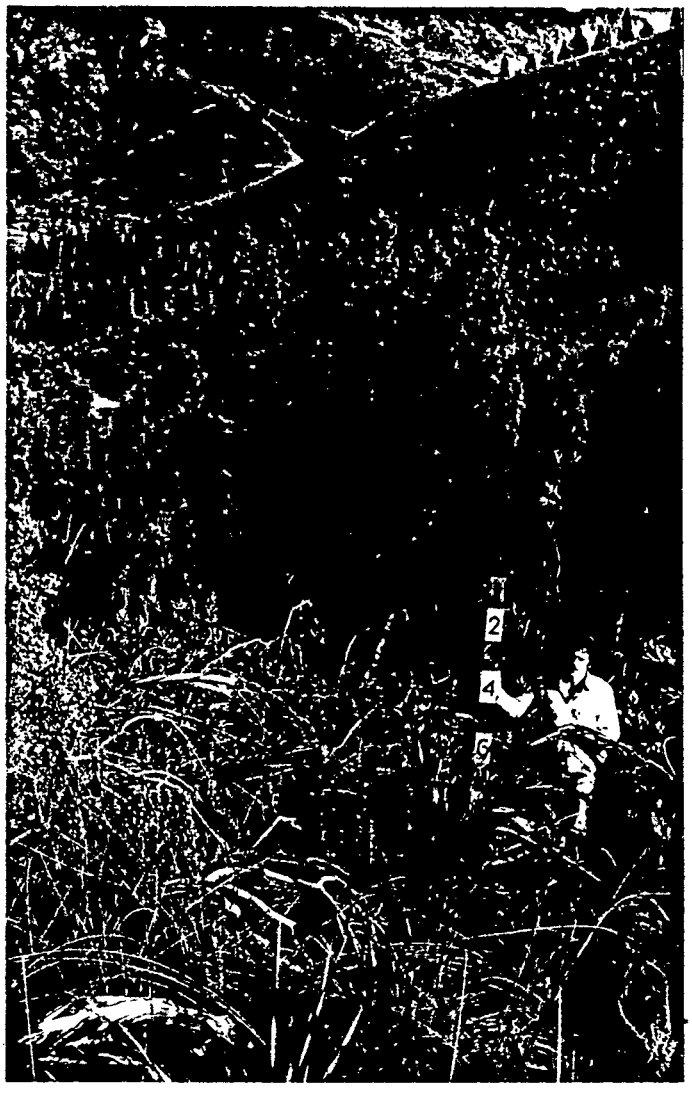


Figure 4: Thirty-seven year old vegetation showing the high percentage of dead Protea shrubs in the foreground. The trees in the background are Widdringtonia nodiflora.

area and were subjectively placed within areas of similar altitude, aspect and soil type. These areas were first selected on stereoscopically viewed colour aerial photographs of the area and later checked in the field. All vascular plants occurring in the quadrats were identified and listed, and assigned cover-abundance estimates on the Braun-Blanquet scale, as described by Küchler (1967). A comprehensive reference herbarium is available at Jonkershoek, and scrap specimens were collected from species which could not be identified in the field for comparison with herbarium specimens. Further records for each site included slope, aspect, geology and soils as well as estimates of total cover and stratification of vegetation. Each site was photographed and a number of heights of prominent species in each plot were measured.

RESULTS

Life forms

All species present in the survey were classified into the following life forms: Trees, shrubs greater than one meter in height, low shrubs (between 0,25 and 1 m), dwarf shrubs (less than 0,25 m), Restionaceae, Cyperaceae, Poaceae and other herbs plus ferns. Members of these were classified according to mode of regeneration after fire as vegetative (v), germinative (g - germinative, regeneration from seed only), or unknown (u). The mode of post fire regeneration

was determined from field observation, or knowledge of their behaviour elsewhere (van der Merwe 1966).

Percentage cover values for each species record were assigned to the cover-abundance scale as follows: r = 0,1; + = 0,5; 1 = 3; 2 = 15; 3 = 37,5; 4 = 62,5 and 5 = 87,5 percent. These values were accumulated for each life form in each plot to calculate means for the sample. Data appear in Table 1.

Total cover

Total cover of the vegetation was estimated at each site. Mean total cover and standard deviation were calculated for each treatment class and data are presented in Table 2.

Plant height

The heights of a few species are presented in Table 3 for purposes of comparison. Where species were not measured in a given treatment class, this is indicated by means of dashes, and does not necessarily mean that the species did not occur in that treatment class.

Species diversity

Measures of species diversity are presented in Table 4. Dominance concentration was measured by means of Simpsons index, calculated for each plot as $C = \sum^{s} p_i^2$ where s = the number

TABLE 1: MEAN COVER OF VEGETATION BY LIFE FORMS FOR THE DIFFERENT FIRE REGIMES (SEE TEXT)

LIFE FORMS	MODE OF REGENERATION	37 YEARS OLD (S ASPECT)	21 YEAR OLD (N ASPECT)	4 YEAR OLD (S ASPECT)	4 YEAR OLD (N ASPECT)
Trees	V	1,05	0,05	0	0
	G	2,31	0	0	0
Shrubs	V	28,34	33,80	13,18	28,15
(> 1m)	G	39,00	87,80	1,95	2,35
Low shrubs	V	52,56	30,11	52,09	45,55
(0,25-1 m)	G	32,80	11,10	33,46	22,45
	U	5,45	7,60	6,43	0,60
Dwarf shrub	V	18,40	15,50	24,47	12,55
(<0,25 m)	G	0,51	3,95	6,56	4,05
	U	0,01	0,10	0	0
Restionaceae	V	45,67	17,25	85,43	125,35
Poaceae	V	46,52	17,60	48,38	39,46
Cyperaceae	V	33,81	20,90	60,85	43,55
Others	V	73,36	55,21	86,71	48,40
	G	4,86	0,05	4,65	0,50
	U	3,05	9,05	2,25	0,10

TABLE 2: MEAN TOTAL COVER OF VEGETATION UNDER DIFFERENT FIRE REGIMES

TREATMENT CLASS	MEAN TOTAL COVER	STANDARD DEVIATION	NUMBER OF OBSERVATIONS	CONFIDENCE INTERVAL p = 0,95
37 year old (South aspect)	90,05	5,55	40	± 1,48
21 year old (North aspect)	94,80	3,65	10	± 2,12
4 year old (North aspect)	80,50	5,99	10	± 3,47
4 years old (South aspect)	87,88	5,47	40	± 1,48

TABLE 3: MEASURED HEIGHTS FOR SOME COMMON SPECIES (SEE TEXT FOR EXPLANATION)

SPECIES	MODE OF REGENE-RATION	VEGETATION AGE CLASSES								
		37 years old			21 years old			4 years old		
		Mean Height	S.D.*	N+	Mean Height	S.D.*	N+	Mean Height	S.D.*	N+
Brunia nodiflora L.	V	123,1	42,19	105	-	-	-	77,2	22,71	57
Widdringtonia nodiflora (L.) Powrie	V	436,5	16,19	23	-	-	-	75,7	19,88	7
Protea nitida Mill.	V	240,0	155,56	2	-	-	-	116,2	63,16	4
P.repens (L.) L.	G	217,5	55,00	4	329,2	69,35	64	-	-	-
P.neriifolia R.Br.	G	201,6	97,43	81	268,0	94,81	15	-	-	-
Cliffortia ruscifolia L.	G	223,3	32,15	3	163,2	58,57	41	35,0	10,00	10
Penaea mucronata L.	V	79,0	25,72	10	82,7	36,88	30	41,5	10,43	30
Rhus angustifolia L.	V	136,9	59,34	8	173,5	42,46	10	-	-	-
Erica hispidula L.	G	63,3	20,60	60	-	-	-	40,8	20,18	30
Corymbium villosum L.F.	V	26,6	4,71	20	-	-	-	27,0	4,29	10
Bobartia indica L.	V	101,8	26,03	200	97,9	23,07	7	100,9	21,66	254
Restio gaudichaudianus Kunth.	V	70,7	17,97	20	-	-	-	54,7	10,97	30
R.tritiseus Rottb.	V	50,6	10,44	103	-	-	-	44,7	8,95	30
Merxmeullera stricta (Shrad) Conert	V	29,4	13,89	99	-	-	-	36,3	13,22	30
Pentaschistis collorata (Steud.) Stapf.	V	19,4	9,19	29	-	-	-	31,3	10,22	110
Cymbopogon marginatus (Steud.) Stapf.	V	45,40	10,82	30	42,2	13,91	40	33,0	12,43	30
Tetraria ustulata (L.) C.B.Cl	V	46,2	8,00	24	44,2	15,41	20	41,0	10,53	60
T.involucrata (Rottb.) C.B.Cl	V	51,8	11,08	19	-	-	-	73,7	13,36	20
Watsonia paramidata (Andr.) Stapf.	V	95,5	28,56	10	96,3	13,48	20	80,5	16,57	10

*Standard deviation + Number of Observations

TABLE 4: SPECIES DIVERSITY DATA FOR THREE POST-FIRE AGES OF FYNBOS AT JONKERSHOEK

	VEGETATION AGE (YEARS)			
	North Aspect (4 yrs old)	South Aspect (4 yrs old)	North Aspect (21 yrs old)	South Aspect (37 yrs old)
Number of species in sample	93	175	71	188
Mean per plot	37,50	35,35	24,20	32,60
Standard deviation	4,12	5,19	6,18	8,42
Maximum per plot	45	45	35	54
Minimum per plot	33	19	13	21
Mean Simpsons Index	0,0368	0,0418	0,0776	0,0510
Standard deviation	0,0057	0,0087	0,0295	0,0176
Mean Shannon-Wiener Index	1,5124	1,4696	1,2581	1,4149
Standard deviation	0,0527	0,0744	0,1308	0,1266
Number of plots surveyed	10	40	10	40

of species in the sample and p_i = the proportional abundance of the i th species (Whittaker 1972). The Shannon-Wiener index, which reflects evenness of relative species abundance in the community, was calculated as $H = -\sum^{s} p_i \log_{10} p_i$ (Whittaker 1972).

Relative abundance of species in each treatment class

Mean cover values were calculated for each species in the same manner as for life forms. The mean cover values and frequencies of some prominent species are presented in Tables 5 and 6. Table 5 contains data for north facing plots (21 and 4 years old) and Table 6 contains data for south facing plots (37 and 4 years old).

DISCUSSION

The relative abundance of life forms as presented in Table 1 quantifies what can be seen at a glance when one looks at the vegetation itself. Trees are absent from younger vegetation, and start to appear only in much older stands. Larger seed-reproducing shrubs are almost totally eliminated from areas burnt on shorter rotations. Such shrubs assume great importance in mature (21 year old) vegetation, but decrease in importance again in older vegetation due to mortality among "over-mature" adult shrubs. Resprouting large shrubs are not as drastically effected, and are only marginally more important in mature stands. Smaller shrubs are also less effected by fire regime,

TABLE 5: CALCULATED COVER PERCENTAGE AND FREQUENCY OF SOME PROMINENT SPECIES ON NORTH ASPECT PLOTS

FAMILY	SPECIES	MEAN COVER (PERCENT) 21 yr old	4 yr old	FREQUENCY (NUMBER OF PLOTS)* 21 yr old	4 yr old
Proteaceae	Protea repens (L.) L.	29,5	0	10	0
	P.neriifolia R.Br.	10,5	2,0	7	1
	P.nitida Mill.	4,0	3,0	6	4
	P.acaulos (L.) Reichard	1,5	3,5	3	7
	Leucadendron salignum Berg.	2,5	8,0	4	9
Poaceae	Cymbopogon marginatus (Steud.) Stapf	9,5	10,0	8	10
	Merxmeullera rufa (Nees) Conert	0	0,5	0	1
	Pentaschistis curvifolia (Schrad.) Stapf	0,5	15,0	1	10
	Themeda triandra Forsk.	3,5	0,6	3	2
Restionaceae	Restio gaudichaudianus Kunth	2,5	2,0	5	3
	R.filiformis Poir.	0	11,5	0	10
	R.cuspidatus Thunb.	0,5	5,5	1	7
	R.triticeus Rottb.	7,5	9,5	8	9
	Cannomois virgata (Rottb.) Steud.	1,0	2,5	2	3
	Elegia juncea L.	1,0	3,0	2	5
	Hypodiscus albo-aristatus (Nees) Mast.	1,0	5,75	2	5
	H.willdenowia Mast.	0	1,5	0	3
	Thamnochortus dichotomus (Rottb.) R.Br.	0	6,5	0	5
Cyperaceae	Tetraria cuspidata (Rottb.) C.B.Cl.	1,0	2,0	2	3
	T.ustulata (L.) C.B.Cl.	10,0	5,0	8	6
	Ficinia deusta (Berg.) Levyns	0,5	1,0	1	2
	F.filiformis (Lam.) Schrad.	2,0	4,5	4	8
Ericaceae	Erica hispidula L.	1,5	1,5	3	3
	E.articularis L.	0	1,0	0	2
	E.nudiflora L.	0	0,5	0	1
	E.plukeneti L.	1,5	1,0	3	2
	E.sphaeroidea Pelfer	0,5	1,0	1	2
	E.cerinthoides L.	0	1,5	0	3
	Eremia lotta (Thunb.) D.Don	3,5	0	3	0
Asteraceae	Berkheya herbacea (L.f.) Druce	2,0	2,0	4	4
	Osteospermum junceum Berg.	0	5,0	0	5
	O.tomentosum (L.f.)Norl.	0	2,5	0	5
	Haplocarpha lanata Less.	0,5	2,0	1	4
	Corymbium glabrum L.	0	7,5	0	10
	Euryops abrotanifolius (L.) DC.	0	2,0	0	4
	Helichrysum rutilans (L.) Less.	3,0	0	4	0
	Cazania serrata DC.	0	1,0	0	2
	Erocda imbricata (Lam.) Levyns	0	1,5	0	3
	Gerbera crocea (L.) O.Kuntze	0	3,5	0	6
	Metalasia muricata (L.) R.Br.	0	3,0	0	6
Anacardiaceae	Rhus rosmarinifolia Vahl	2,0	3,5	3	7
	R.angustifolia L.	3,0	0,5	3	1
	R.tomentosa L.	1,5	0	3	0
Ebenaceae	Diospyros glabra (L.) De Winter	5,0	1,0	5	1
Rutaceae	Diosma hirsuta L.	1,5	4,0	3	8
Rubiaceae	Anthospermum ciliare L.	3,0	1,0	5	2
	A.aethiopicum L.	0,5	0	1	0
Adiantaceae	Pellaea pteroides (L.) Prantl	1,0	0	2	0
Rosaceae	Cliffortia cuneata Ait.	16,0	2,5	8	4
	C.ruscifolia L.	10,5	0,5	7	1
Oleaceae	Olea africana Mill.	0,5	0	1	0
Santalaceae	Thesium carinatum A.DC.	0	1,0	0	2
	T.spicatum L.	0	1,0	0	2
	T.densiflorum A.DC.	0	0,5	0	1
	T.strictum Berg.	0	2,0	0	4
Umbelliferae	Centella glabrata L.	2,0	5,0	4	8
Polygalaceae	Muraltia heisteria (L.)DC.	0	3,5	0	6
Geraniaceae	Pelargonium myrrhifolium (L.) Ait.	3,5	0	4	0
Euphorbiaceae	Clutia alaternoides L.	4,0	4,5	5	9
	C.polygonoides L.	0,5	2,5	1	4
Lauraceae	Cassytha ciliolata Nees	6,5	0	4	0
Lamiaceae	Salvia africana-coerulea L.	1,0	0	10	0
Fabaceae	Rafnia capensis (L.) Druce	0	4,5	0	4
Thymelaeaceae	Struthiola ciliata (L.) Lam.	0	2,5	0	5
Lobeliaceae	Lobelia coronopifolia	00	1,5	0	3
Rhamnaceae	Phylica imberbis Berg.	00	1,0	0	2

*Ten plots in each treatment were sampled.

TABLE 6: CALCULATED COVER PERCENTAGE AND FREQUENCY OF SOME PROMINENT SPECIES ON SOUTH ASPECT PLOTS

FAMILY	SPECIES	MEAN COVER (PERCENT) 37 yr old	MEAN COVER (PERCENT) 4 yr old	FREQUENCY (NUMBER OF PLOTS)* 37 yr old	FREQUENCY (NUMBER OF PLOTS)* 4 yr old
Proteaceae	Protea nitida Mill.	0,75	0,375	2	1
	P.neriifolia R.Br.	12,125	0,025	30	1
	P.repens (L.) L.	0,875	0	3	0
	P.acaulos (L.) Reichard	1,875	3,15	15	20
	Leucospermum lineare (Thunb.) R.Br.	0,375	1,525	3	12
	Leucadendron salignum Berg.	2,0	0,875	8	5
	L.gandogeri Schinz ex Gandoger	0,25	0	2	0
	L.spissifolium (Salisb. ex Knight) I.Williams	5,75	10,125	31	33
	Mimetes cucullatus (L.) R.Br.	0,625	0,15	2	2
Poaceae	Cymbopogon marginatus (Steud.) Stapf	3,625	2,875	15	14
	Merxmuellera rufa (Nees) Conert	6,25	8,625	26	33
	M.stricta (Schrad.) Conert	11,0	4,875	35	19
	Pentaschistis curvifolia (Schrad.) Stapf	0,25	1,125	2	9
	P.steudelii (Nees) McClean	0,875	3,25	7	22
	P.juncifolia Stapf.	0	0,875	0	3
	P.colorata (Steud.) Stapf	3,375	7,0	12	16
	Ehrharta ramosa Thunb.	0,625	0,625	2	3
Restionaceae	Restio gaudichaudianus Kunth	5,875	6,375	24	31
	R.filiformis Poir.	2,0	6,125	11	33
	R.cuspidatus Thunb.	0,375	4,25	3	22
	R.triticeus Rottb.	5,375	5,625	11	27
	Elegia juncea L.	3,4	6,25	24	28
	Staberoha cernua (L.f.) Dur. et Shinz	0,75	1,125	5	7
	Hypodiscus albo-aristatus (Nees) Mast.	2,125	4,25	14	23
	Thamnochortus dichotomus (Rottb.) R.Br.	1,0	0,5	5	3
	Cannomois virgata (Rottb.) Steud.	6,0	6,875	12	16
Cyperaceae	Tetraria cuspidata (Rottb.) C.B.Cl.	4,0	8,125	19	26
	T.involucrata (Rottb.) C.B.Cl.	5,0	4,875	20	22
	T.cappillacea (Thunb.) C.B.Cl.	0,625	7,5	3	6
	T.ustulata (L.) C.B.Cl.	2,625	4,0	10	11
	Ficinia deusta (Berg.)Levyns	0,125	0,5	1	4
	F.filiformis (Lam.)Schrad.	2,875	7,125	7	35
	F.grandiflora Arnold (Lam.) Pfeiffer	0,75	0,875	5	6
	F.nigrescens (Schrad.)J.Raynal	1,25	1,625	8	12
Ericaceae	Erica hispidula L.	8,9	3,925	33	25
	E.coccinea L.	3,875	2,5	15	14
	E.articularis L.	0,625	1,25	5	8
	E.mudiflora L.	0,875	0,375	7	2
	E.plukenetii L.	0,875	0,15	4	2
	E.calycina L.	1,4	2,5	11	11
	E.grandiflora L.f.	0,125	0,25	1	2
	E.sphaeroidea Dulfer	0,9	0,125	6	1
	E.coriathoides L.	1,75	1,15	14	10
Asteraceae	Berkheya herbacea (L.f.) Druce	3,625	5,125	29	34
	Helichrysum crispum (L.) D.Don.	1,75	0,75	7	6
	H.felinum Less.	2,0	0,125	12	1
	H.rotundifolium (Thunb.) Less.	0,875	0,125	6	1
	Osteospermum junceum Berg.	0,125	1,625	1	8
	O.tomentosum (L.f.) Norl.	1,875	2,375	11	14
	Stoebe plumosa Thunb.	1,275	0,75	9	6
	S.capitata Berg.	0,625	2,875	5	15
	Haplocarpha lanata Less.	1,0	3,25	8	26
	Leontonyx spathulatus Less.	0,25	1,5	2	12
	Gerbera asplenifolia Spreng.	0,375	1,625	3	10
	Corymbium glabrum L.	1,25	8,5	8	28
	C.villosum L.f.	2,625	3,125	9	13
	Senecio pinifolius (L.) Lam.	0,5	1,25	4	9
	Ursinia crithmoides (Berg.) Poir.	0	0,425	0	4
	Gnaphalium undulatum L.	0,5	1,625	3	13
	Pteronia camphorata L.	1,0	0	2	0
Rosaceae	Cliffortia ruscifolia L.	0,625	0	2	0
	C.cuneata Ait.	3,15	0,025	12	1
Bruniaceae	Brunia nodiflora L.	9,375	5,875	26	15
Cupressaceae	Widdringtonia nodiflora (L.) Powrie	3,15	0,15	11	2
Flacourtiaceae	Kiggelaria africana L.	1,55	0	9	0
Celastraceae	Maytenus oleoides (Lam.) Loes.	1,025	0	9	0
	M.acuminatus (L.f.) Loes.	0,025	0	1	0
Oleaceae	Olea africana Mill.	0,25	0	1	0
Anacardiaceae	Rhus angustifolia L.	2,325	0,025	15	1
	R.rosmarinifolia Vahl	1,5	1,625	7	9
	R.tomentosa L.	0,4	0	4	0
Myrsinaceae	Myrsine africana L.	0,875	0	6	0
	Rapanea melanophloeos (L.) Mez	0,025	0	1	0
Fabaceae	Rafnia capensis (L.) Druce	0	3,375	0	11
Euphorbiaceae	Clutia alaternoides L.	0,625	0,125	3	1
Penaeaceae	Penaea mucronata L.	3,25	0	15	0
Rutaceae	Diosma hirsuta L.	6,875	3,375	31	22
Santalaceae	Thesium spicatum L.	0	0,25	0	2
	T.densiflorum A.DC.	0	0,25	0	2
	T.strictum Berg.	0	0,25	0	2

*Forty plots in each treatment were sampled

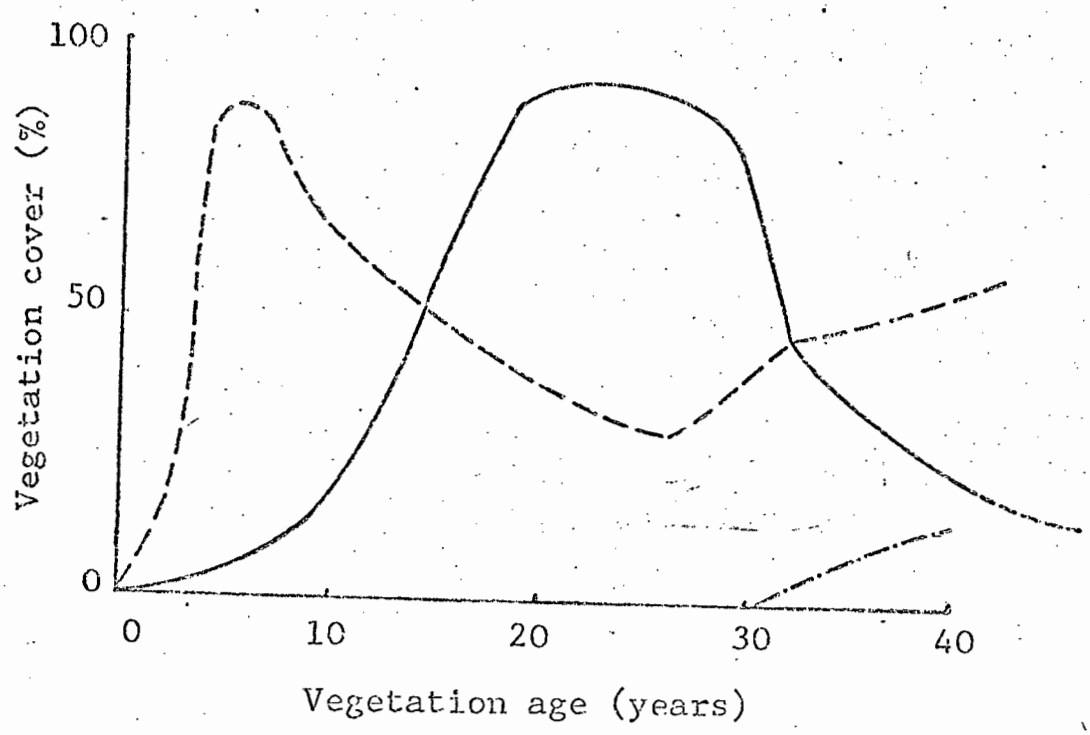


Figure 5: The relationship between post-fire age and vegetation cover. The lines represent large seed-reproducing shrubs (————), graminoid and herbaceous plants (– – – –) and trees (—·—·—).

periods.

The mean heights of some species (given in Table 3) are included to give an indication of how these species react to differing fire frequencies. Some larger shrubs and trees (for example Brunia nodiflora and Widdringtonia nodiflora) manage to survive fires by resprouting from the bases but are severely reduced in height; others, such as Protea nitida, resprout from epicormic buds and are not as severely affected. Some shrubs show a drop in height in the old vegetation due to partial dieback with increasing age (e.g. Protea neriifolia), while some continue to increase in height (e.g. Cliffortia ruscifolia). Grasses, restios and other herbs do not show much difference in height for different vegetation ages, although grasses such as Pentaschistis collorata and Merxmeullera stricta are significantly taller in four year old vegetation when compared to 37 year old vegetation at the 5 percent level of significance. Large effects of fire regime on plant height appear to be limited to the larger shrubs.

The mean number of species per plot (Table 4) is significantly lower in 21 year old vegetation when compared to the other age classes, which do not differ significantly from each other. This must be interpreted together with information presented in Tables 5 and 6. Mature 21 year old vegetation is dominated by large shrubs with smaller plants, noticeably

the Restionaceae and Asteraceae, being of far less importance resulting in a relatively species-poor vegetation. The increase in species richness in much older vegetation can probably be ascribed to the recovery of understorey plant species due to mortality among dominant proteaceous shrubs, as well as the increased importance of trees and other shrubs. A direct comparison of the 37 year old with 21 year old vegetation is not valid due to drastic differences in aspect and geology resulting in differences in the plant communities present, and this may account for at least some of the increase in species diversity as well.

CONCLUSION

The assumption upon which this study is based, namely that certain environmental combinations determine the climax vegetation, may be open to objection. Mistakes or ommissions of important variables in defining environmental subgroups could possibly lead to erroneous interpretation of results. However, certain factors justify this approach. The areas studied are in very close proximity to each other and therefore do not vary climatically. In addition, a representative range of aspect, altitude and soil types were sampled. An alternative approach would be to use a permanent plot study. This technique is being applied elsewhere (see van Wilgen and Kruger 1980) but due to long burning rotations of up to 12 years being tested, urgently needed results will be outstand-

not seen at higher altitudes on shallower soils or on sandstone soils.

In conclusion, it can be stated that the apparent optimum fire frequencies necessary to maintain healthy fynbos at Jonkershoek would be about once in 15 to 25 years. Short burning rotations result in the elimination of certain species, most notably the longer-lived seed regenerating shrubs. Long protection from fire results in the degeneration of the vegetation with accompanying buildup of high fuel levels and a reduction of reproductive potential. Further development to forest would be on limited areas only.

Similar investigations should be carried out in other areas of fynbos to determine whether conclusions drawn here are valid in areas of lower rainfall or differing geology.

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PART IV

GENERAL CONCLUSIONS

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4.1 SURVEY METHODS USED

The study was undertaken in order to obtain data on the effects of fire frequency on fynbos in a relatively short space of time. Ideally such a study should be undertaken on permanent plots (see van Wilgen and Kruger 1980), but this is of course an extremely long term undertaking while data are presently urgently required. This examination of adjacent areas has provided some data on the effects of fire frequency. This information should be interpreted with the problems involved in such surveys in mind.

One of the major difficulties facing a field ecologist working in fynbos is that of accurate species identification in the field. This is not only due to the vast number of species encountered (see Wicht 1945, Acocks 1953, Werger et al 1972, Boucher 1972), but also because the taxonomic status of many groups is poor and many species are easily confused in the vegetative state. There does not seem to be any easy answer to this problem. It may be possible to study certain common and easily recognizable species; the response of such species (to fire or whatever treatment is being tested), could be used to extrapolate the effects on the vegetation as a whole. Using this approach, the selection of representative species poses a problem. Another approach would be to use all species classified into life forms instead of species,

as was done in part of this study, but this technique may mask the response of individual species to a given treatment.

A further problem in a survey of the type reported here, is that it presupposes that the same vegetation will exist on adjacent sites with the same soil type, geology and fire regime. This is not always true, especially so in fynbos, and for this reason the results presented here can only be regarded as broad trends. Subtle differences in vegetation have probably remained undetected. Nevertheless, the data obtained is of value in illuminating some of the broader effects of fire regime. This will be discussed later.

Lastly, it should be emphasized that similar studies should be undertaken in other fynbos zones, such as in arid fynbos in the Cedarberg. The Jonkershoek area has a high rainfall when compared to many other fynbos areas and this, combined with geological factors, must be taken into account when extrapolating these results to other areas.

4.2 FIRE AND SPECIES LIFE CYCLES

The hypothesis that certain species such as fire lilies (Levyns 1971), the marsh rose (*Orothamnus zehyeri*)(van der Merwe 1975) and the blushing bride (*Serruria florida*) (Taylor 1972) need frequent fire to complete their life cycles has been questioned by Moll et al (1980). This study has revealed that

Protea neriifolia at Jonkershoek has a life span of about 30 years whereafter the plants die in large numbers. Similar observations have been made on Leucadendron laureolum in the Kogelberg. Some germination does occur under such senescent stands, but this is on a very limited scale. On the other hand, fire in mature stands of Protea neriifolia is followed by mortality of adults and large scale germination of seed. Work in the Swartberg by Bond (1980) has shown that burns in senescent stands of vegetation (45 to 50 years old) dominated by Proteaceae (Protea repens, P.eximia, P.punctata and Leucadendron spp.) results in very poor seed germination when compared to burnt mature (18-20 year old) vegetation. He postulates that this is due to a reduction in viability in canopy and soil stored seed, a decline in seed production and continual seed predation. The role of nutrients and chemical germination inhibitors (if any) in fynbos is not understood and data on these aspects are lacking. Any hypothesis on these can therefore only be speculation at this stage. It would, therefore, appear that fire is necessary for the successful completion of life cycles of Protea neriifolia and others, and that this fire should take place at the mature stage.

The life cycle of Widdringtonia nodiflora is less easily explained. Widdringtonia resprouts following fire, and has remained a vigourous and dominant component of the vegetation

for 37 years without showing any signs of senescence. I know of no case where seedlings of this species have been observed immediately following fire, but seedlings have been found in the old stands of fynbos in Langrivier. The fact that resprouting species do rarely produce seedlings in older stands of fire-adapted vegetation is discussed by Zedler (1977). This is the case for Quercus dumosa in Californian chaparral, and he postulates that evolutionary constraints may have made it impossible for this species to evolve the proper combination of fruiting phenology, seed behaviour, predator protection, dispersal and reproductive effort that are required to successfully exploit the post-fire environment. The advantages of reseeding instead of resprouting may be genetic, in other words reseeding following fire would mean a greater number of sexual generations, resulting in a greater frequency of natural selection (Wells 1969). This hypothesis is questioned by Keeley (1977) who points out that nonsprouters do not appear to have any obvious advantage over sprouters, which are very successful components of Californian chaparral. The fact that seeders and sprouters coexist shows the weakness of the hypothesis. Widdringtonia would appear to be a successful resprouter with some relic reseeding occurring.

4.3 EFFECTS OF SHORT ROTATION BURNING

Continual short rotation burning (6 to 8 years) is detrimental

to fynbos. The major effect of frequent burning is the elimination of larger seed reproducing shrubs, but large resprouting species such as Widdringtonia nodiflora are reduced in height and frequency and may also eventually dissappear. The conclusion that frequent burning drastically reduces the biomass is mainly due to this effect. Normal young fynbos is usually dominated by hemicryptophytes and this is true of the vegetation sampled in this study. The higher biomass of older stands is mainly due to large shrubs. The seedlings of these shrubs are absent in frequently burnt fynbos, and therefore it would appear that biomass will stay at a lower level, unless immigration of larger shrubs occurs. This will depend on the size of the frequently burnt area and on the patterns of seed dispersal for the species concerned (seed dispersal patterns are little understood in the fynbos).

Species diversity is higher in young fynbos, and many species have disappeared or are far less common in mature fynbos. However, these species reappear again after a burn in mature fynbos (van der Merwe 1966) and therefore this cannot be an argument to support short rotation burning.

Short rotation burning does not have as drastic an effect on fynbos as may have been expected (van Wilgen and Kruger 1980). Short rotation burning may be used in some cases as a manage-

ment tool (for example in the control of exotic weeds) and this is probably permissible. The only question unanswered here is that of recolonization by large seed regenerating shrubs. However, these shrubs are in many cases totally replaced by invasive weeds such as Hakea sericea, and elimination of such weeds should take priority.

4.4 EFFECTS OF DEFERRED BURNING

Deferred burning (for longer than 30 years) at Jonkershoek results in senescence of the vegetation, a reduction in total live biomass and an enormous buildup of litter. The appearance of trees on some sites in Langrivier and in other areas of fynbos, for example Orange Kloof on the Cape Peninsula (McKenzie et al 1977), may indicate that limited areas are seral to forest. Fire in such areas may be detrimental i.e. it may prevent the development of forests. On the other hand, however, fire is apparently necessary for the maintenance of healthy fynbos not seral to forest, as the majority of Langrivier would appear to be. The buildup of fuel in very old fynbos will probably cause fires of very high intensities when they do burn. High intensity burns may cause higher mortality among certain resprouting species. This, coupled with the reduction in reproductive potential, would make a long rotation burning regime (greater than 30 years in Jonkershoek) undesirable. High intensity burns in fynbos areas close to human settlement (for example Hermanus)

have resulted in extensive damage to housing and property and this is also an argument (although not ecological), against deferred burning in such areas.

Keeley (1977) argues for long intervals (up to 100 years) between fires in Californian chaparral. His hypothesis maintains that obligate seeders depend on building up of seed pools, and that shorter periods between fires are of greater advantage to resprouting species. Occasional extended periods of time would have worked to favour seeders over sprouters. The sprouters would have suffered higher mortality in the subsequent burn, and large seed pools would have been available. This does not seem likely in fynbos, however, especially in view of the work done by Bond (1980).

4.5 FIRE REGIME AT JONKERSHOEK

The fire frequency required to maintain healthy fynbos at Jonkershoek would appear to be anything between 15 and 25 years. In the limited areas which may be seral to forest, fire should be excluded so that the further development of the stands can be followed. Should a true forest or scrub forest develop, the vegetation on these limited sites would differ from the inflammable fynbos, and may be able to withstand periodic fires around it. For the majority of the area, however, fire is apparently necessary to maintain healthy vegetation.

Fire frequency in fynbos may have varied anything from once in six to once in 40 years under natural fire regimes in the past (Kruger, in Day et al 1979). The idea that longer intervals between fires may be necessary to maintain the flora, is reflected in the gradual lengthening of suggested rotations of prescribed burns in fynbos. These have gone from eight years in 1968 to recommendations for a 15 year rotation in 1979 (Kruger and Lamb 1979), and the need for flexibility has always been stressed. This has been discussed under the general introduction. Fire frequency at Jonkershoek should be varied at random between the limits suggested, as this would probably simulate a more natural situation than a fixed and inflexible rotation. Burning rotations for other areas of fynbos should be separately determined, and based on observations on the flora of the particular area.

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