The conservation of southern African terrestrial ecosystems, with special reference to the role of fire and the control of invasive alien plants

by

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Thesis submitted in partial fulfilment of the requirements for the degree of

Doctor of Science

In the Department of Botany and Zoology, Stellenbosch University

September 2008

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Selected papers on the ecology and management of invasive alien plants

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Part III. Full list of published papers, and analysis of citations.

Introduction

Detailed list of publications

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Preface

The requirements for a D.Sc. degree at the University of Stellenbosch are that a candidate shall have performed "advanced, original research or learned work in the field of the natural sciences"; and that the candidate shall submit "original work of a high standard that has already been published, on a central theme, making a contribution of substance and of high quality to the enrichment of knowledge in the field of the natural sciences".

My work has been in the field of applied ecology. It has had a particular emphasis on the ecological effects of fire, the management of fires in protected areas, and the ecology and management of invasive alien plants. In practice, ecosystem management is not always easily compartmentalized, and this is true for the management of fires and invasive alien plants; the two phenomena interact strongly in many areas, and cannot always be considered in isolation. My work thus has a common theme around ecosystem management. I have not pursued an academic career, but rather a career that seeks to have practical impact through research and the application of research results in practice. This thesis provides the background to my work, and is in three parts.

Part I is in the form of an overview paper. In this paper, I have attempted to review, briefly, the fields of research in which I have been active. The paper provides a perspective, based on my own research and that of others, on the state of fire management, and the management of invasive alien plants, in conserved areas in South Africa.

Part II provides selected examples of published papers, intended to provide a sample of my work. I have chosen 15 papers, five in each of the fields that made up the bulk of my research: (i) fire ecology and management in fynbos ecosystems; (ii) fire ecology and management in savanna ecosystems; and (iii) the ecology and management of invasive alien plants. The papers were chosen as illustrative of the work done over 25 years (from 1982 to 2007). The papers have been selected to illustrate both the results of field research, as well as aspects of the application of research results in practice.

Part III lists the 100 published works in these three fields on which my contribution is to be judged. The list is in four parts, which includes the three fields listed above, plus another field to cover publications that address general aspects of fire ecology that are not specific to either fynbos or savanna ecosystems. The list includes books, papers in learned journals, chapters in scientific books, substantive published research reports, and a small number of semi-popular scientific articles. Many of these publications have been co-authored, and for each of these I have indicated my level of involvement. Where the paper formed part of a submission for another degree, this is also noted. I have also included the number of times that the publication had been cited in the scientific literature as on 15 March 2008, and provided a brief analysis of the contribution in terms of standard bibliometric measures.

Acknowledgements

I have been lucky to share a career in applied ecological research with a large number of friends and colleagues over the past three decades. Each of the 109 co-authors of the papers listed in this thesis have helped me along the way, and it is risky to single any one of them out. Nonetheless, a few individuals did have had a significant impact on my career in a number of ways, and they deserve special mention.

Firstly, I must thank my teachers, the late Professors Christiaan Wicht and Rudolf Bigalke, who introduced me to the science of ecology and fed my hungry mind with fascinating facts and ideas. After graduation, I was fortunate enough in my first professional position to be placed under the guidance of Dr Fred Kruger. Over the next 15 years, it was Fred who above all others provided me with the guidance, assistance and leadership that made a critical difference to me (and many of my colleagues). I have also been fortunate to have worked with a number of dedicated professional ecologists who have had a marked influence on my thinking. Professor William Bond, arguably Africa's leading contemporary fire ecologist, has been an inspiration to me throughout my working career. Professor Dave Richardson has always collaborated enthusiastically on many projects to do with invasive alien species, sharing his wide knowledge with me and many others in an unusually generous fashion. Dr Harry Biggs, with his remarkable capacity for innovation, assistance and networking, has had a huge beneficial impact on my research in savanna ecosystems. My work on invasive species benefited enormously from my association with the Working for Water programme. This would not have been possible had it not been for the dedication, enthusiasm, and astounding work capacity of Dr Guy Preston. Professor Cliff Moran and Dr Helmuth Zimmermann introduced me to the science of weed biological control, and have over the past decade been extraordinarily generous with their time and with imparting their knowledge.

I would also like to thank my employers, initially the South African Forestry Research Institute (SAFRI), and latterly the Council for Scientific and Industrial Research (CSIR), for creating the environment in which I was able to develop. SAFRI funded my post-graduate education and a number of foreign study trips, and gave me access to exciting research opportunities. The CSIR, with its emphasis on the use of research and understanding to generate impact, provided opportunities for me to explore practical ways for using knowledge and experience in a range of implementation projects.

Last (but of course far from least) I would like to thank my life partner Jane, for her support over the past 30 years. Jane has shared my keen interest in nature and its conservation, and has unselfishly provided the stability I needed to get on with my work. Without her support, I doubt whether any of this would have been possible.

Part I.

The evolution of fire and invasive alien plant management practices in South African conservation areas: The role of research.

PART 1. The evolution of fire and invasive alien plant management practices in South African conservation areas: The role of research.

1.1 Introduction

The conservation of nature has always been a passion of mine. According to Edward O. Wilson, such feelings (termed "biophilia") are typical of the connections that human beings subconsciously seek with the rest of life (Wilson 1985). Few people, though, have been privileged enough to pursue a career in this line of work. Because I have always been interested in plants, animals, ecosystems and their collective conservation, I have chosen to do research in this field, and I have attempted to use the results of this research to improve ecosystem management practices. The original opportunities that came my way centred on the management of unique and incredibly diverse fynbos ecosystems of the Western and Eastern Cape provinces in South Africa. In these ecosystems, the two issues that managers debated most were fire and invasive alien plants. Both fire and invasion are important processes that impact on ecosystem integrity, and both provide fertile ground for research, experimentation and the development of science-based management interventions. Not surprisingly, then, these two processes have been at the core of my career as an applied ecologist, as it expanded from its fynbos beginnings to embrace wider and different ecosystems.

Fire is an extremely important ecosystem process. It consumes enormous quantities of plant material in many of the world's ecosystems, including the grasslands, savannas and fynbos shrublands of southern Africa. Fire shapes the contemporary vegetation patterns that clothe our landscapes, and has done so for millions of years (Bond, Woodward and Midgley 2005; Bond and Keeley 2005). As a result, ecosystems are often not only fire-adapted, but also fire-dependant. There is much evidence that plants in fire-prone environments are well adapted to surviving fires, and that in many cases they need fires to survive. Examples include the widespread ability to sprout after fires; serotiny; smoke-stimulated germination; fire-stimulated flowering, and the evolution of flammable properties. Besides their ecological importance, fires can and do cause damage to the crops, plantations and buildings that encroach on natural ecosystems, and they can threaten human life. Human interference can also change the timing and frequency of fires, with possible detrimental consequences for conservation. Because of the ecological and economic importance of fires, managers of fire-prone ecosystems seek to influence or even control the occurrence, timing and extent of fires. It is therefore also important that we develop an understanding of how and why ecosystems burn, as management interventions can only be successful if the link between such interventions and their likely outcomes can be made.

The invasion of ecosystems by alien species is also an increasingly important aspect of ecology. Up until the late 19th century, mountains, large rivers, deserts and oceans provided formidable barriers to the movement and migration of species. In today's rapidly globalising world, however, the ongoing and increasing human redistribution of species to support agriculture, forestry, horticulture and recreation supplies a continuous pool of species from which invasive aliens are recruited. Invasive alien species can come to dominate natural ecosystems, displacing native biodiversity, altering key processes and often reducing the levels of services that are derived from ecosystems. In fire-prone ecosystems, successful alien species are always fire-adapted themselves, and they come to dominate as a result of a combination of superior growth rates and pre-adaptation to frequent fires. In such ecosystems, managers wishing to control such species have to develop a sound understanding of their ecology in relation to fire, in order to develop effective control interventions.

In this review paper, I have attempted to trace the evolution of fire management policies, and related invasive alien plant management policies in South African conservation areas in the 20th century and beyond. My review is based mainly on the areas where I have experience (fynbos and savanna ecosystems). Over the years, management policies have changed in response to a range of factors, including financial constraints, changing political dispensations, changing ecological paradigms, increased levels of understanding arising from research, and perceptions based on a range of factors. My purpose is to examine the role that science and research has played in informing these changes. This overview has three main sections. The first reviews the evolution of fire management approaches in fynbos ecosystems. The second provides a similar review of the situation in regarding the management of invasive alien plants, again with a focus on fynbos ecosystems. Finally, the third part addresses the evolution of fire management approaches in savanna ecosystems. Against this background, I conclude by sketching the main challenges facing ecosystem managers today.

1.2 Fire management in fynbos ecosystems

1.2.1 The importance of fynbos

Fynbos is an indigenous word that describes the shrubland vegetation typical of the nutrient-poor mountain and lowland areas of the Western and Eastern Cape provinces in South Africa (Figure 1.1). Fynbos is recognised as a biome, and fynbos vegetation has high levels of endemism, with over 6200 (69%) of its 9000 plus species being endemic to the biome (Bond & Goldblatt 1984; Goldblatt & Manning 2002). High levels of endemism have led to the biome being regarded as one of the world's six floral kingdoms (Takhtajan 1969). The fact that the Cape Floristic Kingdom covers only 90 000 km^2 also makes it the smallest such kingdom by a large margin. Several of the major nature reserves in the biome were recently elevated to World Heritage Site status in recognition of their global importance as a centre of endemism. Fynbos vegetation is both fire-prone and fire-adapted, and managers of these ecosystems use fire to achieve stated goals. In this section, I briefly sketch of the history of research and its influence on the evolution of fire management in the biome.

1.2.2 Early understanding of the role of fire, and fire policies prior to prescribed burning

Early botanists generally regarded fires as a destructive force in fynbos vegetation, and agitated for protection from fire (Levyns 1924; Pillans 1924; Marloth 1924; Compton 1926, 1934). There were also concerns about the possible detrimental effects of fire on water supplies. For example, a 1926 Drought Investigation Commission expressed the opinion that veld burning was harmful, especially in important watershed areas, and they recommended that such areas should be protected from both grazing and fire (Bands 1977). Thus, for much of the period between the 1920s and 1968, official policy was to protect fynbos areas from fire. Under the Soil Conservation Act of 1946, Fire Protection Committees were established with a view to drawing up fire protection plans, establishing firebreaks and access paths, fighting veldfires, and exercising control over deliberate burning where it was agreed that such burning was absolutely necessary (Bands 1977).

Figure 1.1. Typical fynbos vegetation in the Kogelberg Nature Reserve, Western Cape.

Against this background, there was also growing evidence that fire was not necessarily always detrimental (Phillips 1930), and later that fire was probably necessary. A leading ecologist at the time, Prof. C.L. Wicht (Figure 1.2) proposed in 1945 that "If grazing after burning can be prevented …, this treatment (fire) should have a definite place in any plan for preserving the sclerophyll scrub" (Wicht 1945). Jordaan (1949) used a study of *Protea repens* to demonstrate that fires in summer, at intervals of at least 8 years, were "safe", and pointed out that the principle of safe fire frequencies would almost certainly apply to other fynbos plant species. He later extended the notion of safe and unsafe fire periods to fire seasons as well (Jordaan 1965). A later study (van der Merwe 1966) demonstrated that all of the 448 species that he identified in the Jonkershoek mountains near Stellenbosch were able to survive fire, either by sprouting or by regeneration from seed. However, the realization that fire was not only harmless, but actually necessary was brought home by the spectacular failure of fire protection policies to prevent the decline to apparent virtual extinction of two rare and charismatic plants (the marsh rose *Orothamnus zeyheri* and the blushing bride *Serruria florida*). Equally spectacular was the rapid recovery of these populations following unplanned fires, which stimulated soil-stored seed reserves to regenerate *en masse* (Boucher 1981; Voigts 1982; Worth & van Wilgen 1988). These realizations, combined with observations that protection of fynbos from fire could lead to declines in streamflow (van der Zel & Kruger 1975) led to the introduction of a policy of prescribed burning in 1968 (Bands 1977).

Figure 1.2. Prof. C.L. Wicht, who made the first serious suggestion of prescribed burning as a management option in fynbos vegetation in 1945.

1.2.3 The introduction of prescribed burning

A memorandum accepting prescribed burning as a management practice in the Department of Forestry was issued in 1968, and the first prescribed burn under this policy was conducted in the same year to stimulate germination in a senescing population of *Orothamnus zeyheri* (van Wilgen, Richardson & Seydack 1994). The introduction of prescribed burning in fynbos catchment areas had, as a primary objective, "the maintenance of maximum permanent sustained flow of silt-free water" (Bands 1977). The rationale behind the change from fire protection to a policy of prescribed burning lay in the assumption that maintaining a healthy cover of fynbos vegetation by regular burning was the best way of protecting the soil, and thus ensuring a sustained yield of water from catchment areas (Kruger 1977a). On public land, the goal of nature conservation enjoyed equal status with the goals of water and soil conservation (Bands 1977).

Policy documents and reviews written at the time (for example van Wilgen 1984b) indicate that the introduction of a prescribed burning programme had three clear ecological aims. The first was to "rejuvenate the vegetation" by removing moribund plants, and stimulating seed release and germination. Although never stated in such terms, this goal clearly implied that if the vegetation was not actively burnt, fires would not occur frequently enough, and local extinctions would occur as populations of fire-dependent species reached senescence. The second goal was to reduce the number and extent of unwanted and harmful wildfires. This was to be achieved through the creation of a mosaic of vegetation of different post-fire ages, thus breaking up large, continuous accumulations of dead, dry fuel. Again, an un-stated assumption behind this goal was that large, harmful wildfires are the result of an accumulation of fuel, and were only likely to occur in large, continuous tracts of vegetation that had not been burnt for some considerable time. The third aim of prescribed burning was never actually stated as an aim. It involved the integration of fire management and operations aimed at the control of invasive alien trees and shrubs (mainly pines and hakeas).

Research to support fire management

In order to develop a better understanding of fynbos ecology and management, the Department of Forestry initiated a research programme in the early 1970s, under the leadership of Fred Kruger. A second initiative, the Fynbos Biome Project, was established in 1977, under the guidance of Brian Huntley of the CSIR, with the purpose of funding and co-ordinating research (Huntley 1987). These two undertakings were responsible for a rapid expansion in the understanding of fynbos ecology, and the role of fire. New understanding was gained regarding the ecological effects of fire (Kruger & Bigalke 1984; van Wilgen *et al.* 1992); of how fire protection led to vegetation senescence and poor regeneration after long fire-free intervals (Bond 1980; van Wilgen 1982); and of how to define acceptable as well as unacceptable seasons for burning (Bond, Vlok & Viviers 1984; Bond 1984; van Wilgen & Viviers 1985). On the termination of the Fynbos Biome Project in 1990 (Cowling 1992), it was possible to provide fairly detailed prescriptions regarding the management of fynbos by means of prescribed burning (Figure 1.3). These included acceptable inter-fire periods, seasons, and weather conditions under which fires would achieve the desired ecological outcomes, and systems for their management (van Wilgen, Bond & Richardson 1992; Richardson *et al.* 1994; Juhnke & Fuggle 1987).

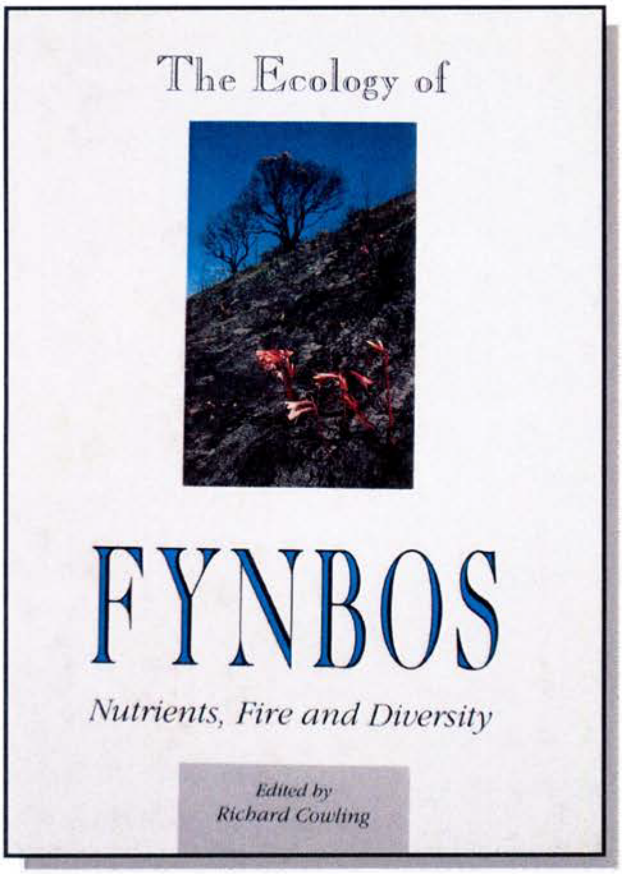

Figure 1.3. The termination of the Fynbos Biome Project was marked by the publication of a synthesis volume (Cowling 1992), compiled by a number of authors who had been active in the project. It contains detailed guidelines for the use of fire in the management of fynbos ecosystems (van Wilgen, Bond & Richardson 1992).

Box 1.1. Quotable quotes: Fynbos

The quotes below reflect the changing attitudes towards fire and its role in the ecology and conservation of fynbos ecosystems in the 20th century. These changes resulted largely from increased understanding provided by ongoing research.

"*the burning of the scrub on the Cape mountains is, in the long run, entirely destructive and absolutely indefensible*" (Compton 1924).

"*it is doubtful whether the evidence is available at present to judge the full effects of burning*" (Wicht 1945).

"*In spite of major gaps in knowledge, … a coherent account of … the ecological role of fire can be presented*" (Kruger & Bigalke 1984).

"*The application of fire is the major management practice in fynbos biome ecosystems*" (van Wilgen, Bond & Richardson 1992).

"*the very existence of fynbos plants can be attributed to the increasing importance of fire over the past few million years. Without fire, fynbos plants perish, leaving no offspring and confounding the biological imperative to reproduce*" (Cowling & Richardson 1995).

1.2.4 The practical implementation of prescribed burning

During the 1970s, managers of fynbos catchments and conservation areas made good progress with the implementation of a program of prescribed burning. Conservation areas were divided into large "compartments" and these were burnt on a planned frequency of 12 – 15 years. Compartment size ranged from 500 – 1000 ha, and sizes were determined by the availability of suitable (natural of artificial) firebreaks, and the area in which a burning operation could be completed in a single day. By 1981, an average of 40 such burns were carried out in the fynbos biome per year (van Wilgen, Everson & Trollope 1990).

However, a steady decline in the areas subjected to prescribed burns followed policy directives that restricted prescribed burning to the late summer/early autumn period. This arose from research that suggested that burning in spring would have detrimental effects on the vegetation (Bond, Vlok & Viviers 1984; van Wilgen & Viviers 1985), thus eliminating the possibility of burning in September and October, the months with the safest weather for burning (Figure 1.4) (van Wilgen & Richardson 1985; van Wilgen, Everson & Trollope 1990). This change in policy resulted in a decline of 75% in the area burnt in prescribed burns by 1988 (van Wilgen, Everson & Trollope 1990).

There were other factors that constrained the application of prescribed burns in fynbos ecosystems in the late 1980s. Most important among these were declining funding, the need to incorporate the pre-fire treatment of invasive alien plants, and growing concerns about the safety of prescribed burning and legal liability in cases where prescribed burns escaped. In response, several new approaches were proposed, varying in the degree of interference in fire regimes from prescribed burning (where all fires were to be management fires) through to "natural burning zones", where no prescribed burning was to be done, and natural (lightning-ignited) fires were allowed to burn (Seydack 1992). In addition, an increasing focus on the conservation of biodiversity led to calls for variation in fire regimes. The rationale behind this was that different species would be favoured by fires in different seasons, or at different intervals, or at particular intensities. It was also recognised that the effects of management on biodiversity would be difficult to monitor, but that variation on fire regimes could be more easily monitored, and could thus serve as a surrogate measure for ensuring the maintenance of biodiversity (van Wilgen, Richardson & Seydack 1994). The approach also recognised the need to incorporate inevitable wildfires into planning and monitoring (van Wilgen, Everson & Trollope 1990), and was formalised in the development of a GIS-based system for the management and monitoring of fires in fynbos areas (Richardson *et al.* 1994).

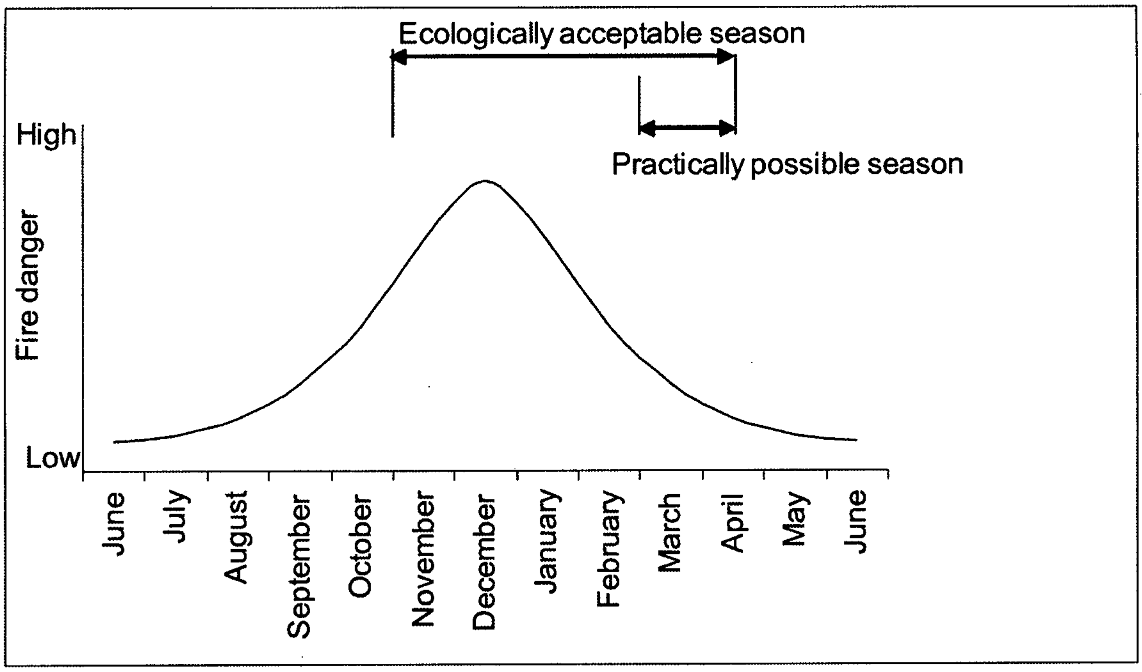

Figure 1.4. The ecologically acceptable season for fire in the fynbos biome co-occurs with the occurrence of high and moderate fire danger. Fires during the season of low fire danger are regarded as ecologically unacceptable. In practical terms, managers are restricted to a narrow window of opportunity for prescribed burning, when the ecologically acceptable season for burning co-occurs with moderate fire danger.

1.2.5 Effects of prescribed burning on fynbos fire regimes

One of the stated aims of prescribed burning was to reduce the number and extent of wildfires, by reducing fuel loads and creating a mosaic of vegetation patches of varying post-fire age. Whether or not this goal had been achieved was first examined in the Cedarberg, by comparing fire records collected between 1956 and 1972 (when fire suppression was practiced) with records form 1973 – 1986 (when prescribed burning was practiced) (Brown *et al.* 1991). During the period following the introduction of prescribed burns, the number of wildfires decreased, but the mean size of wildfires doubled. In fact, three of the four largest fires on record (> 10 000 ha) occurred during the prescribed burning era. It was also established that extensive fires were possible when the vegetation had reached a post-fire age of 5 years, and were thus not reliant on large, continuous areas of older vegetation. This study concluded that "the effects of prescribed burning (on wildfire occurrence) are not yet evident", although it could have been stated otherwise to reflect the lack of any evidence to support the hypothesis that prescribed burning will reduce wildfire occurrence.

A similar detailed analysis of a 70-year fire record was recently completed for the Swartberg Mountain Range (Seydack, Bekker & Marshall 2007). In this area, a succession of fire management policies focused on grazing, then fire control, and then biodiversity conservation. It was found that the extent of burning followed climatic cycles, that fires occurred more extensively during periods of high temperatures and summer rainfall, and were largely unaffected by the absence or presence of fire control measures.

The latest comprehensive analysis of fire records from 10 large nature reserves in the Western Cape over the past 40 – 50 years (Forsyth & van Wilgen 2007; 2008) showed that modern fynbos fire regimes are in fact dominated by wildfires, which account for > 80% of the total area burnt, and that prescribed burning has played a relatively small role in contributing to these modern fire regimes. In addition, fynbos fire regimes are currently dominated by *a few* large wilfires. For example, of the 150 fires on record in the Cedarberg between 1945 and 2006, the 10 largest burnt 66% of the total area burnt. In addition, the occurrence of large wildfires appears to be increasing, with very large fires (> 5000 ha) burning 75% of the total area burnt between 1990 and 2006, compared to only 48% of the area between 1945 and 1969 (Forsyth & van Wilgen 2007). Finally, some concern has been expressed that, in some areas, fires are becoming more frequent. For example, the area subjected to short (< six years) intervals between fires covered > 16% of the Table Mountain National Park in the last two decades, compared to ~ 4% in the previous two decades (Forsyth & van Wilgen 2008).

The above findings prompt the following conclusions:

- The implicit assumption that prescribed burning would be necessary to prevent vegetation senescence and loss of species is not supported by evidence arising from recent analyses. It appears that prescribed burning plays a minor role in modern fire regimes, and that wildfires alone should provide sufficient opportunities for regeneration and “rejuvenation”.

- The assumption that prescribed burning would reduce and fragment fuel loads, leading to a reduction in the number and extent of wildfires, is also not supported by recent evidence. It appears that reductions in fuel do not consistently prevent the spread of wildfires, which can burn through 5 year post-fire vegetation provided that hot, dry, and windy conditions prevail.

- It appears possible that the incidence of fire is increasing in some areas as a result of increasing human population densities and access, leading to increased opportunities for ignitions to take place (Forsyth & van Wilgen, 2008). In other words, fynbos fires are not fuel-dependent (except when the vegetation is very young), but rather dependent on the co-occurrence of weather conducive to wildfires, combined with a source of ignition.

Similar conclusions are being drawn regarding fire and prescribed burning in California. For example, Keeley, Fotheringham & Morais (1999) demonstrated that fire frequency and human population density were correlated in Californian chaparral shrublands, and they concluded that the expansion of the urban-wildland interface would be a key factor influencing the degree of destruction (to houses) that could be expected. It was also shown that there was not (as commonly assumed) a strong relationship between the post-fire age of chaparral and the probability of fire. Rather, the risk of fire increased only moderately with time since the last fire (Moritz *et al.* 2004). These authors called for a serious re-evaluation of fire management and policy, which in California is based on fuel reduction through prescribed burning.

1.2.6 Current ecological understanding of the role of fire in fynbos

Current understanding of the role of fire in fynbos ecology is relatively robust. Most species in fynbos vegetation are resilient to a fairly wide range of fire return intervals. For example, van Wilgen & Forsyth (1992) established the regeneration strategies of 210 co-occurring fynbos species; of these, most were able to resprout after fire, and 200 out of the 210 species could survive fire return intervals of between 10 and 40 years. Only 29 species were classified as obligate seeders: species that have their growth cycle terminated prematurely by fire, and are unable to sprout. Large, serotinous shrubs with relatively long juvenile periods are an important component among obligate seeders in fynbos communities. These species, typically in the family Proteaceae, are killed by fire and rely on canopy-stored seed for regeneration (Bond, Vlok & Viviers 1984). While only a small proportion of the total number of species fall into this category (van Wilgen & Forsyth 1992), they can be the dominant component (in terms of cover and biomass) of the vegetation. Short intervals (less than the juvenile periods of obligate re-seeding plants) between fires can eliminate these species from the vegetation, and cause dramatic structural changes (van Wilgen 1982). As a result, they are usually the species that are used to determine acceptable fire return intervals (van Wilgen, Bond & Richardson 1992). For example, Kruger & Lamb (1979) proposed that the minimum interval between prescribed fires in fynbos should be equivalent to the time needed for at least 50% individuals in a population of the slowest-maturing of the obligate reseeding species to have flowered and set seed for at least three successive seasons. Application of this rule normally suggests a minimum period of 10 to 12 years between fires.

At the other end of the scale, excessively long fire-free periods (greater than the longevity of obligate seeding species – about 30 years or so) can lead to senescence, and elimination of these species from the vegetation. When prescribed burning was introduced in 1970, one of the reasons given for its introduction was the removal of what was seen as the threat of over-protection that would lead to senescence.

Fire season is also important. Serotinous shrubs (notably the genera *Protea* and *Leucadendron*) are sensitive to fire season, and the highest number of seedlings per parent plant occur after fires in summer and early autumn (Bond, Vlok and Viviers 1984; van Wilgen and Viviers 1985). This has led to strong recommendations to burn fynbos at this time of the year (van Wilgen, Bond and Richardson 1992). However, it was recognised as early as 1984 (van Wilgen 1984a) that management fires should be restricted to the summer-autumn period in the western and inland zones, but that fire season was less critical in the eastern coastal zone. Recent work by Heelemann *et al.* (2007) in the eastern coastal areas of the fynbos biome has shown that the most favourable recruitment periods for proteoids were late summer to autumn (February – March) and late winter to early summer (August – October), both of which coincided with the bimodal rainfall peaks recorded for the eastern fynbos biome. Heelemann and his co-workers were able to show that flowering shifted from winter to summer along a west-east gradient, with flowering concentrated in winter west of about 22° E. The strict adherence to the seasonal constraints that apply in the western half of the biome may not be required in the eastern half, and this will increase the number of available, suitable days to conduct safe prescribed burning, especially east of 24° E.

There is also evidence that *variation* in fire regimes is necessary to maintain plant diversity in the landscape (Cowling & Gxaba 1990; Thuiller *et al.* 2007). Variation in the intervals between fires, in fire season, or fire intensity will induce variation in the density of overstorey shrubs (for example *Leucadendron laureolum* on the Cape Peninsula); and this variation is in turn associated with the maintenance of diversity in understorey species (Cowling & Gxaba 1990; Thuiller et al. 2007). Pre-fire stand densities may also affect the density of post-fire recruitment (Bond *et al.* 1995); resulting in alternating densities and species diversity on the same site between different fires. Thuiller *et al.* (2007) concluded that recurrent fires will buffer plant populations from extinction, by ensuring stable co-existence over time, despite localised extirpation by individual fires. This finding was based on two surveys of plant composition on fixed sites 30 years apart which (importantly) have not been subjected to really short-interval (< 6 years) fires. Fynbos may therefore not be as resilient in areas subjected to repeated, short-interval fires. Where fire sizes are much larger than typical seed dispersal distances (see Bond 1988; Schurr et al. 2005), more than one fire-cycle may be required for the species to re-colonise its former habitat by dispersal from adjacent areas. It is well known that repeated frequent burning can eliminate important overstorey shrubs in fynbos (van Wilgen 1981, 1982). It has also been shown that increased fire frequency favoured sprouting species in the Swartberg, and that increases in sprouters led to overall decreases in plant diversity (Vlok & Yeaton 2000). While variation in fire regimes may be acceptable, and even necessary, there are probably limits beyond which elements of the vegetation may well suffer. Repeated, widespread, short-interval fires will almost certainly be undesirable from a conservation point of view.

1.2.7 Managing fire regimes: future challenges

Fire regimes are defined as the typical combination of frequency, season, intensity and type of fires that characterise a region (Gill 1975). Each individual fire event contributes to the regime, but ecosystem managers tend to view fires as events, and their responses are typically event-driven. So, for example, many management decisions are around suppression and containment responses to an unplanned fire, or predicting weather suitable for a prescribed burn. The response of ecosystems, on the other hand, depends not only on the effects of a single fire, but also on the legacies inherited from previous fires (Gill, Bradstock & Williams 2002). In other words, ecosystems respond to fire regimes where managers often respond to fire events. Moving beyond the management of fires as isolated events, and towards the concept of managing fire regimes, will require a far better understanding of whether and how fire regimes can be managed. Fire regimes are more difficult to study than fire events, as there is a need to evaluate responses in relation to fire history. This concept has been well articulated by Parr & Andersen (2006), who coined the terms "visible mosaic" (to describe the footprint left by the last fire), and "invisible mosaic" (to describe the patterns of all other past fires). With the advent of modern GIS analysis capabilities, invisible mosaics can be made visible to a certain extent, provided that good spatial fire records are kept. It is now theoretically possible to determine the range of variability encompassed by modern fire regimes, and therefore to examine the responses of species in terms of this variation. One of the major changes needed in terms of setting ecosystem and conservation goals will be to assess responses to fire regimes at a landscape scale, which will implicitly involve the consideration of a set of fire regimes (Gill, Bradstock & Williams 2002). Plant populations may fluctuate considerably over time, with local extinctions and re-colonisations taking place within a much larger landscape (see, for example, Thuiller *et al.* 2007). Managers need to be able to distinguish between acceptable and unacceptable limits to landscape-scale variations in elements of the fire regime, and whether and how they can influence them where deemed necessary. This implies the need for an approach of adaptive management, where information on fire regimes and ecosystem responses are regularly collected and assessed,

Impending global changes to climate also hold significant implications for fynbos fire managers. The future climate of the fynbos biome is likely to be one that is warmer and drier than at present, according to a number of current model projections. Recent temperature trends reveal appreciable warming in the Western Cape over the past three decades, which support these projections (Midgley *et al.* 2005). A future that is warmer, and possibly drier, will encompass a range of consequences that will affect the ecological integrity of the fynbos biome. We need to develop a better understanding of how this will influence fire regimes. Fire will be influenced both directly and indirectly. Direct impacts may come about as a result of changes in the weather that allows large fires to occur. Indirect changes may come about as a result of changes ecosystem productivity (and thus fuel accumulation rates), or species dominance (and thus fuel structure). Feedback loops will complicate responses. These changes would have consequences for conservation as well as safety in neighbouring areas, and much needs to be done to understand these so as to be able to adapt in such a way as to avoid the worst consequences.

Controlling invasive alien plants, and avoiding or minimising their impacts in a fire-prone environment poses arguably the biggest challenge to managers of fynbos ecostystems. These species are spread by fire, and they also increase fuel loads, fire intensity, and impact on soil stability. This is *the* major threat to biodiversity, as well as to catchment integrity, in extant fynbos ecosystems. The issue is considered in more detail in the next section.

1.3 Invasive alien plant management in fynbos ecosystems

1.3.1 Invasive alien plants in fynbos ecosystems

There are over 150 species of alien plants that are listed as invasive in the fynbos biome (Henderson 1998). However, many of these species are not widespread, or invade only disturbed areas, and are not of major ecological significance. Van Wilgen *et al.* (2007) identified 30 invasive alien plant species (17 trees, 8 shrubs, 3 grasses, 1 succulent and 1 annual) as important in the fynbos biome, by establishing which species occurred in at least 10% of the biome. Of these the most important species, or groups of species include the pines (*Pinus* species), wattles (species in the genera *Acacia* and *Paraserianthes* from Australia), hakeas (*Hakea* species), and gum trees (in the genus *Eucalyptus*, notably *Eucalyptus camaldulensis*). All of these are trees or large shrubs, and two groups are of particular interest because of their wide distribution in the biome.

The first are the pines and hakeas (Figure 1.5). These serotinous trees and shrubs produce copious amounts of seeds held in cones or follicles, which are released on the death of the parent plants in fires. The seeds are winged, and can spread over great distances after fires. Pines and hakeas are therefore widespread, occurring in all areas of the biome, including remote areas. They can and do form dense and impenetrable stands. The second group is the wattles. These species typically produce copious amounts of seeds, but these are released on maturity. The seeds are hard-coated, and accumulate in the soil. The seeds can either be spread by water transport in rivers or streams, or sometimes by birds. Soil-stored seed banks are stimulated to germinate by fires, and dense stands of seedlings usually appear after fires. Gum trees are a special case, in that the one species that appears to be aggressively invasive (the Red River gum *Eucalyptus camaldulensis*) is restricted to river courses in lower-lying areas.

Figure 1.5. Fynbos vegetation with a light infestation of pine trees, Kogelberg, Western Cape. Without regular and effective control operations, repeated fires in areas such as this will lead to the total dominance of the ecosystem by pines.

1.3.2 Control methods available

Invasive alien plants are notoriously difficult to bring under control. They are for all practical purposes impossible to eradicate (unless the population is very small and confined to a restricted area), and experienced managers speak of control rather than eradication. Integrated control refers to a combination of approaches that are aimed, collectively, at the sustainable and effective control of invasive alien plant infestations. The combination of elements in the design of an appropriate integrated control programme for an area or species depends on the characteristics and dynamics of the ecosystem being invaded, the life history attributes of the weed, the time since introduction, and the size of invasive population.

- Prevention involves the development and enforcing of policies about the importation of new species into the country, minimising the risks of accidental introductions, effective policing at border posts, and so on.

- Early detection and eradication requires widespread vigilance on the part of knowledgeable people, to identify problem plants as early as possible. Eradication is also only possible when populations of invasive species are very small, and confined to a limited area.

- Mechanical control involves the clearing, felling, or removal of invading alien plants, often in conjunction with burning. It can be labour-intensive, and requires several follow-up treatments to ensure that all individuals have been found and removed.

- Chemical control involves the application of herbicides, either directly to infestations of invasive plants, or in conjunction with mechanical clearing.

- Biological control involves the use of species-specific insects, mites and diseases from the alien plant's country or region of origin to either kill the target alien plant species, or lessen its 'weediness' by reducing its vigour or lessening the number of seeds it produces.

- Ecosystem rehabilitation is necessary to restore the stability of ecosystems once invasive alien plant infestations have been removed.

In fynbos ecosystems, pines and hakeas are most easily controlled by means of mechanical control alone. Infestations of these species are felled, allowing seeds to be released into the unburnt vegetation, where most are consumed by rodents, and some germinate. The area is then burnt about 1 – 2 years after felling, killing seedlings before they can mature and set seed, and allowing the natural, fire-adapted vegetation to recover. This method is usually very successful, but it suffers from the drawbacks of being expensive, and ineffective in large, remote areas. It also requires a degree of risk to be taken in burning the area. Alternately, leaving it exposes the area to wildfires, which can be detrimental (Holmes *et al.* 2000).

Australian wattles are more difficult to control. Most of the species are able to sprout after felling, necessitating the use of herbicides to kill cut stumps. The soil-stored seeds are also protected by the soil from the heat of fires, and they germinate en masse following a fire, necessitating either hand-pulling huge numbers of seedlings, or again using foliar herbicides. Costs escalate exponentially as the density of infestations increases (Marais, van Wilgen & Stevens 2004), making wattles extremely expensive to control.

Biological control options are available for some, but not all, of the invasive alien plant species in the fynbos (Zimmermann, Moran & Hoffmann 2004). Hakeas and several wattles have a suite of seed-feeding and gall-forming insects which can reduced seed loads. However, conflicts of interest often preclude the use of other biological control agents. For example, the existence of a wattle industry (based largely on black wattle, *Acacia mearnsii*) in South Africa means that plant (rather than seed) attacking insects cannot be used. Similarly, a promising project seeking seed-destroying insects for pines (Moran *et al.* 2000) had to be terminated because of fears that the proposed insect would assist the infection of pine trees by pitch canker. Biocontrol projects need to be carefully integrated with fire management projects, especially where the control agents have their populations reduced by fire, and where re-introduction, or the protection of "reserves" of the weed species from fire (to allow re-colonization) needs to be considered.

1.3.3 Research into the impacts and control of invasive alien plants in fynbos

Concerns about the impacts of invasive alien plants in South Africa are not new. As early as the 1890s, for example, the invasive cactus *Opuntia monocantha* was recognised as a problem along the eastern coastal strip of South Africa, precipitating the release of biological control agents in 1913 (Zimmermann, Moran & Hoffmann 2004). Early botanists, including Peter MacOwan (in 1888) and Rudolf Marloth (in 1908) raised concerns that alien plants would replace natural vegetation (Stirton 1978). In a landmark publication in 1945, Prof. C.L. Wicht stated that "one of the greatest, if not the greatest, threats to which the Cape vegetation is exposed, is suppression through the spread of vigorous exotic plant species" (Wicht 1945).

In June 1982, the General Assembly of the Scientific Committee on problems of the Environment (SCOPE) identified the invasive spread of plants, animals and micro-organisms introduced by humans into areas remote from their centres of origin as a problem of global concern. A large international project was initiated, with the purpose of addressing three specific questions:

- What factors determine whether a species will be invasive?
- What properties determine whether an ecosystem will be prone or resistant to invasion?

- What management approaches should be developed using the knowledge gained from these two questions?

The South African component of this work led to the publication of a synthesis volume in 1986 (Macdonald, Kruger & Ferrar 1986), in which the current understanding was set out. Work in this field continued under the auspices of the South African Forest Research Institute (SAFRI) (for fynbos invasive weeds), the Percy Fitzpatrick Institute of African Ornithology (for overall synthesis under the ongoing SCOPE programme), and the Plant Protection Research Institute (for research into biological control). A good deal of useful work was done during this period. For example, research was initiated by SAFRI which examined the underlying reasons for differences in the invasive potential of closely-related plant species (van Wilgen & Siegfried 1986; Richardson, van Wilgen & Mitchell 1987). This work ultimately led to the development of the first fairly robust model of invasive potential in a large group of plants (Rejmánek & Richardson 1996).

Most of the research conducted under the auspices of the SCOPE programme attracted no more than academic interest. It was not until researchers were able to demonstrate that invasions would have significant economic impacts on water resources that the issue went beyond academic debate and into the realms of action. Even then, it took a radical change of government to initiate the implementation of invasive plant clearing programmes (dealt with in the next section). The idea that invasive alien trees could have negative impacts on streamflow (in much the same way as commercial forestry did) was first raised by Fred Kruger in 1977 (Kruger 1977b). It was raised again during the SCOPE synthesis (Versfeld & van Wilgen 1986), and at the conclusion of the Fynbos Biome project (van Wilgen 1991; van Wilgen, Bond & Richardson 1991). This led simply to small funding grants for more research to quantify the impacts more clearly.

The first such attempt to estimate the impacts of invasive alien trees on water resources came about in 1996, when a spatially explicit model was developed (Le Maitre *et al.* 1996). The model simulated five important processes: the occurrence of fire; the spread and establishment of alien plants after fire; rainfall to runoff ratios; growth and changes in biomass between fires; and effects of these changes on streamflow. The estimations of streamflow reductions due to invasive alien plant infestations make use of an "age-biomass-streamflow reduction model" This model allows biomass to be estimated separately for tall trees, medium trees and tall shrubs. Streamflow reduction is driven by this estimated biomass and distinguishes between riparian and non-riparain streamflow reduction conditions (Figure 1.6). The simulations predicted that the cover of alien plants would increase from an initial estimate of 2.4% to 62.4% over 100 years, decreasing streamflow from the catchment by 347 m^3 per hectare (equivalent to 30% of the water supply to the city of Cape Town). Based on this work, van Wilgen, Cowling & Burgers (1996) estimated the costs of "generating" water from catchments where alien plants were either controlled, or not. Their study suggested that despite higher costs overall when alien plant management projects were implemented, the costs per unit of water "produced" would be lower when such projects were in place. Another study (van Wilgen *et al.* 1997) suggested that investing in the management of alien species in the catchments of existing dams would be more cost-effective than constructing new dams, while simultaneously allowing the catchments of existing dams to become invaded (it also showed that an early investment in alien plant control programs would pay off, rather than leaving them for control at a later date).

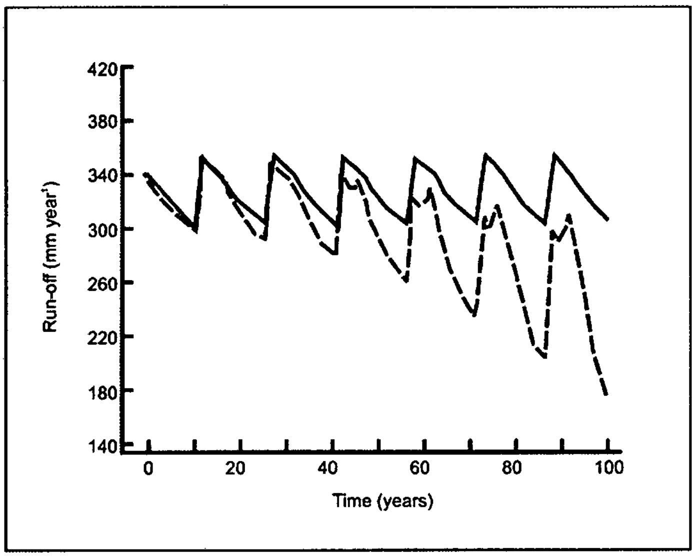

Figure 1.6. Streamflow runoff over time from a fire-prone fynbos catchment under two scenarios: without alien plants (solid line), where streamflow varies as plant biomass responds to repeated fires; and with alien plants (dashed line) where plant biomass increases due to the spread of invasive trees after fires, and streamflow decreases correspondingly. Figure from Le Maitre et al. 1996).

Since these earlier studies, several other papers have estimated the economic consequences of alien plant invasions in fynbos ecosystems and elsewhere. All of these papers (Higgins *et al.* 1997; Hosking & Du Preez 1999; Turpie & Heydenrych 2000; De Wit, Crookes & van Wilgen 2003) provide estimates showing that clearing invasive alien plants makes economic sense (in that they deliver positive cost-benefit ratios). However, all of these findings rely heavily on the positive impacts predicted using the age-biomass models described above, and all do not account for the total economic value which would consider the full suite of economic costs and benefits (Turpie 2004).

Perhaps the biggest threat to water yields comes from the combined effects of unplanned wildfires and alien plants. Unplanned fires in fynbos result in additional costs in invaded areas, in one of a number of forms, depending on the action taken. First, invasive alien plant seedlings germinate after fires, and usually increase the density of infestation (in terms of the number of plants per unit area) compared to the pre-fire density. It is necessary to control these flushes of seedings to prevent them becoming dominant over the next few years. Extensive unplanned fires will require additional effort in the form of "follow-up" operations. CapeNature has estimated that these additional costs would amount to R17.5 million following fires in 40 000 ha in 2006 (Bekker 2006). Alternately, if funds or capacity do not allow for immediate follow-up, the costs of control rise as the plants grow. If the infestations were to be left for 10 years, CapeNature estimate that control costs would rise almost four-fold to R65 million on the same 40 000 ha (Bekker 2006). On average therefore, if control operations were carried out within 5 years of an unplanned fire, additional costs could amount to around R1000 per ha. Finally, if the problem is not dealt with (because of a lack of capacity or funds), then the environmental impacts (for example in the form of water losses) would represent a cost attributable to wildfires. The 4.3 million ha of extant fynbos is subjected to a fire return period of 15 years, so roughly 286 000 ha burns every year. Data from Versfeld *et al.* (1998) (Table 3.6) indicates that 33% of the three major catchments in the Western Cape are invaded to some degree; thus approximately 95 000 ha of *invaded* fynbos will burn per year. This means that the additional costs to control these infestations (and prevent even worse environmental losses) would be around R100 million annually.

The quest for finding biological control solutions for invasive alien plants in the fynbos biome has also led to some innovative research and significant advances in understanding. Research started in the biome with a search for seed-feeding insects in the 1960s. It expanded over the next two decades to include releases on the invasive alien genera *Ageratina*, *Hypericum*, *Acacia* (8 species), *Paraserianthes*, *Leptospermum*, *Sesbania*, and *Hakea* (2 species). Many of these projects were innovative; for example they made use of gall-forming and seed-feeding insects that had not been used elsewhere; the emphasis on weeds in conservation areas (as opposed to weeds in agricultural crops); and the predominance of woody invaders that have been targeted for biological control (Zimmermann, Moran & Hoffmann 2004). Many of these releases have resulted in the target invasive species being brought under substantial or complete control.

1.3.4 Management responses

Attempts at the control of invasive alien plants began in the fynbos biome as early as the 1930s. In this regard, it is important to note that when control efforts started in the second half of the 20th century, they were done mostly for reasons of conserving natural vegetation, and not for any hydrological or agricultural benefits that might have accrued. The initial attempts at the control of invasive plants were at best uncoordinated and erratic, and did little to stem their spread. Although few campaigns were adequately documented, the existing evidence shows that poor understanding of the ecology of invasive species, as well as a lack of follow-through when clearing was done, led to much wasted effort and money. For example, Macdonald, Clark & Taylor (1989) reviewed 47 years of control attempts on the southern Cape Peninsula, and concluded that they were “almost totally ineffective for the first 35 years”. The early, erratic control efforts were replaced later by co-ordinated control programmes in the 1970s and 1980s (Fenn 1980). At the same time, considerable efforts were put into research (described above), in order to develop sound, scientifically-based control options.

The momentum of this work was sadly lost in the late 1980s. There were many contributing factors. The seasonal restrictions on burning (mentioned in the previous section) meant that many prescribed fires, necessary for the control of seedlings after felling operations, could not be carried out. The government also split the functions of its forestry department, with plantation management becoming privatised, conservation management being devolved to unprepared and inexperienced provincial authorities, and the research arm being transferred to the CSIR. The net result of these changes was a fragmentation or loss of capacity and experience. The government of the day, beleaguered by anti-apartheid sanctions, had to cut funding, resulting in further losses of capacity. The net result was that invasive alien plant control programs fell behind, and cleared areas were under threat of re-invasion.

The development of economic arguments, based essentially on the predicted impacts of alien trees on water resources in the fynbos biome, coincided with the formulation of South Africa's first democratically-elected government. This government created the Working for Water programme, an initiative that sought to reduce the impacts of invasive alien plants on water supplies through the employment of poor people in rural areas (Figure 1.7). The events that led to the formation of the Working for Water programme have been documented by van Wilgen *et al.* (2002), but in essence this intervention was only possible because a particular set of factors coincided to create a unique opportunity. These included leveraging political support, emphasising emergent benefits (employment), taking a novel approach by linking several benefits into an attractive "package", putting together a dedicated team, publicising early successes, and avoiding bureaucracy (van Wilgen *et al.* 2002).

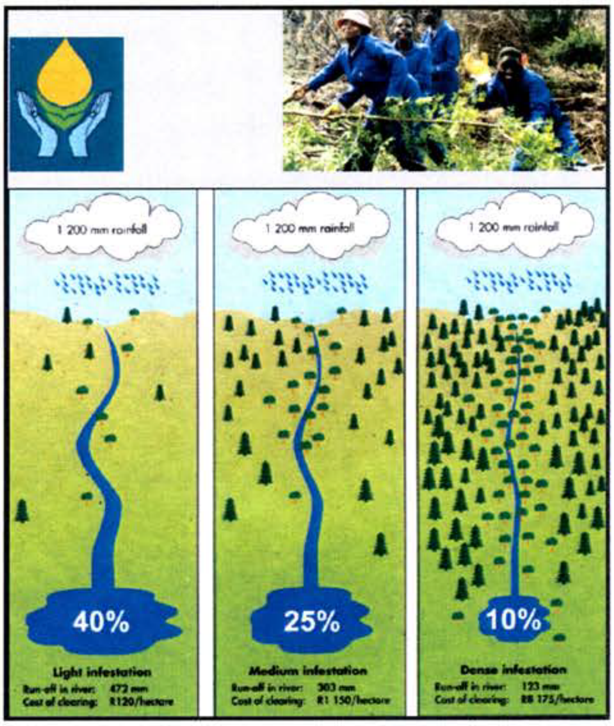

Figure 1.7. Promotional material from the Working for Water programme, based on predictions from the biomass model. This poster emphasizes the degree to which invading alien woody species reduce water yield (from a 1200 mm annual rainfall) as the invasive trees gain increasing dominance in the system (percentages indicate water yields). The photo at top shows local people employed in the clearing of invasive species from the land.

The Working for Water programme has been very successful in terms of attracting funding and gaining local and international acclaim, but it relies heavily on political support and remains vulnerable for this reason. Political support for this programme relies almost entirely on its employment creation, upliftment and empowerment benefits. The economic benefits of invasive alien plant clearing projects (as opposed to employment benefits) are often viewed with some scepticism by decision-makers, for a number of reasons. These include:

The benefits of alien plant control, especially those in natural (rather than agricultural) environments are often "public good" benefits. In such cases, the individual marginal benefit (the amount of benefit gained by any one person) is small. Where individual marginal benefits are small, people tend not to take them seriously, despite the total benefit being very large (as there are many people);

Many of the projected benefits of alien plant control come about from avoiding future impacts rather than removing current impacts (for example, by preventing further spread of a weed that has not yet reached its full potential, see van Wilgen *et al.* in press). People find it difficult to appreciate (or gain political benefit or advantage from) the avoidance of future impacts that are not yet manifesting themselves; and

The inaccurate valuation of costs and benefits can lead to cost: benefit ratios that people have little faith in. It is notoriously difficult to estimate the full suite of impacts associated with a particular weed species, and the process becomes particularly difficult when a species has both positive and negative effects (so-called conflict of interest species).

The fact remains that invasion by alien plants (especially woody species) poses arguably the greatest threat to the conservation of fynbos ecosystems and the services that they provide to humanity. The problem is exacerbated by the fact that fynbos is fire-prone and that fires are inevitable. Fire-adapted invasive species thrive in such environments, so bringing them under control is the biggest challenge for managers of these ecosystems.

1.3.5 Prognosis for control

Whether or not current control attempts are having real impacts on the overall status of invasive alien plant infestations in the fynbos biome is an important question. For example, the Working for Water programme was initially put forward as a 20-year activity, but it appears that achieving the goal of clearing major infestations within that timeframe will not be possible. Data from the Working for Water programme suggest that, at current rates of clearing, infestations of several important species would only be cleared within 30 – 85 years (Marais, van Wilgen & Stevens 2004). These estimates are extremely conservative. Marias and his co-worker's approximations made a number of assumptions, each of which reduced the estimate of time that would be needed to clear existing infestations; the estimates are therefore probably serious underestimates. The assumptions included: (1) that infestations are static, and will not spread further while clearing operations are under way; (2) that clearing a site will eradicate the invasive alien species; (3) that areas require only one follow-up treatment; (4) that funding levels will remain at the levels sustained over the past few years; and (5) that we know how big the problem is. They also do not address the emergence of new weed species. More realistic indications are that, at current rates of management, the problem will not be contained; at best, only some species will be controlled, and some areas will be kept clear of invasive species. This is a sobering prognosis, and it highlights the need to find sustainable solutions if significant impacts are to be avoided, and management efforts optimised.

The above analysis underscores the importance of biological control solutions to invasive alien weed problems, wherever they can be found. Biological control is seen by its proponents (for example, Moran, Hoffmann and Zimmermann 2005) as a particularly attractive option because:

- it is cost effective and very safe compared with the expense and risks associated with herbicide development and deployment;
- biological control can be successfully integrated with other management practices;
- and, most compelling of all, biological control is self-sustaining.

There are however, counter-arguments to the use of biological control (see, for example, Simberloff amd Stiling 1996; Louda and Stiling 2003). The argument against biocontrol maintains that the outcomes of an introduction cannot be predicted precisely enough *a priori* to know with some certainty that the benefits will outweigh the environmental costs. Proponents of this view often point to examples of unintended consequences, such as impacts on non-target species, and the disruption of food webs in support of their views. The evidence suggests that these concerns are often groundless, but they are nevertheless responsible for serious barriers to biological control. In my view, a resolution to this debate remains one of the most important challenges to ecosystem managers if invasive alien plants are to be controlled.

The other important aspect is, as far as possible, to integrate prescribed burning and alien weed control operations. Fire regimes are difficult to manage, and wildfires are inevitable (as discussed in the previous section). There is therefore an urgent need to become more flexible with regard to follow-up operations after fires, in order to avoid either significantly increased control costs, or alternatively to suffer increased impacts. The degree to which managers are able to overcome resistance to biological control, and to gain a degree of control over fire regimes, will ultimately determine the fate of the unique fynbos vegetation.

1.4 Fire management in savanna ecosystems

1.4.1 The ecology of African savannas

Savanna vegetation is characterised by the co-existence of two major life-forms: grasses and trees. Savannas constitute one of the largest biomes of the world, covering about 20% of the land surface. Most savannas occur in Africa, with smaller areas in South America, India and Australia (Shorrocks 2007). In South Africa, savannas make up 35% of the land area, and are the basis of two major industries: cattle ranching and wildlife-related tourism (Scholes & Walker 1993). Savannas have existed in Africa for at least 30 million years, and their distribution and structure is determined by water availability, nutrient availability, fire and herbivory.

The the mechanisms that allow trees and grasses to co-exist is central to the understanding of savanna ecology. This coexistence is traditionally explained by either equilibrium or disequilibrium models (Scholes & Archer 1997). Equilibrium models propose that grass-tree coexistence is possible, for example, because of separation of the rooting niche, with trees having sole access to water in deeper soil horizons and grasses having preferential access to, and being superior competitors for, water in the surface soil horizons (Walter 1971). In this equilibrium model, climatic variability precludes dominance by either life form, and coexistence is possible in a variety of states (Walker & Noy-Meir 1982). Disequilibrium models, on the other hand, propose that there is no stable equilibrium, and that frequent disturbances prevent the extinction through competition of either grasses or trees by periodically biasing conditions in favour of alternative competitors. Higgins, Bond & Trollope (2000) have proposed a disequilibrium model in which interactions between life history characteristics of trees (sprouting ability, fire survival at different life stages, and mortality) and the occurrence of fires (which prevent recruitment of trees into adult life classes) could explain coexistence. This model identified the critical need for variability in fire intensity as a prerequisite for grass-tree coexistence, and suggested that the imposition of fire regimes of homogenous intensity (such as those associated with regular prescribed burning) could lead to dominance by grasses.

The relevance of disequilibrium models is greater in areas of higher mean annual rainfall. Sankaran *et al.* (2005) have demonstrated that the maximum woody cover in savannas receiving a mean annual rainfall of less than 650 mm is constrained by the amount of rainfall (Figure 1.8). These are arid and semi-arid savannas that could be considered as "stable". The scarcity of water constrains woody cover, and allows trees and grasses to co-exist. In these arid and semi-arid systems, fire, nutrients and herbivory can interact to reduce woody cover below the upper bound that is determined by rainfall (Figure 1.8). Where mean annual rainfall exceeds 650 mm, there is sufficient moisture to allow trees to attain canopy closure, but this is prevented by fire and herbivory. Sankaran and co-workers regard these as “unstable” savannas, where the co-occurrence of grasses and trees require regular disturbance.

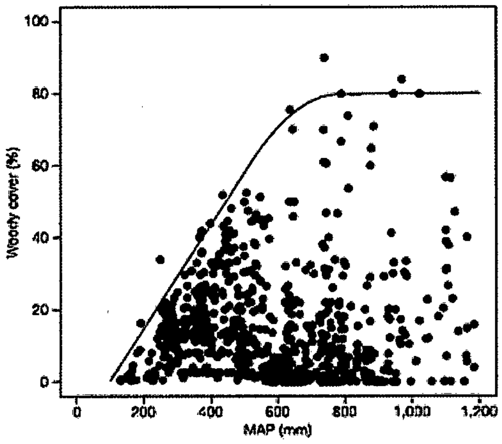

Figure 1.8. Change in woody cover of African savannas as a function of mean annual precipitation (MAP). Trees are typically absent where mean annual rainfall is <100 mm. Where mean annual rainfall is > 650 mm, tree canopy closure is possible, but is prevented by regular disturbance by fires and herbivory. Data are from 854 sites across Africa. Figure from Sankaran et al. (2005).

1.4.2 Fire management in savannas

Early views on the role and use of fire in savanna vegetation were ambiguous (see Phillips 1930 for a review). Some early writers, and particularly the Drought Investigation Commission (1926) believed that “veld burning is contrary to the interests of the country as well as to the principles of all veld and soil conservation”. Others, including Busse (1908), Bews (1918) and Staples (1926) recognised that deliberate burning of grasslands had several beneficial features. In his 1930 review, Phillips urged the careful consideration of “all regional circumstances in the light of scientific experience, before we definitely decry the practice of firing”. Much later, Phillips was to reminisce about the early days of fire ecologists as follows: “We knew very little about fire ecology in 1929, when I drafted, on a mountain massif at the edge of the Massai Steppe, Tanganyika, the paper later published in the South African Journal of Science in 1930” (Phillips 1984). The impact of the Drought Commission’s views on the fire management of savannas in South Africa was similar to that experienced in fynbos. Strict conditions for the use of fire were laid down, and the practice of prescribed burning in arid savannas was virtually eliminated (Trollope 1984). Trollope (1984) reports that “except for the wildlife areas, the general attitude regarding the practical use of fire tends to be negative, and veld burning is applied as a last resort”.

The use of fire, and research into its effects, in conservation (wildlife) areas has led to a greater understanding of the role of fire in South and southern Africa. A growing recognition of the inevitability of fires in the 1950s led to the establishment of a large, replicated fire experiment in the Kruger National Park in 1954 (van der Schijff 1958). Over the next few decades, managers of southern African savanna conservation areas embraced the belief that fires were inevitable and necessary, and developed fire management policies in line with this. Examples include:

- In the Kruger National Park, regular prescribed burning every 3 years was introduced in 1957, and continued until 1980, following the recognition that fires were an integral part of the ecology of the area (van Wilgen *et al.* 2003). This was followed by a more flexible approach to prescribed burning between 1981 and 1991. From 1992 – 2001, a "natural" fire policy was in place, in which all lightning-ignited fires were allowed to burn freely, while at the same time attempts were made to prevent, suppress or contain all other fires. From 2002 – present, point ignitions have been used to start fires in areas where fire is deemed necessary, and wildfires are tolerated where fire is deemed to be necessary (Biggs & Potgieter 1999; van Wilgen, Govender & Biggs 2007; van Wilgen, Govender & MacFadyen 2008).

- In the Hluhluwe/Umfolozi Park, fire was used in the 1980s primarily in an attempt to control the visibly encroaching acacias. A major change in approach to fire management, initiated in the mid 1980s, eliminated the strict application of block burning, and adopted an approach where fire was used to create patchiness in the vegetation through point source ignitions and broadening the season of ignition. This shift was justified by arguing that optimal management of a conservation area should include managing fire in a manner "that most closely resembled a natural state as well as in an attempt to create a mosaic of patches with a range of fire histories, in an attempt to promote biotic diversity" (Balfour & Howison 2001).

- In the Etosha National Park, the use of fire was forbidden in the 1970s, but the policy allowed for backfires to contain and limit any wildfires that did occur (Siegfried 1981). In 1981, the deliberate use of fire was introduced, but no guidelines were available, and thus its use was haphazard (du Plessis 1997). In the 1990s, an approach was developed that sought to guide the use of intentional burning. The approach used seasonal rainfall, the time since the last fire, and fuel loads in an attempt to simulate the incidence of lightning fires (Stander, Nott & Mentis 1993; du Plessis 1997).

- In the Pilanesburg National Park, a patch-mosaic burning system was developed to create a diverse fire regime (Brockett, Biggs & van Wilgen 2001). In this system, the area burnt per year is a function of the grass fuel load, and the number of fires per year is a function of the percentage area burnt. Fires are point-ignited, under a range of fuel and weather conditions, and allowed to burn out by themselves. The seasonal

> distribution of planned fires over a year is dependent on the number of fires. Early dry season fires (May–June) tend to be small because fuels have not yet fully cured, while late season fires (August–November) are larger. More fires are ignited in the early dry season, with fewer in the late dry season. The seasonality, area burnt, and fire intensity are spatially and temporally varied across a landscape. The aim of this approach was to impose a variable fire regime on the landscape, on the assumption that this would promote heterogeneity and the conservation of biodiversity.

Arguably the largest changes in fire management approaches in savanna ecosystems came about as a result of changing paradigms in both conservation and ecology (Mentis & Bailey 1990; Bond & Archibald 2003). For over a century, the primary conservation goal in savanna ecosystems was the protection of large mammals. The commonly-used name of "game reserve" betrays the intention to conserve animals ("game") for hunting (and later tourism) purposes. A global trend towards the conservation of biodiversity (rather than particular, often charismatic, species) led to these goals being challenged, and in many places they were replaced by goals that required the conservation of all facets of biodiversity. Changes in ecological thinking also came about with the growing realisation that ecosystems were far from stable, and management aimed at the maintenance of a particular state was doomed to failure. The adoption of a heterogeneity paradigm in savanna ecology, with variability as a central concept (Mentis and Bailey 1990; Rogers 2003) has required thinking about the use of fire in ways quite different to the fixed-area, fixed-return interval approach, aimed at the maintenance of a stable vegetation structure, that characterised the 1950s to 1980s.

The difficulties facing mid- and late-20th century ecosystem managers who sought to impose a fire regime of their choice on savanna ecosystems are reflected by the experience in the Kruger National Park. Despite adopting different approaches to the use of fire (described above), the total area burnt was found to be predominantly determined by grass fuels loads, in turn determined by rainfall over the past two years (van Wilgen *et al.* 2004), and was unaffected by the management approach (Figure 1.9). Further evidence regarding the difficulty of applying desired fire regimes came from experimental burning plots. The attempt to impose a series of fire regimes (annual, biennial and triennial fires, and protection from fire) on small (7 ha) plots was also not entirely successful. The degree of success was higher in areas of higher (and thus more reliable) rainfall, but even in these cases, there were some years in which fires were not possible; in addition, some of the plots intended as controls (protection from fire) were burnt in accidental fires (Figure 1.10). Given that it was not possible to "impose" a fire regime consistently on small plots, even with large budgets going into attempts to do so, it follows that imposition of fire regimes onto very large areas would be much less likely to succeed.

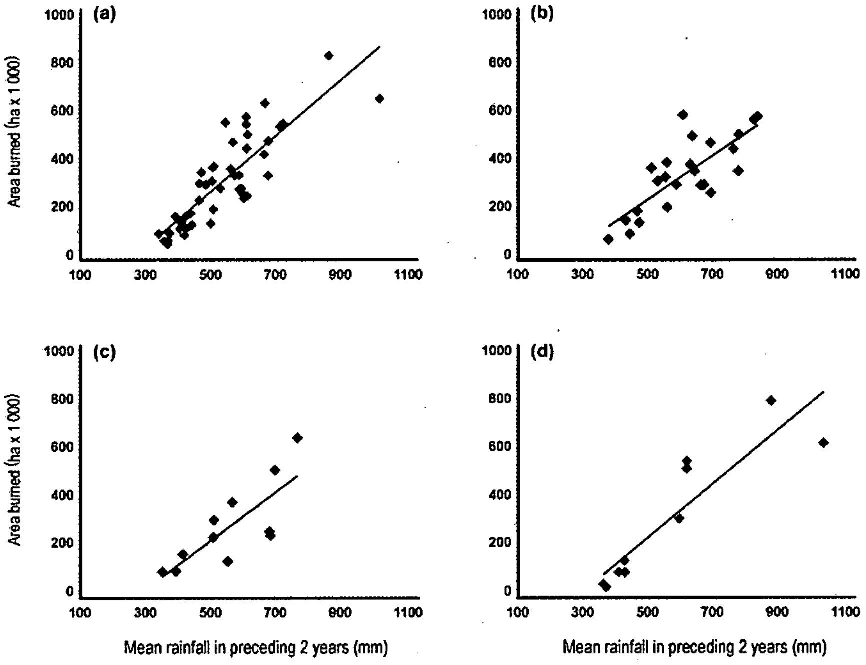

Figure 1.9. Relationship between mean annual rainfall over the preceding 2 years and the extent of fires in the Kruger National Park. Data are for (a) all years between 1957 and 2001; (b) 1957–1980, when regular prescribed burning took place; (c) 1981–1991, when flexible prescribed burning took place; and (d) 1992–2001, when a policy of lightning-driven fires was in place. Lines for different management eras did not differ significantly. Figure from van Wilgen et al. (2004).

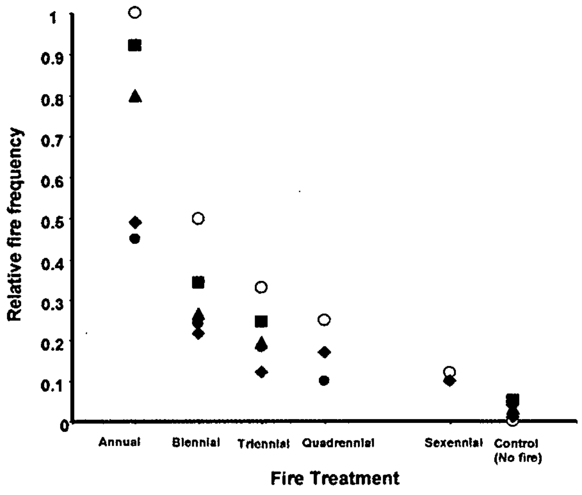

Figure 1.10. The relative fire frequency (calculated as x/y, where x = the number of fires applied and y = the years of existence of the treatment) achieved for different fire treatments (various frequencies or protection from fire) on experimental burning plots in the Kruger National Park in Sourveld (■) (mean annual rainfall = 705 mm), Combretum (▲) (mean annual rainfall = 572 mm), Knobthorn-Marula (♦) (mean annual rainfall = 507 mm) and Mopani (●) (mean annual rainfall = 451 mm) vegetation types. Open circles (○) indicate the intended level of treatment. Figure from van Wilgen, Govender & Biggs (2007).

In the Kruger National Park, the concept of adaptive management by 'thresholds of potential concern' was introduced in the mid-1990s (Biggs and Rogers 2003). Under this framework, upper and lower thresholds were defined for a range of ecosystem indicators. If a threshold is reached, then management interventions are considered; alternately, the threshold could be recalibrated. In line with this policy, a range of thresholds relating to fire patterns was proposed (van Wilgen, Biggs & Potgieter 1998). The framework included thresholds relating to fire-return periods, the seasonal distribution of fires, the range of desired fire intensities, the size-class distribution of fires and the cause of fires (whether they were "natural" lightning fires, or fires initiated by humans). Deviations from these thresholds were intended to alert managers to the possibility that fires were either too frequent, too infrequent, or otherwise deviating from acceptable limits in the area concerned. When management by 'thresholds of potential concern' was introduced to replace prescribed block burning, the goal was to encourage a "natural" (lightning-driven) fire regime in the park. After a decade, however, it became apparent that this would not be possible, as fires ignited by people dominated the fire regime (van Wilgen, Govender & Biggs 2007). This led to the introduction of the park's current fire management objectives, which reflect the ongoing need for better understanding of the ecological role fire. This need remains despite considerable research into the ecological role of fire in the park (see van Wilgen Govender & Biggs 2007 for a recent review). Besides safety considerations, the specific ecological objectives within the park are to understand the role of fire as a natural process, and its relationship with other interacting co-drivers, so as to develop an informed context for management (van Wilgen, Govender & MacFadyen 2008). The sub-objectives include the need to fill important knowledge gaps with respect to the effects of fire on elements of biodiversity, as well as the use of new understanding to recommend feasible fire management policies and procedures.

Box 1.2. Quotable quotes: Savanna

The quotes below reflect the changing attitudes towards fire and its role in the ecology and conservation of savanna ecosystems in the 20th century. These changes reflect the evolution of thought that at first regarded fire as detrimental, later as necessary to maintain "stable" states, and later as an integral factor for the maintenance of heterogeneity and diversity.

"veld burning is contrary to the interests of the country as well as to the principles of all veld and soil conservation" (Drought Investigation Commission 1926).

"we should consider all regional circumstances in the light of scientific experience, before we definitely decry the practice of firing" (Phillips 1930).

"Until it is proved wrong, ...as an interim policy, ... all grass which has become long and rank (will) be burnt every three years" National Parks Board resolution in 1954, regarding the use of fire in the Kruger National Park, quoted in van Wyk & Wager (1969).

"Fire is recognised as having an important ecological role .... in the maintenance of .... stable savanna communities" (Trollope 1984).

"An appropriate fire regime .... spans a range of return periods, seasonal timings, intensities and spatial extents so as to preserve .... diversity" (Mentis & Bailey 1990).

"There is no such thing as a savanna that does not burn: the only management choice is between planned fires and unplanned fires" (Scholes & Walker 1993).

"Fire management in conservation areas in South Africa is currently in a state of flux. Practices maintained for nearly 50 years have been challenged, and in some parks, completely replaced with radically different alternatives" (Bond & Archibald 2003).

1.4.3 Lessons from research and adaptive management

Many lessons have been learned about fire management in savannas, arising both from result as well as the application of fire in different ways and in different areas. As a result, a number of principles can be recognised:

- Fire is a vital ecological process in maintaining the structure of savannas in relatively moist areas. In moist savannas (where mean annual rainfall > 650 mm) the tree layer is not constrained by a lack of moisture, but is prevented from reaching closure because of repeated fires and pressure from herbivores. In such areas, the elimination of fire will result in dominance by woody vegetation. The incidence of fires in these ecosystems is also more regular, as less variable rainfall results in the more regular accumulation of sufficient fuel to support a spreading fire.

- Fire is a less important ecological process in relatively arid areas. In arid savannas (where mean annual rainfall < 650 mm) the tree layer is effectively prevented from reaching closure, as it is constrained by a lack of moisture. In these systems, the elimination of fire will not lead to *total* dominance by woody vegetation. The incidence of fires in these ecosystems is also more erratic, as variable rainfall and herbivory often prevent the accumulation of sufficient fuel to support a spreading fire.

- Fires do not act alone in shaping the vegetation. The regular removal of grass by a variety of grazing species affects fuel loads, and thus the occurrence and intensity of fires. Damage to woody plants by a range of animals (such as porcupines, Yeaton 1988, and elephants, van Wilgen, Govender & MacFadyen 2008) affects their post-fire survival, their ability to compete with grasses, and thus their abundance and relative dominance in the vegetation.

- Savannas are resilient to a wide range of fire regimes. Long-term fire experiments in the Kruger National Park have shown that the effects of fire on the vegetation were most marked in extreme treatments (burning every year, burning in the summer wet season, or long periods of fire exclusion), and that these effects were greater in areas of higher rainfall (van Wilgen, Govender & Biggs 2007). However, the widespread and repeated application of such regimes on the vegetation would be impossible to achieve in practice. In addition, faunal communities, and soil physiology, were largely unaffected by fire.

- The ability of managers to control fire regimes is often limited, especially in more arid areas. Fuel loads respond to variations in rainfall more than to post-fire age, and many uncontrollable sources of ignition combine with the regular occurrence of weather suitable for fires to ignite grass fuels.

- The belief that diverse fire regimes are necessary for conservation remains unproven. In a recent critique of the "patch burning" approach, Parr & Anderson (2006) pointed out that the relationship between pyrodiversity and biodiversity, if any, is at best poorly understood; that in robust and resilient ecosystems (such as African savannas), a wide range of fire regimes have little effect on the ecosystem anyway; and that the dogma of "pyrodiversity begets biodiversity" is often accepted unquestioningly by managers. All of these are valid criticisms. As was pointed out in the original paper that proposed the thresholds for the Kruger National Park (van Wilgen, Biggs & Potgieter 1998), there is a need for ecological studies to assess the impacts of fire regimes, and the validity of thresholds.

- The management of fire in savannas will become more complex in future. As in the case of the fynbos, changes in global climate will have both direct and indirect impacts on fires and their effects; increases in CO_2 concentrations in the atmosphere will affect the balance between grasses and trees; and invasion by alien plants may also have significant impacts. Some of these issues are addressed in the next section.

1.4.4 Future challenges to fire management in savannas

The key to a better understanding of fire ecology, and the development of effective management interventions appear to lie in the adoption of a system of adaptive management. Parr & Andersen (2006) recommend that any patch mosaic burning system should incorporate an effective feedback process involving systematic monitoring. Effective feedback requires timely and accurate mapping of burned areas,
combined with monitoring both of fire heterogeneity and effects on biota. While modern geographic information systems can assist greatly in the analysis of fire patterns, the two weak links at present are obtaining and curating accurate fire maps, and establishing effective monitoring of biotic responses. In the first case, obtaining accurate fire maps will depend on the diligence and co-opetation of "on-the-ground" managers, which varies both within and between protected areas. The second lies in the challenge of identifying appropriate indicator elements to monitor, and maintaining accurate records over time and under scenarios of limited funding. In addition, other challenges face savanna fire managers, and these are covered briefly in the next section.

As stated by Bond & Archibald (2003), fire management in South African savanna conservation areas is in a state of flux. This has followed two key changes in thinking over the past two decades. The first relates to the move away from the conservation of large and charismatic fauna, to the conservation of all biodiversity and landscapes. In fire management terms, this requires managers not only to think of what is good for animals, or the conservation of rangelands that support them, but also to consider all other life forms. This has led to the embracing of concepts of variability, and "natural" fire regimes. The second relates to the replacement of concepts of ecosystem stability, and succession towards climax, with concepts of heterogeneity and flux across space and time, within a system best explained by disequilibrium models. This too has led to the promotion of management that seeks to establish variable fire regimes over space and time. Much remains to be done before these new concepts can become an integral part of routine savanna management. Currently, managers have been adopting the the paradigm of "pyrodiversity begets biodiversity" too easily (Parr & Andersen 2006), and without clear guidelines on the ranges of diversity that are possible, that are needed, or that may be detrimental. The challenge here will be to understand the limits within which fire regimes can be managed, and more importantly to what the ecological effects of this variation will be.

Two other concerns that will affect the role of fire in savanna ecosystems are currently being vigorously debated. The first relates to CO_2 enrichment, and its effects on the balance between grass and trees in savannas. The phenomenon of "bush encroachment" (increases in woody vegetation at the expense of grasses) has long been recognised as a major problem in South Africa (Hoffman 1997). It is usually attributed to the elimination of the indigenous browsing fauna (including elephants), and overgrazing by cattle. Both would have given woody plants a competitive advantage over grasses, the first directly, and the second indirectly, as lower grass fuel loads associated with overgrazing would have led to less intense fires. Recent research has also suggested that low levels of atmospheric CO_2 would have been a significant factor in the reduction of trees during glacial times, both because they would have experienced slower growth (and thus been more susceptible to fires), and because, under these conditions, fire would have promoted the spread of competing grasses (Bond, Midgley & Woodward 2003). Rising CO_2 levels (from 270 ppm in pre-industrial times to 370 ppm, and increasing, in modern times) could possibly explain the recent bush encroachment in savanna conservation areas, despite the presence of large mammalian browsers. Bond & Archibald (2003) argue that attempts to recreate "natural" fire regimes that simulate pre-colonization fire regimes will be inappropriate under scenarios of global change and higher CO_2 levels. The reversal of woody plant encroachment, and accompanying losses of biodiversity, will require the application of high-intensity, and possibly dangerous, fires to control woody plant growth. This is likely to present significant challenges to managers of savanna ecosystems.

The second remaining concern relates to the interactions between elephants and fire. Concern is often expressed about declining numbers of large trees in the Kruger National Park, which are at least in part due to fire, and interactions between fire and herbivory by elephants (Eckhardt, van Wilgen & Biggs 2000, Edkins *et al.* 2007). The exclusion of one of either fire or elephants, and the presence of the other, both result in the dominance of large trees; the co-occurrence of both apparently erodes the number of large trees (van Wilgen *et al.* 2003). Elephants do considerable damage to woody vegetation, and increase the susceptibility of trees to damage during fires (Figure 1.11). It is therefore tempting to consider either the manipulation of fire regimes, or reductions in elephant numbers, as possible means of slowing or preventing declines in large trees in the presence of elephants. However, there are a number of underlying principles that need to be considered before such interventions can be proposed (Owen-Smith *et al.* 2006). These include: (i) the absence of a benchmark against which to judge an "ideal" vegetation state for the park; (ii) the possibility that large trees present today may have established during a time when elephants had been eliminated from the area as has happened elsewhere (Dublin *et al.* 1990), and which is itself an unnatural situation; and (iii) the fact that observed declines in large trees took place despite limiting the elephant population through culling for over three decades. Owen-Smith *et al.* (2006) also point out that manipulation of one component of an ecosystem is likely to be ineffective because poorly understood feedbacks are not taken into account and that "perpetual tinkering" to meet aesthetic objectives should be avoided. There is also growing recognition that ecosystems are in a state of flux (Rogers 2003) and that stable or semi-stable states are both unattainable and undesirable. Owen-Smith *et al.* (2006) have proposed that thresholds for the maintenance of tree populations need to be made spatially explicit, for example so that the elimination of large trees can be tolerated in some areas as long as they survive in others. Clearly, the issue of interactions between fire regimes, herbivory and other factors requires better understanding if concrete recommendations about the use of fire are to be made.

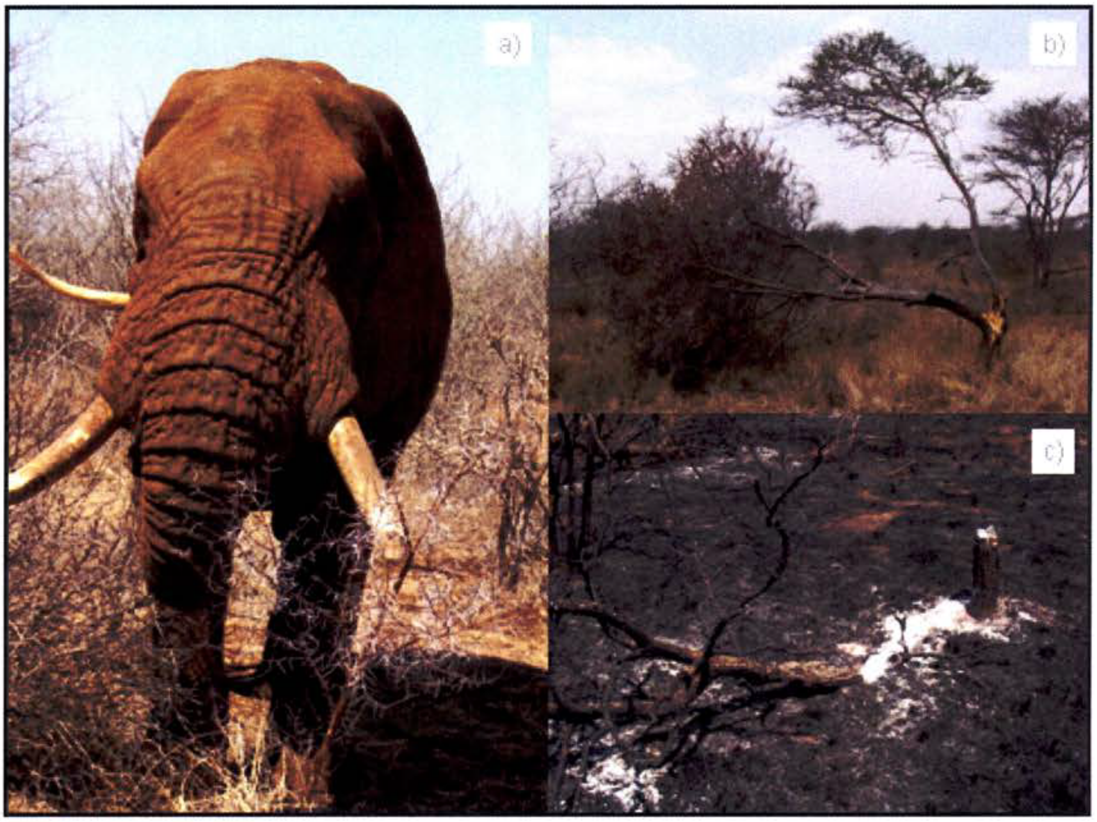

Figure 1.11. Impact of elephants on woody vegetation in combination with fire in the Kruger National Park. a) = elephant chewing a large woody stem that it has broken from a living tree; b) = typical elephant damage to Acacia nigrescens tree; c) = specimen of A. nigrescens that has been burnt off in a fire following elephant damage to the stem. Such a tree would normally survive fires of moderate or even high intensity.

1.5 Conclusions

The evolution of fire management in southern Africa over the past century has reflected increasing levels of ecological understanding. Attitudes towards fire and its management have changed dramatically from the views of the 1920s, when fire was regarded, in an ecological sense, as a detrimental force that needed to be controlled. These views were slow to change, but over the next few decades fire came to be viewed by many as something that was not always bad, and had to be tolerated and understood. As a result, many critically important long-term burning experiments were initiated in the 1950s and 1960s. As ecological understanding advanced further, fire was finally recognised as a key ecosystem process that was both inevitable and necessary.

The evolution of fire management approaches and philosophies reflected this advance in understanding. During the early 20th century, fire prevention and suppression was the order of the day. With the later acceptance of prescribed burning as a management practice, policies were developed with a view to imposing a desired fire regime onto the landscape. Under these policies, managers focussed on the implementation of particular prescriptions, without critically assessing whether or not strategic ecological objectives were met. More recently, in South Africa and elsewhere, there has been much progress towards attempts to influence fire regimes, rather than to maintain a "command-and-control" approach (Andersen 1999). There is nonetheless still much to be learnt. While we are beginning to understand the degree to which fire regimes can be influenced, surprisingly little is known about the ultimate ecological outcomes of altered fire regimes. There is thus an ongoing emphasis on setting management goals (both in terms of fire regimes and their outcomes), monitoring the outcomes closely, and making adjustments as understanding increases.

While our understanding of fire ecology has come a long way, new and significant challenges are being brought about by global change. The introduction of fire-adapted alien species has added a complex dimension to fire management. This has meant that otherwise beneficial fires now have to be regarded as a serious threat in terms of their contribution to the spread and dominance of these fire-adapted aliens. This problem is particularly acute in the fynbos biome, where all conservation areas are invaded to some degree, with many being seriously invaded. The prognosis for gaining control of this threat is not good, but it underscores the need to understand how fires can be managed to reduce the threat. More flexibility with regard to implementing control operations after unplanned fires will be needed, as will the maximum use of long-term, sustainable biological control options. Global changes in climate and atmospheric CO_2 concentrations will also have many ecological consequences, and will require ecologists to develop new approaches to the management of fires.

Our ability to deal with dynamic ecosystem management challenges in a rapidly-changing world of imperfect understanding will be determined by how well, and how fast, we can learn from experience. The recent adoption of adaptive management approaches is certainly a step in the right direction, but it needs to be expanded and strengthened. Adaptive management is hard work, and will require managers to set measurable (and meaningful) goals, collect and curate considerable volumes of data, and to continually assess new evidence, and change approaches, as understanding increases. In South Africa, we are fortunate to have a strong tradition of ecological research, and consequently understanding, on which to build. This tradition must be passed on to young South Africans if science is to maintain its important role in informing management and conservation.

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Part II.

Selected published papers.

Part II. Selected published papers

This section includes15 published papers, 5 in each of the three main fields in which I have done research:

- fire ecology and management in fynbos ecosystems;
- fire ecology and management in savanna ecosystems; and
- the ecology and management of invasive alien plants.

The papers were chosen as illustrative of the work done over 25 years (from 1982 to 2007). A full list of publications in each of these fields, as well as papers that address the broader field of fire ecology, and included at the end of this section.

Fire ecology and management of fynbos ecosystems

My early research concentrated on the ecological effects of fire in fynbos shrublands. The papers included here cover aspects of the ecological effects of fire on fynbos, and the role of vegetation structure in allowing forests to persist in fire-prone fynbos. As much of my work has focussed on the development of a sound ecological basis for fynbos fire management, I have included a review paper which illustrates how a knowledge of the biology and ecology of plants and animals can be used to arrive at rational management rules. In addition, I have included a paper that describes the development of a computer-based system for fire management in fynbos areas.

The five papers are:

- van Wilgen, B.W. (1982). Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *Journal of Ecology* 70, 217-225.

- van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. (1990). The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78, 210-222.

- van Wilgen B.W., Bond, W.J. and Richardson, D.M. (1992) Ecosystem management. *The Ecology of Fynbos: Nutrients, Fire and diversity* Ed: Cowling, R.M. Oxford University Press, Cape Town, pp 345-371.

- van Wilgen, B.W. & Forsyth, G.G. (1992). Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. *Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof.* Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 54-80.

- Richardson, DM, van Wilgen, BW, Le Maitre, DC and Higgins, KB, and Forsyth, GG (1994) A computer-based system for fire management in the mountains of the Cape Province, South Africa. *International Journal of Wildland Fire* 4, 17 -32.

Fire ecology and management in savanna ecosystems

My work on the ecological effects of fire in savanna ecosystems has been based largely on research in the Kruger National Park. The papers included here cover the documentation of fuels, fire behaviour and fire regimes in this area. An understanding of fire regimes has provided the basis for a system of adaptive management, based on "thresholds of potential concern" with regard to selected aspects of the fire regime. I have also included two papers which critically examine the role of research, and research findings, in shaping fire management policies, as well as the role of fire management in influencing aspects of the fire regime.

The 5 papers are:

- Stocks, BJ, van Wilgen, BW, Trollope, WSW, McRae, DJ, Mason, JA, Weirich, F and Potgieter, ALF (1996). Fuels and fire behaviour dynamics on large-scale savanna fires in Kruger National Park, South Africa. *Journal of Geophysical Research* 101 (D19), 23541 - 23550.

- van Wilgen, BW, Biggs, HC, and Potgieter, ALF (1998). Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe* 41, 69 - 87.

- van Wilgen, BW, Biggs, HC, O'Regan, S and Mare, N (2000). A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. *South African Journal of Science* 96 167 - 178.

- van Wilgen, BW, N. Govender, H.C. Biggs, D. Ntsala and X.N. Funda (2004). Response of savanna fire regimes to changing fire management policies in a large African national park. *Conservation Biology* 18, 1533 - 1540.

- van Wilgen, B.W., Govender, N., Biggs, H.C. (2007). The contribution of fire research to fire management: A critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16, 519 – 530.

The ecology and management of invasive alien plants

Much of my work has addressed the problem of invasive alien plants. This interest arose largely because the management of fire-prone ecosystems requires that attention be paid to the issue of fire-adapted invasive alien plants. The first paper included here addresses the effects of alien plant invasions on fuel structure and fire behaviour (an important impact of invasions). The second investigates whether certain features of closely-related invasive species could be used to predict their success in fire-prone environments. It is one of the earliest papers to illustrate that selected features of species could explain their invasive potential. The next two papers describe the potential impacts of shrub and tree invasions in key watershed areas. These papers provided the scientific justification for the initiation of the government's Working for

Water programme, a billion-rand project aimed at the control of invasive species to secure water resources and to provide employment opportunities in impoverished rural communities. The final paper proposes data-based approaches towards the prioritization of control projects.

The five papers are:

- van Wilgen, B.W. and Richardson, D.M. (1985). The effect of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *Journal of Applied Ecology* 22, 955-966.
- Richardson, D.M., van Wilgen, B.W. and Mitchell, D.T. (1987). Aspects of the reproductive ecology of four Australian Hakea species (Proteaceae) in South Africa. *Oecologia* 71, 345-354.
- Le Maitre, D.C., van Wilgen, B.W., Chapman, R.A. and McKelly, D. (1996). Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology* 33, 161 - 172.
- van Wilgen, B.W., Cowling, R.M. and Burgers, C.J. (1996). Valuation of ecosystem services: a case study from the fynbos, South Africa. *BioScience* 46, 184 - 189.
- van Wilgen, B.W., Nel, J.L. and Rouget, M. (2007). Invasive alien plants and South African rivers: A proposed approach to the prioritization of control operations. *Freshwater Biology* 52, 711 – 723.

Selected papers on the fire ecology and management of fynbos ecosystems.

First paper: Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *Journal of Ecology* (1982).

Journal of Ecology (1982), **70**, 217–225

SOME EFFECTS OF POST-FIRE AGE ON THE ABOVE-GROUND PLANT BIOMASS OF FYNBOS (MACCHIA) VEGETATION IN SOUTH AFRICA

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SUMMARY

(1) The South African vegetation type fynbos (macchia) is fire-adapted and fire-dependent.

(2) Four sites which differed in the frequency with which they had been burned were sampled towards the end (4–37 yr) of a period between fires.

(3) The above-ground shoot biomass was determined from clipped plots and regression analysis. Shoots smaller than 6 mm diameter were considered to be potential fuel.

(4) The biomass was 670 g m^{-2} 4 yr after burning; all of this was potential fuel. Fynbos 21 yr after burning had a biomass of 5100 g m^{-2} of which about half was potential fuel. Fynbos protected from fire for 37 yr had a biomass of 7600 g m^{-2}, of which more than half was potential fuel.

(5) Frequent burning keeps the biomass low. Protection from fire for longer than 30 yr results in a decline in *live* biomass and an accumulation of litter and potentially burnable vegetation. Fires in such senescent stands are usually very severe.

INTRODUCTION

Fynbos is an indigenous South African word for vegetation characteristic of large areas of the south-western Cape Province, including the types described by Acocks (1953) as macchia, false macchia and coastal macchia. Physiognomically, fynbos is characterized by three elements: restioid, ericoid, and proteoid. The restioid element comprises the Restionaceae and similar aphyllous grass-like plants up to 1 m tall, while ericoid plants are usually short shrubs with small, narrow and often rolled leaves. Taller shrubs with moderate-sized sclerophyllous leaves comprise the proteoid element, which may be absent in certain habitats. The Cape Floristic Region and its flora have been described by Goldblatt (1978), Taylor (1978) and Kruger (1979).

Fynbos vegetation has been burned periodically for probably 100 000 yr, and possibly since the early Pleistocene (Kruger 1979), and is adapted to survive fires (Van der Merwe 1966). In order to accumulate enough fuel to burn, more than 4 yr must have elapsed since the previous fire, but the period between fires is usually 12–20 yr. Vegetation which has not been burnt for more than 30 yr is rare. Fires may be caused by human action or by natural phenomena such as lightning or falling rocks (Bands 1977; Kruger 1979). Recently, there has been increased interest in the above-ground plant biomass of fynbos communities and preliminary results have been reported by Kruger (1977) and Rutherford (1978). Biomass values may be used to calculate primary productivity and to predict fire intensity and behaviour (see, for example, Specht 1969b; Countryman & Philpot 1970; Kruger 1977). Here I report the biomass of fynbos stands protected from fire for up to 37 yr.

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THE STUDY AREA

The Jonkershoek Valley (33°57′S, 18°55′E) has been described by Wicht, Meyburgh & Boustead (1969); it runs from east to west. At the western end it is open, while on the other three sides it is enclosed by mountains, formed predominantly from sandstones of the Table Mountain Group (Cape Supergroup). Faulting has resulted in a difference in altitude of the Table Mountain Group on the north (610 m) and south (426 m) sides of the valley. The north-facing slopes are underlain by sandstones, or sandstone-granite mixtures, whereas the south-facing slopes are underlain by granite. Although colluvial material from the sandstones above affects all the soils of the area, their influence is less on the south-facing slopes. The north-facing aspect has a higher potential evapotranspiration which results in more xeric plant communities than on the south-facing slopes (Holland & Steyn 1975).

The climate is mediterranean, Köppen's (1931) humid-mesothermal (type Csb), with a dry summer and the average temperature of the warmest month below 22 °C. Rainfall patterns in the valley are described by Wicht, Meyburgh & Boustead (1969); the value of the mean annual rainfall for the sites is included in Table 1. About 60% of the rain falls in the period from May to August.

The mature vegetation of the area is an approximately 4-m tall closed shrubland (Plate 2). The predominant species are *Protea neriifolia* R. Br. and *P. repens* (L.) L. (Proteaceae). On south-facing slopes *P. repens* is less abundant while *Widdringtonia nodiflora* (L.) Powrie (Cupressaceae), a small tree, and *Brunia nodiflora* L. (Bruniaceae), a fynbos endemic shrub, are prominent. In addition, certain moisture dependent shrubs, not found on the north-facing aspect, occur. The understorey contains other smaller shrubs, together with restioid, graminoid and forb components, although these form a relatively small part of the total biomass in mature vegetation.

PLATE 1. Young frequently burnt vegetation, typical of sites 1 and 2, photographed 4 yr after a fire. Graminoid and restioid plants predominate; large shrubs are absent. Scale is 2 m tall and divided into 20 cm segments. (Photograph by B. W. van Wilgen.)

PLATE 2. Mature vegetation 21 yr after a fire on site 3. Large shrubs (especially *Protea* spp.) predominate; firebreak in foreground. Scale as on Plate 1. (Photograph by B. W. van Wilgen.)

PLATE 3. Senescent vegetation 37 yr after a fire on site 4. Dead *Protea neriifolia* shrubs in foreground; large trees of *Widdringtonia nodiflora* in middle distance. Scale as on Plate 1. (Photograph by B. W. van Wilgen.)

In the early stages of the succession after fire large shrubs are absent and hemicryptophytes (chiefly belonging to the families Restionaceae, Poaceae, and Cyperaceae) predominate (Plate 1). These diminish in importance as the shrub canopy closes. On south-facing slopes vegetation protected from fire for 37 yr has reached a senescent stage. Of the predominant species *Widdringtonia nodiflora* remains healthy and apparently vigorous, while much of the *Brunia nodiflora* is dead. Most of the *Protea neriifolia* has died and surviving plants often have only one or two live branches (Plate 3).

METHODS

Four 50 × 50 m sites in areas differing in the time since they were last burned (and in their frequency of burning) were sampled during 1979. All were in the grounds of the Jonkershoek Research Station. Table 1 shows the principal features of the four sites which were carefully selected to give pairs of sites with similar rocks, soil, altitude and aspect. Two of these sites (sites 1 and 2) were in firebreaks that had been burnt frequently (in 1942, 1948, 1954, 1960, 1968 and 1975) and were sampled 4 yr after a fire. Another (site 3) was in vegetation burnt in 1927, 1942 and 1958—21 yr prior to sampling. The last (site 4) was last burnt 37 yr ago. The history of the sites prior to the dates given is unknown. The effects of the season at which the vegetation was burned were not considered.

TABLE 1. Principal features of the fynbos sites at Jonkershoek.

Site	Altitude (m)	Aspect (°)	Slope (°)	Mean rainfall* (mm yr^{-1})	Predominant rocks	Time since burnt (yr)
1	470	235	14	1800	Cape Granite	4
2	455	20	20	1625	Table Mountain Sandstone	4
3	425	31	28	1600	Table Mountain Sandstone	21
4	425	241	26	1950	Cape Granite	37

* Mean value, by interpolation from Wicht, Meyburgh & Boustead (1969).

Young vegetation (*sites 1 and 2*)

Biomass was determined by clipping aerial plant parts, as close to the soil surface as possible, from twenty-four 1 × 2 m quadrats, distributed on each site in a stratified random manner, following the ranked set sampling procedure of Halls & Dell (1966). Litter was collected from the soil surface; dead plants were included as litter. Clipped material was separated into growth-form categories.

The following categories were used (Kruger 1977):—

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

(ii) Sub-shrubs: sub-woody 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 (Adamson 1931).

(v) Forbs: non-woody species not included in the above categories, and including ferns.

The samples were stored (for up to 10 days) and then oven dried at 105 °C for 24 h (or, in the case of large branches, until weight changes were insignificant) and their mass determined.

Mature vegetation (*site 3*)

Biomass was estimated as for young vegetation, but *Protea repens* and *P. neriifolia* were not collected. In order to estimate the amount of fuel available, the clipped material was divided into those pieces with diameter less than 6 mm and those of greater diameter;

branches were cut across where their diameters reached 6 mm. This arbitrary division follows the rule of thumb (e.g. Countryman & Philpot 1970) that material with a diameter greater than 6 mm does not burn.

Estimation of the biomass of the two predominant shrubs was carried out by regression analysis. Twenty-two *Protea neriifolia* and twenty-four *P. repens* shrubs, selected to cover a representative range of diameters, were harvested from outside the site after measuring their diameters 20 cm above ground-level. They were divided into potential fuel (pieces less than 6 mm diameter) and larger pieces. Each component was weighed and subsampled for moisture content to estimate the oven-dry weight of the original material. Linear, power and exponential regressions were fitted (Daniel & Wood 1971) and tested for goodness-of-fit using Furnival's (1961) index. In all cases power curves provided the best fit. The following equations were obtained for *P. neriifolia* where x is the diameter (cm) 20 cm above ground-level, y (kg) is the dry weight and n is the total number of shrubs measured:—

(i) diameter and total dry weight:

$$\log_e y = -2{\cdot}23 + 2{\cdot}26 \log_e x \quad (n = 105, r^2 = 0{\cdot}91); \tag{1}$$

(ii) diameter and dry weight of large branches:

$$\log_e y = -2{\cdot}23 + 2{\cdot}12 \log_e x \quad (n = 105, r^2 = 0{\cdot}87). \tag{2}$$

A similar allometric model for *P. repens* gave:—

(i) diameter and total dry weight:

$$\log_e y = -2{\cdot}70 + 2{\cdot}46 \log_e x \quad (n = 241, r^2 = 0{\cdot}92); \tag{3}$$

(ii) diameter and dry weight of large branches:

$$\log_e y = -2{\cdot}89 + 2{\cdot}36 \log_e x \quad (n = 241, r^2 = 0{\cdot}84). \tag{4}$$

The diameter of each bush of *P. neriifolia* on the site was measured and its total biomass and that of its large branches calculated from Eqns (1) and (2). These estimates were adjusted to allow for bias resulting from logarithmic transformations by the correction factor of Mountford & Bunce (1973). The fuel component was estimated by subtraction. The same procedure was followed for *P. repens* but using Eqns (3) and (4).

Senescent vegetation (*site 4*)

Biomass estimation was carried out as for the mature vegetation on site 3, but using a regression model (based on twenty trees) for *Widdringtonia nodiflora* only. The methods used were as for *Protea* spp. except that cones were designated as an additional component. The equations were:—

(i) diameter and total dry weight:

$$\log_e y = -2{\cdot}82 + 2{\cdot}34 \log_e x \quad (n = 247, r^2 = 0{\cdot}97);$$

(ii) diameter and dry weight of fuel:

$$\log_e y = 3{\cdot}19 + 1{\cdot}94 \log_e x$$
$$(n = 247, r^2 = 0{\cdot}94);$$

(iii) diameter and dry weight of cones:

$$\log_e y = 7{\cdot}83 + 3{\cdot}42 \log_e x$$
$$(n = 247, r^2 = 0{\cdot}79).$$

RESULTS

The regressions of diameter against total dry weight for the two *Protea* species (Eqns 1 and 3) did not differ significantly. Despite the apparent similarity between total and branch mass regressions (Eqns 1 and 2 and Eqns 3 and 4) they are significantly different (at $P = 0{\cdot}05$), as are the two branch regressions (Eqns 2 and 4). A regression using total mass data for both *Protea* species was compared with the regression for *Widdringtonia nodiflora*. There was no significant difference between the residual variances or slopes but the difference in intercept was significant.

Biomass results for each site are presented in Tables 2 and 3. The largest diameters used in calculating the regressions were 14·3 cm for *Protea neriifolia*, 14·8 cm for *P. repens* and 14·0 cm for *Widdringtonia nodiflora*; larger diameters were encountered on the sites, and biomass estimates from these were extrapolated.

The values in Table 2 show large confidence intervals for biomass of older vegetation due to its structural heterogeneity. The confidence interval of the total biomass was not estimated, as results from clipped plots and regressions were added, but the estimates from regressions contributed most to the estimate of live biomass (89% for site 3 and 72% for site 4), and the regressions do account, in most cases, for more than 90% of the observed variability. The estimates for litter (Table 2) on sites 1 and 2 do not differ significantly, whereas those from sites 3 and 4 are different from each other and from sites 1 and 2 ($P < 0{\cdot}01$).

The results are most easily considered, initially at least, as three points in a single time-series, ignoring the fact that the sites differ in the frequency with which they have

TABLE 2. Above-ground live plant biomass and litter on clipped plots at four sites with fynbos vegetation of different post-fire age. For each site $n = 24$.

Site:	1	2	3	4
Time since last fire (yr):	4	4	21	37
(a) Above-ground live biomass				
Dry mass (g m^{-2})	660	590	410‡	630‡
*Coefficient of variation (%)	12	15	62	87
†Confidence interval (g m^{-2})	±33	±38	±106	±232
(b) Litter				
Dry mass (g m^{-2})	53	33	1430	5330
*Coefficient of variation (%)	71	35	54	28
†Confidence interval (g m^{-2})	±16	±5	±330	±630

* $s/\bar{x}$.

† $P = 0{\cdot}95$.

‡ Excluding shrubs, see Table 3.

TABLE 3. Above-ground total plant biomass at four sites with fynbos vegetation of different post-fire age.

	Total biomass (g m^{-2})				*Potential fuel (g m^{-2})	
Site:	1	2	3	4	3	4
Time since last fire (yr):	4	4	21	37	21	37
Large shrubs:						
Protea neriifolia	<1	<1	930	0†	270	0†
P. repens	<1	<1	2310	0†	810	0†
Widdringtonia nodiflora	<1	<1	<1	1650	<1	440
Other shrubs	92	52	94	556	71	310
Sub-shrubs	<1	1	21	<1	<1	<1
Restioid plants	180	170	63	26	63	26
Graminoid plants	310	290	49	16	49	16
Other forbs	85	83	182	35	180	35
‡Total live biomass	660	590	3650	2300	1450	820
Litter	53	33	1430	5300	1250	3500
‡Total	710	620	5100	7600	2700	4300

* Pieces less than 6 mm diameter (see text).

† Included in 'other shrubs'.

‡ Rounded value.

been burnt. It is evident (Table 3) that total live biomass is greater 21 yr after a fire than it is either 4 or 37 yr after, but that the amount of litter increases with time since the last fire, up to 37 yr at least. The apparent continued increase in *total* biomass with age on site 4 (Table 3) is due to the contribution of *Widdringtonia nodiflora*, which was absent on site 3. Live biomass on site 3 can be expected to decline sharply once *Protea* shrubs start to die. This occurred at a post-fire age of about 25 yr on site 4.

Graminoid and restioid plants with shoot diameters less than 6 mm predominate in communities 4 yr after burning (Kruger 1977). Thus the total biomass of sites 1 and 2 is nearly all potential fuel. Estimates of the fuel components on sites 3 and 4 are given in Table 3. At 21 yr after burning much of the potential fuel consists of live material.

DISCUSSION

Fynbos compared with other vegetation

Kruger (1977) compared the biomass of fynbos communities with that of mediterranean-type ecosystems elsewhere. The maximum biomass was 4970 g m^{-2} for 13-yr-old garrigue (France) and 4910 g m^{-2} for 37-yr-old chaparral (California) of which 2180 g m^{-2} was standing dead wood (Specht 1969a). The maximum biomass for fynbos was 2570 g m^{-2} for a 17-yr-old sclerophyll scrub community at Jonkershoek. The values reported in this paper are the highest for mediterranean-type ecosystems.

Jonkershoek is not entirely representative of fynbos communities mainly because of soil differences and higher rainfall. Most fynbos soils are derived from sandstones alone, whereas soils at Jonkershoek are partly derived from granite. However, growth rates in fynbos are affected by soil moisture availability more than by soil fertility (Kruger 1977).

The effects of burning

In fires burning under cool and moist conditions (for example, those started deliberately) much of the potential fuel in old fynbos remains unburnt. In very dry weather, however, fires will burn vigorously in the shrub crowns and consume much of the fuel. In vegetation older than 30 yr since the last fire, most of the biomass is dead and dry, and much has fallen to the ground as litter. Under normal summer weather, fires will be intense and will burn much of the coarser litter as well as the fine material. Under severe drought a fire would probably consume all the litter and most of the live vegetation. The ability of the vegetation to recover after such severe fires is little understood. McLachlan & Moll (1976) observed that areas not burnt for 20–25 yr recovered better than did areas burnt at shorter intervals of about 12 yr. On the other hand, the accumulation of litter in old fynbos results in very intense fires. Observations after a fire in 40-yr-old fynbos in the Cedarberg mountain range showed that an unusually large proportion of species which normally survive by vegetative regeneration had died; 32% of *Heeria argentia* (E. Mey.) O. Knutze trees were killed (F. J. Kruger, personal communication). Rourke (1972) found that the degree of recovery after burning of some resprouting species of *Leucospermum* (Proteaceae) depended largely on the intensity of the fire. Bond (1980) reported little seed regeneration following fire in 45-yr-old fynbos due to a reduction in both seed production and stored seed; this again indicates that the vegetation is not adapted to long intervals between fires.

Frequent burning drastically reduces the biomass, due to the elimination of most of the seed-reproducing shrubs (Jordaan 1949; Van Wilgen & Kruger 1981). Young fynbos is usually dominated by hemicryptophytes which sprout again following fire. The greater biomass of older stands is mainly due to large seed-reproducing shrubs, the seedlings of which are absent in frequently burnt fynbos as potential parents do not have time to mature between fires. It appears that the biomass will remain low unless larger shrubs immigrate. Bond (1980) found that seed dispersal in fynbos was inefficient, and that abundant regeneration depended on a healthy population of adults before a fire. Frequent burning may therefore result in permanent loss of these shrubs, especially if the burnt areas are large.

Protection of communities from fire for periods longer than 30 yr results in a decline in total live biomass and a considerable increase in the amount of litter and fuel. There is evidence that communities on sandstone soils have not reached the same state of degradation as those studied here (E. J. Moll, personal communication); these communities may have a longer cycle, but will probably follow a similar course to those at Jonkershoek. What would happen if communities were to be protected from fire for much longer periods can only be surmised. There are some forest precursor species on the moister sites (for example *Kiggelaria africana* L., *Rapanea melanophloeos* (L.) Mez and *Olea africana* Mill.) but it is doubtful if a true forest could develop due to the shallow rocky soils and summer drought.

ACKNOWLEDGMENTS

I thank L. T. Arends and G. G. Forsyth for assistance with field work, and Dr E. J. Moll, F. J. Kruger and W. J. Bond for useful comments on the manuscript.

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(*Received* 29 *May* 1981)

Second paper: The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* (1990).

Journal of Ecology (1990), **78,** 210–222

THE ROLE OF VEGETATION STRUCTURE AND FUEL CHEMISTRY IN EXCLUDING FIRE FROM FOREST PATCHES IN THE FIRE-PRONE FYNBOS SHRUBLANDS OF SOUTH AFRICA

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SUMMARY

(1) South African fynbos is fire-prone, but contains non-flammable forest patches which seldom burn. Although fuel structure and foliar chemistry are often hypothesized to be important in determining flammability, the fuel properties of these vegetation communities are poorly known.

(2) Biomass, the size and vertical distribution of plant parts as fuel, foliar moisture contents, heat yields, and crude fat contents were determined in the two vegetation communities, to test if differences would explain the inability of fires to penetrate forest patches. The data were also used to define fuel models and to simulate fire behaviour in the two communities, using a modification of Rothermel's fire model for multi-layered vegetation.

(3) Fuel mass in fynbos was less than half that in the forest. The forest also differed from fynbos in being taller, and having a pronounced separation between the litter layer and tree canopies. The ratio of fuel volume to fuel-bed volume of forest species was half that of fynbos species, reflecting the sparse nature of the crowns. Foliar moisture contents of forest trees were 50–100% higher than in fynbos plants.

(4) Heat yields were marginally higher (21 860 J g^{-1}) in fynbos than in forest species (20 703 J g^{-1}). Crude fat contents of forest species averaged about 3% of dry mass. The fat contents were more variable among the fynbos species, but some species had high (6–10%) fat contents.

(5) The modified Rothermel model predicted flame lengths of 0·7–4·9 m in fynbos under low to extreme fire hazard conditions, but predicted that fires would fail to burn in forest vegetation under the same conditions.

(6) The physical and chemical make-up of fynbos favours fire. It is more flammable than Chilean mattorral, but is less flammable than Californian chaparral or Australian *Eucalyptus* woodlands due to lower crude fat contents and higher foliar moisture contents. Although narrow forest strips may be scorched by intense fires in adjacent fynbos, it seems unlikely that extensive forest patches would burn under the conditions usually selected for prescribed burning operations.

INTRODUCTION

Fynbos shrublands cover large tracts of mountain land in the southern and southwestern Cape Province of South Africa. Fynbos usually burns about once every twenty years (Van Wilgen 1982; Kruger & Bigalke 1984), and fires can be relatively intense when compared to those in other similar shrublands (Van Wilgen, Le Maitre & Kruger 1985). Fynbos is managed by prescribed burning in order to rejuvenate the vegetation, reduce fire hazard, and control woody weed species. In mountain areas, landscapes dominated by fynbos contain small patches of evergreen (Afromontane) forest; these patches do not burn except under severe conditions (see, for example, Everard 1986). Despite concern that regular burning would erode forest patches (Van der Merwe 1966; Everard 1986), there is little information on their sensitivity to repeated fire. An understanding of the dynamics of the boundary between flammable and non-flammable communities would promote their efficient management.

Cursory examination of the forest–fynbos boundary reveals abrupt differences in structure between the two types. Fynbos contains graminoid and restioid herbs and ericoid shrubs with fine leaves, and significant proportions of dead material held aloft to form a porous fuel bed about 1 m deep. Larger proteoid shrubs (2–3 m tall) dominate above this fuel bed, and burn readily under warm, dry conditions. Forests are dominated by large trees (up to 25 m tall) with canopies of live foliage. Dead material is restricted to the compact litter layer below the tree canopies. Fires in forest patches could be either crown fires (fires that burn in the canopies of trees) or surface fires (in the fuel layers on the ground). Usually crown fires are sustained by surface fires below them (dependent crown fires), but under severe conditions fires can advance through the crowns of trees leaving the surface fire some distance behind (independent crown fires). Whether or not forest patches in fynbos will burn depends on whether or not crown fires can develop in the canopies of trees.

Fire behaviour in multi-layered vegetation can be simulated using an approach based on Rothermel's (1972) fire model. This model was designed to predict fire behaviour in a single continuous stratum of fuel on the ground. Fire-behaviour predictions from the model are based on the physical and chemical make-up of the fuel and the environmental conditions under which it is expected to burn. Fuel characteristics such as estimates of fuel loads, fuel particle sizes, fuel-bed depth and heat yields are summarized in fuel models (Deeming & Brown 1975). The assumption of single stratum in the vegetation leads to inaccurate predictions of fire behaviour where vegetation displays vertical discontinuities. Kessell *et al.* (1978) modified Rothermel's model to allow for multi-layered vegetation fuel models. This was done by accommodating separate fuel models for up to three strata, and calculating the rate of spread for individual strata, which could vary in cover. Fuel inputs for the three-strata model include: (i) fuel loads divided into the litter layer (first stratum), live grass and herbs with standing dead fuel of <6 mm, 6–25 mm and >25 mm (second stratum), and shrub foliage and shrub branchwood (<6 mm) (third stratum); (ii) a percentage cover value for each stratum; and (iii) a packing ratio for each stratum. The size classes for dead fuel follow the convention used for estimating available fuel in fuel models (Countryman & Philpot 1970; Deeming & Brown 1975; Van Wilgen 1982). Packing ratios are defined as the ratio of bulk density (fuel mass per unit volume occupied by fuel and air) to the specific gravity (fuel mass per unit volume occupied by fuel alone). A stratified-fuel-modelling approach could allow for the simulation of conditions likely to lead to crown fires in forest patches.

In this study, the structural and chemical properties of fynbos and forest vegetation across the boundary between the two communities were examined in order to establish differences in their fuel properties. It is postulated that the inability of forest patches to burn could be due to one or more of the following factors: (i) a higher moisture content in the live foliage of forest trees when compared to fynbos shrubs and herbs; (ii) a higher proportion of crude fats in fynbos compared to forest plants; (iii) higher heat yields in fynbos than in forest plants; (iv) differences in the packing ratios of plant (fuel) parts, and in the ratio of live to dead material. These differences were formalized by constructing stratified fuel models for the two vegetation types and simulating fire behaviour under various conditions.

MATERIALS AND METHODS

Study site

The Swartboskloof Valley (373 ha in extent), forms part of the Jonkershoek Valley (33°57′S, 18°55′E) in the Hottentot's-Holland mountain range, southwestern Cape Province. Swartboskloof is a fan-shaped valley ranging from 285 m to 1200 m a.s.l., and has an equatorial (north-facing) aspect. Sandstones of the Table Mountain Group (Cape Supergroup) are underlain by Cape granite. The climate is characterized by cool wet winters and a warm dry summer; annual rainfall is about 1600 mm, of which about 60% falls in the period from May to August. The area was last burnt in November 1977.

The vegetation of the area is described by McDonald (1988). The dominant vegetation is a tall (2–3 m) shrubland dominated by *Protea neriifolia* and *Brunia nodiflora.* The understorey contains smaller shrubs, restioid, graminoid and forb components. Forests (up to 25 m tall) occur on less than 10% of the area, and are restricted to the fringes of perennial streams and rocky scree slopes. The major tree species include *Cunonia capensis, Ilex mitis, Maytenus oleoides* and *Brabejum stellatifolium.* Nomenclature in this paper follows Bond & Goldblatt (1984).

Biomass and fuel loads

Biomass and fuel loads were determined in the fynbos and forest sites separately. In fynbos, all plant material, other than the dominant shrub *Protea neriifolia,* was clipped from a random sample of ten plots (each 2 m × 2 m). Clipped material was divided into litter and standing dead, woody shrubs (other than *P. neriifolia*), and herbaceous (non-woody) plants. These categories were further subdivided into size classes (< 6 mm, 6–25 mm and > 25 mm for dead material and < 6 mm and > 6 mm for live material). Samples were oven-dried and weighed to determine dry mass. The mass of *P. neriifolia* was estimated from existing regressions of biomass, and mass of material < 6 mm, on stem diameter (Van Wilgen 1982). The stem diameter of each *P. neriifolia* shrub occurring on two random transects of 2 m × 30 m was measured and the dry mass of the shrubs calculated from the regression equations.

Forest litter and understorey shrubs up to 1·5 m tall were clipped from a random sample of ten plots (each 2 m × 2 m). Clipped material was divided as above. Tree canopies in the sample area were up to 15 m tall, and were sampled from ten random plots, each 1 m × 2 m. Scaffolding was erected to gain access to the canopies. Plots were delimited by means of four metal rods extending from ground level to above the tree canopies. Frames equal to the plot size were used to hold the rods together. Stems of trees and live branches > 6 mm in diameter were not included because of logistical difficulties in doing this, and because they do not normally burn. All plant material within the volume defined by the rods, and above 1·5 m from the ground, was collected. Plant material was divided into dead material (< 6 mm, 6–25 mm and > 25 mm), and live foliage and small branches (< 6 mm). These were weighed in the field and subsampled for moisture content to estimate dry mass.

Vegetation height and stratification

Vegetation height and stratification were assessed from a transect (1 m × 25 m) across the boundary between the forest and fynbos communities. A level reference line was spanned across the transect. The following data were recorded: (i) mean depth of the litter layer at 0·5-m intervals; (ii) the distance to the ground from the reference line; and (iii) the height, crown diameter and height to the lowest leaves of each plant on the transect. Tree heights were measured from the reference line using a telescopic height rod. Plants were recorded as evergreen trees, microphyllous shrubs such as *Protea neriifolia*, leptophyllous shrubs such as *Erica* species, orthophyllous shrubs such as *Halleria elliptica*, evergreen herbaceous plants such as *Restio* species, ferns, or standing dead plants (see Table 1 for definition of leaf categories).

Packing ratios

Twelve species (Table 1) were selected to represent dominant forest trees, and fynbos shrubs and herbs. An estimate of bulk density was obtained from three representative individuals of each species. The crown volume was measured in the field. Each plant was then harvested, all pieces < 6-mm diameter were removed, oven-dried and weighed. For large trees, single branches only were harvested. Specific gravity values were determined from the volume and mass of ten freshly collected samples of each species. Volumes were determined using the method of Burdett (1979). The samples were then dried and weighed. Packing ratios were calculated as the ratio of bulk density to specific gravity.

Moisture, energy and crude fat contents of plants

Foliar moisture contents of the species (Table 1) were monitored monthly for one year. Each month, five samples of the live foliage of each species were collected, sealed in air-tight bottles to prevent moisture loss, weighed and oven-dried. The percentage moisture content was calculated on a dry-weight basis. The energy contents of three samples of each of the species, collected in January 1989, were determined using standard bomb calorimetry. Oils, fats, waxes and terpines (hereafter referred to as crude fats) of five samples of each of the species were extracted with ether using the Soxhlet extraction apparatus (Peters, Hayes & Hieftje 1974). This was done separately for samples collected in July (winter), September (spring), December (summer) 1988 and March (autumn) 1989. Extracts were expressed as a percentage of the dry mass.

TABLE 1. Details of twelve species selected for analysis of fuel properties along a forest–fynbos gradient in Swartboskloof, Cape Province. The leaf categories are as follows: Sc = sclerophyllous (hard-leaved); Op = orthophyllous (soft-leaved); Mp = microphyllous (leaf area 225–2025 mm^2); Np = nanophyllous (leaf area 25–225 mm^2); Lp = leptophyllous (leaf area < 25 mm^2); Ap = aphyllous (without leaves).

Species	Growth form	Leaf category	Maximum height (m)	Vegetation community
Kiggelaria africana	Tree	Mp, Op	10	Forest
Cunonia capensis	Tree	Mp, Op	25	Forest
Brachylaena neriifolia	Tree	Mp, Sc	5	Forest
Maytenus oleoides	Tree	Mp, Sc	10	Forest
Ilex mitis	Tree	Mp, Op	25	Forest
Brabejum stellatifolium	Tree	Mp, Sc	15	Forest
Ischryolepis gaudichaudiana	Restioid herb	Ap	1	Fynbos
Protea neriifolia	Shrub	Mp, Sc	3	Fynbos
Erica plukenetii	Shrub	Lp, Sc	1	Fynbos
Brunia nodiflora	Shrub	Lp, Sc	2	Fynbos
Cliffortia cuneata	Shrub	Np, Sc	3	Fynbos
Widdringtonia nodiflora	Tree	Lp, Sc	6	Fynbos

TABLE 2. Above-ground biomass (g $m^{-2} \pm 1$ S.E.) of vegetation components in forest and fynbos sites in Swartboskloof, Cape Province ($n = 10$).

Vegetation community	Fynbos	Forest
Tree canopies (above 1·5 m)		
Live foliage and twigs (< 6 mm)	0	1824 (169)
Dead material (< 6 mm)	0	443 (78)
Dead material (6–25 mm)	0	221 (55)
Protea neriifolia		
< 6 mm	248†	0
> 6 mm	973†	0
Other shrubs		
< 6 mm	500 (54)	53 (12)
> 6 mm	187 (37)	not sampled
Herbaceous plants (< 6 mm)	68 (12)	69 (43)
Dead material (below 1·5 m)		
< 6 mm	880 (64)	1296 (147)
6–25 mm	439 (59)	222 (29)
> 25 mm	206 (65)	108 (32)
Total mass (dead + live)	3501†	4236*†
Total fuel (< 6 mm)	1696†	3685†

* Does not include stems of trees or live branches > 6 mm in diameter.
† No estimates of S.E. possible.

Simulation of fire behaviour

Fire behaviour was simulated using the modification by Kessell *et al.* (1978) of Rothermel's (1972) fire model. Fuel loads for use in fuel models were obtained from biomass estimates, cover estimates from the transect data, and packing ratios from the estimates described above. Simulations of fire behaviour were done using the PC-based FIREPLAN package (Gradient Modelling 1985). This package allows users to enter fuel models, together with estimates of fuel moisture, wind and slope, in order to predict fire behaviour under the selected conditions.

RESULTS

Biomass and fuel loads

The mass of plant parts that can be regarded as fuel was higher at the forest site than at the fynbos site (Table 2). The amount of dead material was 1·5 times greater, live plant parts < 6 mm in diameter were 2·4 times greater, and total fuel (all parts with diameters < 6 mm) was 2·2 times greater at the forest site. Total above-ground biomass was not estimated at the forest site, but was obviously much higher than in fynbos (see Fig. 1).

Vegetation height and stratification

In the fynbos, ericoid and proteoid shrubs, herbaceous plants and standing dead material form a vertically continuous fuel bed about 1–2 m deep (Fig. 1). In the forest, tree canopies are about 5 m above the litter layer, and are 5–7 m deep. Rothermel's fire model assumes that fuel beds are homogenous, but this is seldom true in natural vegetation. Although no measure of fuel-bed heterogeneity exists, Fig. 1 provides a visual impression of this feature. Two well-defined and relatively homogenous strata (litter layer and tree

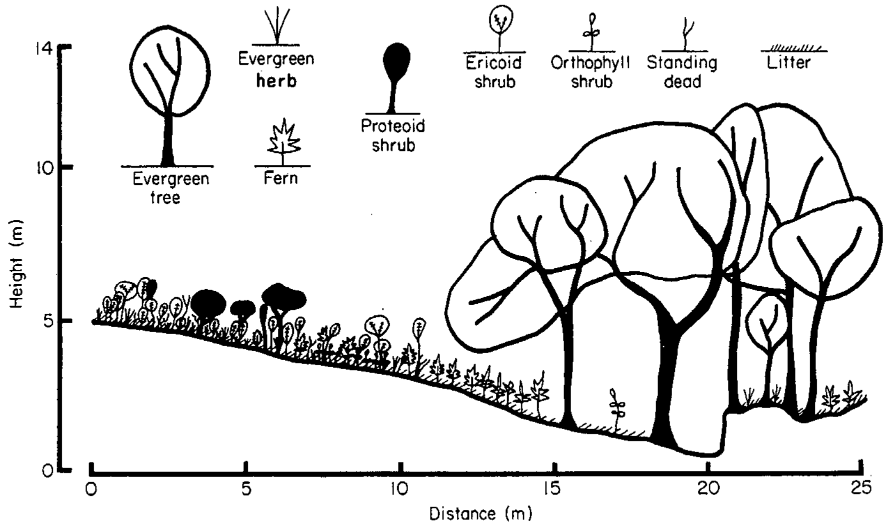

FIG. 1. Profile diagram from a 1-m-wide transect across the boundary between fynbos and forest communities at Swartboskloof, Cape Province.

crowns) exist in the forest. In fynbos, the strata are less well defined. In addition, the shrub stratum is discontinuous, and has two structurally different shrub types (proteoid and ericoid). Abrupt changes in structure between fynbos and forest include an increase in plant height, and a spatial separation of the crowns of dominant plants from the litter layer.

TABLE 3. Mean energy contents, specific gravities, bulk densities and packing ratios for the foliage of six forest and six fynbos species. The figure in parentheses is 1 S.E. ($n = 5$ for specific gravities, and $n = 3$ for energy contents, bulk densities and packing ratios).

Species	Energy content (J g^{-1})	Specific gravity (g m^{-3} × 10^{3})	Bulk density (g m^{-3} × 10^{3})	Packing ratio (bulk density: specific gravity)
Kiggelaria africana	19 752 (466)	371·2 (21)	0·59 (0·1)	0·0016 (0·0002)
Cunonia capensis	20 100 (646)	291·5 (14)	0·83 (0·2)	0·0029 (0·0005)
Brachylaena neriifolia	21 665 (165)	269·4 (27)	0·37 (0·1)	0·0014 (0·0003)
Maytenus oleoides	20 329 (844)	348·7 (5)	3·20 (0·3)	0·0092 (0·0008)
Ilex mitis	20 258 (580)	397·5 (19)	0·64 (0·1)	0·0016 (0·0003)
Brabejum stellatifolium	22 116 (170)	287·7 (31)	1·60 (0·2)	0·0056 (0·0008)
Ischryolepis gaudichaudiana	20 838 (164)	554·5 (18)	4·31 (0·4)	0·0078 (0·0007)
Protea neriifolia	22 695 (452)	495·3 (11)	6·48 (0·8)	0·0131 (0·0002)
Erica plukenetii	20 957 (399)	465·4 (30)	3·57 (1·0)	0·0077 (0·0022)
Brunia nodiflora	23 793 (537)	456·7 (9)	4·30 (0·6)	0·0094 (0·0013)
Cliffortia cuneata	19 683 (586)	300·3 (48)	0·47 (0·1)	0·0016 (0·0001)
Widdringtonia nodiflora	23 195 (917)	378·6 (7)	1·68 (0·8)	0·0044 (0·0022)

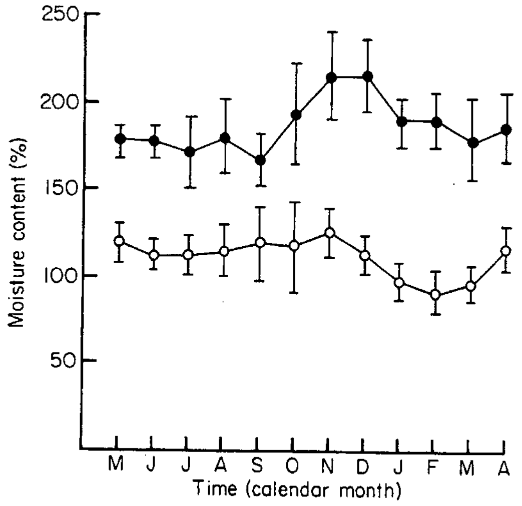

FIG. 2. Seasonal trends in the mean moisture contents of six fynbos (○) and six forest (●) species at Swartboskloof, Cape Province. (see Table 1 for species). Bars are the 99% confidence intervals of the mean ($n = 30$).

Packing ratios

The mean specific gravity of fynbos species is about 33% higher than the mean for forest species (Table 3). The sparse nature of the crowns of forest trees is reflected in a relatively low bulk density, with the exception of *Maytenus*, which had fairly dense

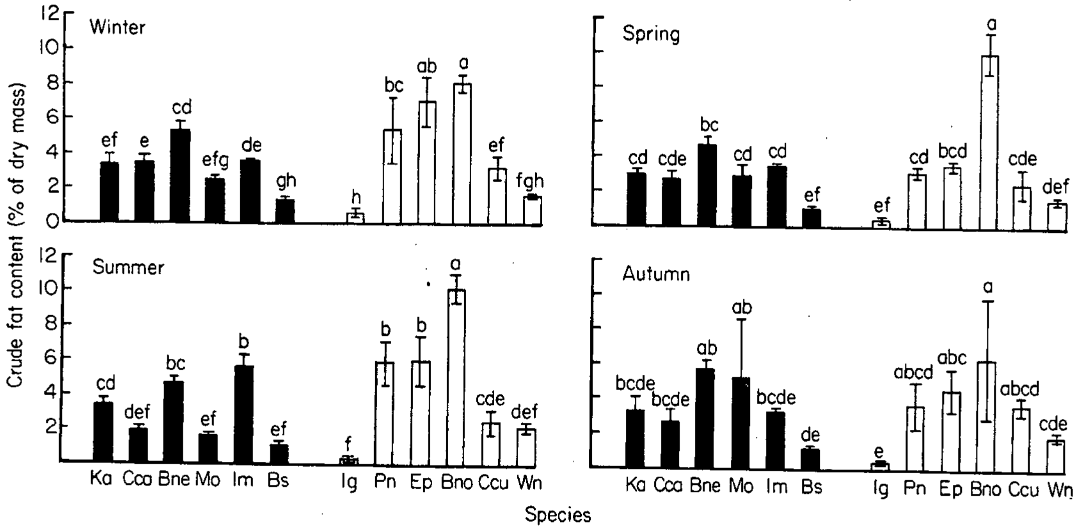

FIG. 3. Mean percentage crude fat contents for six fynbos (□) and six forest (■) species in four seasons at Swartboskloof, Cape Province. Bars show the 95% confidence intervals of the mean ($n = 5$). Values sharing the same letter are insignificantly different at $P = 0{\cdot}05$ (Tukey's Studentized range test). The species are: Ka = *Kiggelaria africana*, Cca = *Cunonia capensis*, Bne = *Brachylaena neriifolia*, Mo = *Maytenus oleoides*, Im = *Ilex mitis*, Bs = *Brabejum stellatifolium*, Ig = *Ischryolepis gaudichaudiana*, Pn = *Protea neriifolia*, Ep = *Erica plukenetii*, Bno = *Brunia nodiflora*, Ccu = *Cliffortia cuneata* and Wn = *Widdringtonia nodiflora*.

TABLE 4. Details of fuel models used to simulate fire behaviour (using the three-strata Rothermel model) in fynbos and forest vegetation.

Variable	Fynbos	Forest
Fuel loads (g m^{-2})		
Stratum 1		
Litter	500	1600
Stratum 2		
Herbaceous plants and low shrubs	275	0
Dead material (< 6 mm)	530	0
Dead material (6–25 mm)	500	0
Dead material (> 25 mm)	220	0
Stratum 3		
Tree or shrub foliage	900	1800
Dead material (all classes)	80	600
Percentage cover by strata		
Stratum 1	80	100
Stratum 2	90	0
Stratum 3	60	100
Packing ratios		
Stratum 1	0·020	0·444
Stratum 2	0·007	0
Stratum 3	0·009	0·002

foliage. The mean bulk density for fynbos species was about threefold that for forest species. Here *Cliffortia*, which has a relatively sparse crown, was an exception. Packing ratios were about twice as high in fynbos as in forest.

The packing ratios of the litter layers in forest and fynbos were calculated from biomass, depth estimates along the transect, and mean specific gravity values. Packing ratios were 0·0444 and 0·0197 for forest and fynbos litter layers, respectively.

Moisture, energy and crude fat contents of plants

The mean monthly moisture content for all individual fynbos species was significantly lower than the mean for any individual forest species in most months (Tukey's Studentized range test, $P=0{\cdot}05$). The moisture data for the six forest species were therefore pooled, as were those from the fynbos. The moisture content of forest plants was consistently 50–100% higher than the mean value for fynbos plants (Fig. 2). The pooled mean energy content for fynbos species was significantly higher (21 860 J g^{-1}) than the mean for forest species (20 703 J g^{-1}, Tukey's Studentized range test, $P=0{\cdot}05$) (Table 3). Fat contents in forest species varied between 2% and 5% (Fig. 3). The range of fat contents between fynbos species was much greater. Very low fat contents (< 1%) were found in *Ischryolepis gaudichaudiana*. *Brunia nodiflora*, on the other hand, had a fat content above 10% at times, while both *Erica* and *Protea* had high (6–7%) fat contents in some seasons. As these shrubs make up the bulk of live biomass in fynbos, it is apparent that the fynbos vegetation can have a higher crude fat content than forest.

Simulation of fire behaviour

Fuel loads in the fynbos and forest fuel models (Table 4) were based on biomass estimates, but for strata with less than 100% cover, the estimates were increased to reflect concentration of biomass within the stratum. For example, strata with an estimated mean biomass of 100 g m^{-2} and a cover of 50%, would have a fuel load of 200 g m^{-2} in the fuel model.

TABLE 5. Wind, slope and fuel moisture conditions, and flame length predictions from the three-strata Rothermel model for forest and fynbos vegetation under varying degrees of fire hazard.

Degree of fire hazard	Low	Moderate	High	Extreme
Windspeed (m s^{-1})	0·5	2	5	7
Slope (degrees)	0	0	0	0
Dead fuel moisture (%)	10	8	6	4
Live fuel moisture (%)				
Fynbos	120	110	100	90
Forest	220	210	200	180
Predicted flame length (m)				
Fynbos	0·7	1·6	3·5	4·9
Forest	0	0	0	0

Estimates of fire behaviour were made for four sets of conditions which represent typical days with low, moderate, high and extreme fire hazard (Table 5). Under conditions of increasing fire hazard, simulated flame lengths in fynbos increased accordingly (Table 5). However, the simulations predicted that fires would fail to burn in forest vegetation under similar conditions.

DISCUSSION

Fynbos and forest as fuel

The chemical and physical features of vegetation in Mediterranean-climate regions are often quoted as favouring the onset and spread of fires (Philpot 1977), but are poorly known for fynbos (Kruger & Bigalke 1984). Crude fats influence burning rate because of their high heat content and availability at low temperatures (Philpot 1977), while higher foliar moisture contents will retard fires (Rothermel 1972). Data on foliar moisture and crude fat contents were assembled for comparison with the results of this study (Table 6). The moisture contents in fynbos plants are equivalent to those found in coniferous trees (*Pinus* and *Pseudotsuga* spp.), but are not as low as those recorded for Californian chaparral shrubs (*Arctostaphylos* and *Adenostema* spp.). Unlike fynbos, chaparral shrubs showed strong seasonal trends, with low (50%) moisture contents at the height of the fire season (Dell & Philpot 1965). Although fynbos has much lower moisture contents than co-occurring forest vegetation, it never drops to the low values found in chaparral shrubs. Some fynbos shrubs have high crude fat contents. They are higher than values for Chilean mattorral shrubs, but are somewhat lower than those found in chaparral shrubs and coniferous trees, and much lower than values for *Eucalyptus* (Table 6). The chemical characteristics of fynbos plants therefore indicate a higher flammability than Chilean mattorral, but a lower flammability than Californian chaparral or Australian *Eucalyptus* woodlands.

Although fynbos fuel loads in this study were half those found in adjacent forest, they can be equivalent to, or higher than forest, in fynbos of greater post-fire age. Fuel loads from this study (Table 2) are 1696 g m^{-2} for fynbos twelve years after fire, compared to 3685 g m^{-2} for forest. Fynbos fuel loads in the Jonkershoek valley increased to 2700 and 4300 g m^{-2} at twenty-one and thirty-seven years after fire, respectively (Van Wilgen 1982).

TABLE 6. Comparative foliar moisture and crude fat contents for selected species or vegetation types.

Region	Species or vegetation	Live foliage moisture content (%)	Crude fat content (% of dry mass)	Source
Cape, South Africa	Fynbos	98–126	0·4–10·3	This study
Cape, South Africa	Forest	167–216	1·0–5·7	This study
Montana and California	*Pinus ponderosa*	85–115	8–10	Philpot (1963); Mutch (1970); Philpot & Mutch (1971)
Montana	*Pseudotsuga menziesii*	70–110	6–9	Philpot & Mutch (1971)
California	*Arctostaphylos viscida*	100–160	—	Philpot (1963)
California	*Arctostaphylos pungens*	50–90	8·0–9·6	Countryman & Philpot (1970); Trujillo (1976)
California	*Adenostema fasciculatum*	48–115	9–11	Dell & Philpot (1965); Philpot (1969); Countryman & Philpot (1970)
California	*Quercus turbinella*	—	2·6–5·6	Trujillo (1976)
California	Chaparral shrubs	—	6·25	Rundel (1981)
Chile	Mattorral shrubs	—	1·87	Rundel (1981)
Australia	*Eucalyptus* sp.	—	19·1	Mutch (1970)
Vietnam	Tropical hardwoods	—	2·9	Mutch (1970)

Why do forest patches not burn?

Surface fires occasionally spread to the crowns of trees, but the phenomenon of crown fires is poorly understood (Albini 1984). Crown fires have only been studied in coniferous woodlands and forests of the northern hemisphere. Van Wagner (1977) proposed a model for predicting conditions that would lead to crown fires in coniferous timber stands. The model assumes that crown fires are dependent on surface fires for active spreading. In order for crown fires to develop, surface fires have to reach a critical intensity (I, kW m^{-1}) and rate of spread (R, m min^{-1}), which varies according to crown bulk density (CBD, kg m^{-3}), foliar moisture content (FMC, %) in the crowns of trees, and the lower crown branch height above the ground ($LCBH$, m). The critical intensity necessary is given by:

$$I=[(0{\cdot}01\ LCBH\,(460+26\ FMC)]^{1{\cdot}5} \qquad (1)$$

The critical rate of spread is given by:

$$R=3/CBD \qquad (2)$$

Assuming 180% foliar moisture content and a lower crown height of 6 m (Figs 1 and 2), eqn 1 yields an estimate of 5415 kW m^{-1} for critical intensity. Assuming a crown bulk densities of 0·8 kg m^{-3} (Table 3) the critical rate of spread needed to sustain a crown fire is 3·75 m min^{-1} (eqn 2). These levels of fire behaviour are often exceeded in fynbos fires (Van Wilgen, Le Maitre & Kruger 1985). Van Wagner's model assumes, however, that the surface fire sustaining the crown fire is burning below the trees, and not in adjacent vegetation. In addition, 'bridging fuels' are often necessary for the onset of crown fires (Van Wagner 1977). Forest patches in fynbos have only dense litter layers to support fires, and lack bridging fuels. This makes the application of Van Wagner's model inappropriate for our conditions.

The structural differences between fynbos and forest, considered together, are sufficient to explain the inability of fires to penetrate forest patches using the three-strata Rothermel model. It is difficult, however, to select the factors chiefly responsible for this. The spatial distribution of fuel would appear to be of overriding importance. Forests have concentrated litter layers with high bulk densities, and sparse crowns with low bulk densities. This arrangement of fuel is less conducive to fire spread, despite higher fuel loads. Coupled to this are the much higher moisture contents of live foliage in forest, and relatively high crude fat and energy contents in fynbos. The complex relationships between the fuel and environmental factors needed to simulate fire behaviour preclude a rigorous sensitivity analysis. In Canada, only coniferous trees support crown fires, but broad-leaved trees and shrubs in other areas, such as Australian *Eucalyptus* species, and chaparral shrubs, do support crown fires. Although crude fats may play a role in this, Van Wagner (1977) argues that foliar moisture content alone will explain the inability of fires to burn in the crowns of broad-leaved trees. For example, moisture content in the foliage of conifers is about 70–130%, while chaparral and *Eucalyptus* species often have foliar moisture contents below 100%. Aspen, birch and maple trees in Canada, on the other hand, have foliar moisture contents of 140–200% (Van Wagner 1977). The high moisture contents of forest trees observed in this study would support this argument.

Will forest patches burn under extreme conditions?

A recent review of fire in southern African forest ecosystems (Granger 1984) highlighted the lack of data in this field, and only early accounts of 'rare' crown fires exist. Charcoal fragments are found in and on the soils throughout the coastal and montane forests of the southern Cape Province. The sources of charcoal have been ascribed to localized lightning fires, the activities of honey hunters, or to the occurrence of fires under rare suitable conditions (Geldenhuys 1987). The hot, dry 'bergwinds' which occur periodically can desiccate most fuels to the extent that they will burn. In addition, bergwinds were shown to induce litterfall of up to 6·5–7 times the normal monthly amount in forests (Geldenhuys 1987). This increased fuel loads by 140 g m^{-2}, and, combined with hot, dry weather, could constitute conditions that would support a fire. In the absence of documented evidence, however, it is not possible to reconstruct the nature of forest fires. It is probable that they would be surface fires in the litter layer, and not crown fires. Surface fires have been observed in forests in the southern Cape under conditions of severe drought (C. J. Geldenhuys, personal communication), where they kill trees simply by burning their root systems.

Forest patches occurring in frequently burnt vegetation such as fynbos or grassland are characterized by abrupt margins which are maintained by fire (Granger 1984; Everard 1986). These margins are scorched by fires, and the degree of penetration into the forest patch will depend on the intensity of the fire in the adjacent vegetation. With narrow (10–20-m) strips of forest along streams, the entire forest patch could be scorched by intense fires in adjacent vegetation, even though they do not support a fire themselves. Swartboskloof contains forest patches up to 100 m wide. The interiors of these patches are presumably safe from fire, particularly under the conditions selected for prescribed burning operations in the Cape mountains (Van Wilgen & Richardson 1985).

Is frequent fire detrimental to forest patches?

Frequent fire leads to lower fuel loads in fynbos, which in turn lead to less intense fires and, presumably, less damage to the forest margin. If fynbos is protected from fire, fuel loads build up rapidly (Van Wilgen 1982). Experience has shown that active protection of fynbos from fire for extended periods (> 40 years) is virtually impossible. The inevitable fire in old fynbos would be very intense and would be more damaging to the forest margin. Frequent fires would prevent the establishment of forest trees along the margin, however. All forest trees are able to sprout and, once established, could survive fires. It would appear, therefore, that frequent fires, although less damaging to the margin, would prevent establishment of trees and, consequently, expansion of forest patches. On the other hand, infrequent but inevitable fires of high intensity could damage the margin of a forest patch that would just be starting to expand. Average fire frequencies that would allow tree species to establish and grow large enough to survive fires of moderate intensity may allow forest patches to expand. Other factors controlling the potential extent of forest patches, such as soil depth and moisture availability as well as the tolerance range of the species concerned, will have to be taken into account. The long intervals between fires in fynbos make field studies on the dynamics of forest margins impractical, and call for experimental work to establish models that could predict the effects of fire management policies on the dynamics of forest patches.

ACKNOWLEDGMENTS

This work forms part of the conservation research programme of the Forestry Branch of the South African Department of Environment Affairs. We thank Gregory Bailey, Tersia Greeff, Gordon Hockey, Claire Jones, Gerard Mostert and Adrian Simmers for assistance with field and laboratory work, and Coert Geldenhuys and Pat Manders for useful comments.

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(*Received 11 April 1989; revision received 6 October 1989*)

Third paper: Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. *Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof.* Springer-Verlag, Heidelberg (1992).

4 Regeneration Strategies in Fynbos Plants and Their Influence on the Stability of Community Boundaries After Fire

B.W. van Wilgen and G.G. Forsyth

4.1 Introduction

An analysis of the range of regeneration strategies present in fynbos communities was a major aim of the work conducted at Swartboskloof. Information on the mechanisms whereby plants survive fire (e.g. Bell et al. 1984) and the attributes which allow them to persist in vegetation subjected to repeated fire (e.g. Noble and Slatyer 1980) is required to develop a sound understanding of the dynamics of vegetation subjected to fire. Such information is often only available for all of the plants if the communities are species-poor (e.g. Hobbs et al. 1984). In species-rich communities, it is usually the case that detailed information is only available for the dominant plants. A detailed knowledge of the responses of the constituent species in fynbos is restricted to the dominant shrubs of the family Proteaceae (e.g. Bond et al. 1984). A few studies have listed survival mechanisms in other species (van der Merwe 1966; van Wilgen 1981; van Wilgen and Kruger 1981), but data on other vital attributes (juvenile periods, longevity, modes of seed dispersal, and seed bank longevity) are not available for the vast majority of fynbos species. Fynbos has a rich diversity of species, and fynbos communities may differ in the spectrum of responses (and therefore in their vulnerability to fire). In this chapter we quantify the range of regeneration strategies manifested in a sample of fynbos plants subjected to fire, and examine the differences between major vegetation communities in terms of these strategies. We also compare the data to those collected in other fire prone ecosystems.

4.2 Survival Mechanisms and Vital Attributes of Species

4.2.1 Systems for the Classification of Species

Several systems for the classification of plant species responses to fire have been developed (e.g. van der Merwe 1966; Noble and Slatyer 1980; Gill

1981a; Bell et al. 1984). In this study we examined the responses of plants and communities to fire in terms of the systems described by Bell et al. (1984) and Noble and Slatyer (1980). The systems are outlined briefly below.

Bell et al. (1984) defined five categories of species response to fire. Fire ephemerals (FE) include monocarpic therophytes and annuals, or short-lived polycarpic perennials which exhibit a degree of fire-stimulated germination. They have fast growth rates, early reproductive maturities, high reproductive efforts proportional to biomass, and relatively short (<4 years) life spans. Obligate seeders (OS) are long-lived (>15 years) and are likely to have their growth cycle terminated prematurely by fire, as they do not possess the ability to sprout. Sprouting species are a diverse group, and three categories are recognized. Obligate vegetative reproducing sprouters (OVS) display great powers of multiplication by vegetative (non-sexual) means, but virtually no ability to reproduce by seed. Facultative sprouter-seeders (FSS) sprout weakly, or only after mild fires, but recruitment from seed is highly effective. Autoregenerating long-lived sprouters (ALS) are both successful sprouters, and generate moderately dense stands of seedlings after fire.

Noble and Slatyer (1980) regarded a set of attributes as important in determining the response of a species to disturbance. These included (1) mechanism of persistence during a disturbance, or arrival of propagules afterwards; (2) ability to become established either immediately after a disturbance or later in the post-fire development; (3) the timing of critical life-history events. In regard to the first of these, species are divided into:

D species: arrival of widely dispersed seeds;
S species: seeds with a long viability, stored in the soil;
C species: seeds with short viability surviving disturbance within protective fruits or cones;
V species: persistence by part of the individual surviving the disturbance, and recovery by vegetative growth, with immature tissue;
U species: as for V species, but sprouting mature tissue;
Δ species: a species with both D and U characteristics.

Similarly, three sets of species were recognized in respect of the second group of attributes:

T species: tolerant species, able to establish at any time, tolerating competition with adults of the same or other species;
I species: intolerant species, able to establish only immediately after disturbance, when competition is reduced;
R species: requiring species, unable to establish immediately after a disturbance, but able to establish once mature individuals of the same or other species are present.

Thirdly, with reference to the times taken to reach certain stages in life history, the following were regarded as critical:

1. The time when a disturbance occurs (o) and the time for propagules to become available on a disturbed site (p);
2. The time taken for individuals to reach reproductive maturity (m);
3. The life span of individual plants of the species (l);
4. The time taken for all propagules to be lost from the community (e.g. for the seed store to become depleted) and for the species to become locally extinct (e).

4.2.2 Selection and Characterization of Species

We studied pre-fire composition and post-fire succession on ten permanently marked quadrats (5 × 10 m). These were placed in proteoid and ericoid-restioid shrublands prior to the March 1987 fire in Swartboskloof (see Fig. 1.3). Quadrats were surveyed once before the fire, and at intervals of 9, 18 and 30 months after the fire. Post-fire surveys were done in the spring (except the first one), when most species are in flower. At each survey, all the plant species occurring on the quadrats were identified and listed. Two more quadrats were laid out in the specialized hygrophilous communities after the 1987 fire, and these were also surveyed at three intervals after the fire.

The quadrats were subdivided into 50 sub-plots of 1 m^2 each. At each survey, the maximum height of the vegetation, and an ocular estimate of the percentage canopy cover was made on each of the 50 sub-plots within each quadrat. In addition, the three dominant species (in terms of visual estimates of live biomass) were listed and ranked on each sub-plot. Species were allocated importance values in proportion to their rank, as follows: rank 1 = 1, rank 2 = ⅔ and rank 3 = ⅓. These importance values were used in comparisons of the relative contribution of fire survival strategies and vital attributes between the major vegetation communities (see below).

We recorded the mode of post-fire regeneration (whether from seed or sprouting) and the date of first flowering after fire for each of the species. Each species was assigned a fire response category, and a description of the mechanism of persistence, based on morphological observations. Non-sprouting species were classified as either C, D, or S based on seed morphology and seed shed characteristics. C species are those where the seeds are retained on the parent plant; D species those with structures (such as wings or pappi) that enable the dispersal of seeds, or fruits that are dispersed by birds. The remaining non-sprouting species were classified as S species. Age to maturity (first flowering), where this was 3 years or less, was obtained from the quadrat data. For species that took longer to mature, data on age to maturity was obtained by searching for mature specimens of

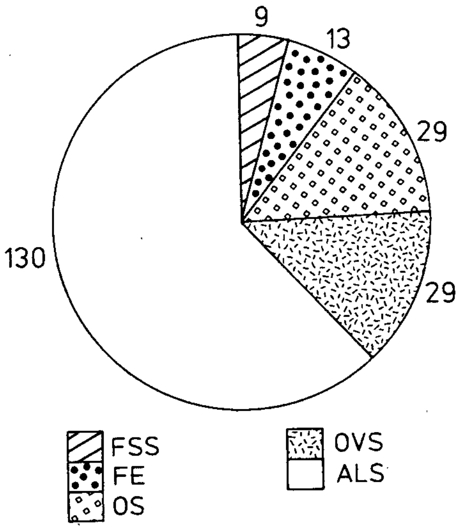

Fig. 4.1. Distribution of fire-response types among 210 plant species from Swartboskloof. The fire-response types are: *ALS* autoregenerating long-lived sprouters; *FE* fire ephemerals; *FSS* facultative sprouter-seeders; *OS* obligate seeders; OVS obligate vegetative reproducing sprouters. The number of species in each life-form is indicated on the diagrams

the species in adjacent areas of known post-fire ages. In addition, the comprehensive herbarium collection at Jonkershoek was searched for data on maturity. Data on longevity were obtained in a similar manner, but for species with longevities that exceeded 45 years (the longest that vegetation in the Jonkershoek valley had survived fire), longevity was simply given as >50 years. Fynbos that survives fire for longer than 50 years is almost unknown, and this assumption will have no effect on comparisons of fire frequencies of less than 50 years. For species which rely on soil-stored seed banks to regenerate, seed bank longevity was estimated as greater than the period between longevity and the occurrence of fire, where the given species was known to have regenerated after fire. For other species, seed bank longevity data were not considered essential to the analysis.

4.3 Results and Discussion

4.3.1 Spectra of Fire Response and Vital Attribute Types

Swartboskloof contains 651 indigenous species of flowering plants and ferns (McDonald and Morley 1988). We encountered 210 species on the 12 quadrats (Appendix 4.1). The most important fire response category (Fig. 4.1) was autoregenerating long-lived sprouters (62% of the species). This category included all of the species where all or most individuals sprouted after fire, and where seedlings of the species appeared after fire. The fate of the seedlings is not known, and many may die before they reach maturity (see Chap. 7). Obligate vegetative reproducing sprouters (14% of the species) included all species which sprouted strongly, but for which we did not find any seedlings. Of the 29 species classified as obligate vegetative reproducing sprouters, 16 were perennial herbs from the family Restionaceae. Species which reproduced by seed were made up by obligate seeders (14%), fire ephemerals (6%) and facultative seeder-sprouters (weak sprouters, 4%).

Of the 51 species that reproduce from seed, most (31) regenerate from soil-stored seed banks (SI and ST, Fig. 4.2). Widely dispersed seeds were found in 18 species, and canopy-stored seeds in only 2 species. Most sprouting species (70%) matured within the first year, and were classified as either U or Δ species. The remainder were classified as V species. Most species (91%) were classified as intolerant (I), while some (7%) were able to establish in mature vegetation and were classified as tolerant (T). Only five species (2%) were classified as requiring (R) a mature overstorey to establish from seed. Obligate vegetative reproducing sprouters were classified as I, but as no seedlings were found, they could be R species. Such a strategy would imply that the species only establish as seedlings if fire-free intervals are very long, as is the case with such species in Californian chaparral (Keeley 1986).

4.3.2 Age at Maturity

Of the 210 species, most (86%) flowered in the first year after fire; a further 7% flowered in the second, 5% in the third, 1% in the fourth, and 2% in the fifth year after fire. Almost all of the sprouting species (148 of 159 species) flowered in the first year after fire. Non-sprouting species were somewhat slower to mature, with 30, 10, 6, 2, and 3 out of 51 species flowering in the first, second, third, fourth and fifth years respectively.

4.3.3 Longevity of Individuals and Seed Banks

Most species in Swartboskloof are long-lived; 173 of the 210 species occur in vegetation with a post-fire age of >45 years as mature, long-established individuals. Twenty species were short-lived (<10 years), and only one annual species (*Sebaea exacoides*) occurred. There were 18 species of moderate longevity (15–40 years). Seed bank longevities were estimated only for those species that rely totally on a soil-stored seed bank in order to survive fires (see Appendix 4.1). Short-lived species, such as some *Aspalathus*, *Roella*, and *Thesium* species, must have fairly long-lived seed banks as they disappear early in the post-fire succession, and reappear after fire from the soil-stored seed bank. For longer-lived species, such as some *Blaeria*, *Cliffortia* and *Phylica* species, seed bank longevity could be much

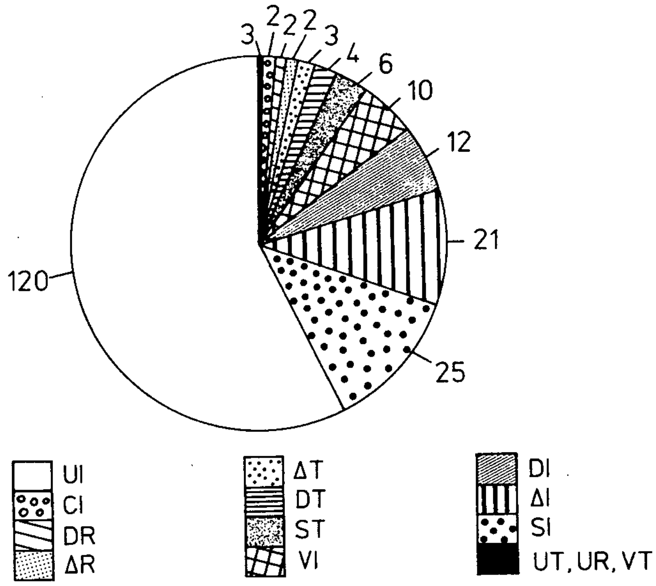

Fig. 4.2. Distribution of vital attribute types among 210 plant species from Swartboskloof. Each type indicates both the method of persistence and the requirement for establishment. The methods of persistence are: *C* canopy-stored seeds; *D* dispersed seeds; *S* soil-stored seeds; *U* sprouting mature tissue; *V* sprouting immature tissue; and Δ U and D features combined. The requirements for establishment are: *I* intolerant; *T* tolerant; and *R* requiring. The number of species in each type is indicated on the diagram

shorter. The population sizes of these species, and many *Erica* species, decline markedly with increasing age, but some individuals do remain in old vegetation.

4.3.4 The Timing of Critical Life History Events

The time at which plants reach critical stages in their life histories can be summarized with reference to the five recognized phases of post-fire succession in fynbos (Kruger and Bigalke 1984; Table 4.1). We recognized nine fire-response patterns (Table 4.2). A given pattern may apply to a range of different vital attributes or fire-response types, as illustrated in Table 4.2. Each of the patterns is discussed below.

The first pattern was the most common, and applied to 160 of the 210 species in the sample. These species persist on, or return to the site and mature within the youth period (1 year after fire). They have life spans in excess of 50 years, or are able to establish in the interfire period, and are found at all stages of the post-fire succession. The vast majority of these species have the ability to sprout, and are classified as ALS or OVS in terms of fire-response types, and as UI or ΔI in terms of vital attributes. Species classified as UI and ALS (the most common combination) may differ considerably in their ecology, although the survival mechanisms and outcomes of disturbances at different stages of their life cycles remain the same. Consider for example *Maytenus oleoides* (a tree) and *Cyrthanthus ven-*

Table 4.1. Post-fire successional phases in fynbos (After Kruger and Bigalke 1984)

Phase	Period after fire (years)	Characteristics
Immediate post-fire	0–1	Seed germination and vegetative regeneration takes place. Most annuals and some geophytes reproduce only in this phase.
Youth	1–5	Graminoid herbs and sprouting shrubs dominate. Canopy cover approaches pre-fire levels.
Transitional	5–10	All plants reach reproductive maturity. Non-sprouting shrubs emerge from the canopy.
Mature	10–30	Tall shrubs reach maximum height and flowering activity. Low shrubs begin to die.
Senescent	30–60?	Mortality of tall shrubs accelerates. Crowns open and litter builds up.

tricosus (a geophyte). Both sprout after fire, and both are long-lived. *Maytenus*, where it occurs, remains a dominant feature of the above-ground vegetation, and flowers and produces fruit annually. *Cyrthanthus*, on the other hand, flowers only immediately after fires, and appears to survive even long interfire periods as a dormant bulb. The first pattern also applies to a small number of long-lived, non-sprouting species, which are killed by fire.

The second pattern is almost identical to the first, but contains species which mature in the immediate post-fire phase (2–5 years after fire), rather than in the first year after fire. About half of these species possess the ability to sprout. The non-sprouters include plants such as the three *Cliffortia* species, which are long-lived but establish only immediately after fire, and

Table 4.2. Fire-response patterns (illustrated by the timing of critical life history events) in 210 species in Swartboskloof, and the range of vital attributes (Noble and Slatyer 1980) and fire-response types (Bell et al. 1984) in each response pattern

Phase of fynbos succession[a]					Vital attributes[b]		Fire-response types[b]		Total number of species
Immediate post-fire	Youth	Transitional	Mature	Senescent					
opm				le	UI	(122)	ALS	(122)	160
					ΔI	(21)	OVS	(26)	
					ST	(5)	OS	(10)	
					DT	(3)	FSS	(2)	
					SI	(4)			
					ΔT	(2)			
					UR	(1)			
					UT	(1)			
					ΔR	(1)			
op	m			le	SI	(10)	OS	(10)	24
					VI	(8)	ALS	(7)	
					DI	(2)	FSS	(4)	
					ΔT	(1)	OVS	(3)	
					ST	(1)			
					DT	(1)			
					VT	(1)			
opm	l			e	SI	(6)	FE	(11)	11
					DI	(5)			
opm			l	e	DI	(4)	OS	(5)	6
					SI	(2)	FSS	(1)	
o		p	m	le	DR	(2)	FSS	(2)	3
					ΔR	(1)	ALS	(1)	
op	m		l	e	DI	(1)	OS	(2)	2
					SI	(1)			
op	m		le		CI	(2)	OS	(2)	2
op	m	l		e	SI	(1)	FE	(1)	1
opm		l		e	SI	(1)	FE	(1)	1

[a] Symbols for critical life history events are: (o), time of disturbance; (p), time at which propagules are available on site; (m), time at which reproductive maturity is reached; (l), local loss of individuals from the community; (e), local extinction from the community.

[b] Abbreviations for vital attributes and fire-response types are explained in the text; number of species in parentheses.

Chrysanthemoides monilifera, which is short-lived but can establish between fires. Sprouting species exhibiting this pattern were classified as V in terms of the mechanism of persistence, as opposed to U, which applies to the first pattern.

The third pattern contains most of the plants classified as fire ephemerals. These species all establish from seed after fire. They complete their life cycles within the immediate post-fire phase, but none are annuals. They then either persist as soil-stored seeds, or disperse back to the site from adjacent areas after the next fire. Of the species that are able to disperse widely, two are exotics; the other three are herbaceous Asteraceae species.

The fourth and sixth patterns are similar, and represent non-sprouting plants that either flower within the first year of fire, or shortly thereafter, respectively. Some of these species, such as *Helichrysum cymosum*, *Pelargonium elongatum* and two *Senecio* species, possess the ability to disperse back into the site after fire. Some, such as *Blaeria dumosa*, and *Pentaschistis malouinensis* rely on a soil-stored seed bank. There are no data on the longevity of soil-stored seed banks for any of the species concerned, and this represents a critical gap in the ability to predict the effects of long interfire periods. *Sebaea exacoides*, the only annual species we encountered, fits this pattern as it is able to establish in the interfire period.

The fifth pattern applies to species which require an overstorey of mature vegetation to establish, and includes two trees (*Maytenus acuminata* and *Kiggelaria africana*) and one shrub (*Myrsine africana*). Seeds of these species are dispersed by birds and establish in the transitional phase of fynbos succession. The two tree species need to reach a large size before they can survive fires by sprouting, but it is possible that, given long (>50 years) interfire periods, the species could establish and create foci for further colonization by tree species with bird-dispersed propagules. Such foci would be fire-resistant (van Wilgen et al. 1990b) and could lead to the establishment of clumped forest patches.

The seventh pattern is essentially the same as the third. It represents plants which could best be described as long-lived fire ephemerals. These plants all regenerate from soil-stored seed banks, and complete their life cycles before the mature stage of fynbos succession is reached. Although no data on seed longevity are available, seed banks must persist for up to 40 years in some cases, as abundant regeneration occurs at some sites after long fire-free periods. The ninth pattern applies to only one species (*Aspalathus ciliaris*), which is a long-lived fire ephemeral that matures in the second year after fire.

The eighth pattern describes two shrub species (*Protea repens* and *P. neriifolia*) which are killed by fire, and rely on seed banks stored in the canopies of the shrubs for regeneration. The species have moderately long life spans (up to 35 years), but seed banks do not persist beyond the life span of the adults. The species will thus not survive fires which occur at intervals of longer than 35 years. Secondly, although the species mature within 3 to 4 years after fire, it takes at least 10 years for adequate seed banks to build up in the canopies of plants. Of the 210 species, these two species were considered the most vulnerable to both short and long interfire periods. Should the species be lost from the community, they represent a small proportion of the total diversity. However, they can contribute up to 89% of the above-ground and 53% of the below-ground biomass in some communities in Swartboskloof respectively (van Wilgen 1982; Higgins et al. 1987). The dominance of these species, combined with their relative vulnerability, has led to fire frequencies in fynbos being prescribed to accommodate these species.

4.3.5 Differences Between Communities

We examined the relative contribution of various categories of fire survival strategies and vital attributes to each of the major vegetation communities (see Chap. 1). The quadrat data from both pre- and post-fire surveys were divided into proteoid shrublands (five quadrats), ericoid-restioid shrublands (three quadrats), specialized hygrophilous communities (two quadrats), and a frequently burnt firebreak (one quadrat). For each sub-set thus defined, the contribution of each category of fire survival strategy and vital attributes to the community as a whole was examined in two ways. Firstly, the number of species in each category was listed for the combined pre- and post-fire data. Secondly, the relative contribution of the various categories in terms of surrogate measures of biomass was calculated for the pre-fire and last post-fire surveys. To do this, importance values for each species on each sub-plot (see above) were totalled per species for each quadrat. A surrogate measure of live biomass was calculated for each species, by multiplying the total importance value (described above) of each of the species per quadrat by the mean cover and height of the vegetation for that quadrat. Data for the quadrats were then pooled to obtain means, and summarized by vital attributes and fire survival strategies for each of the major communities.

The communities are remarkably similar in terms of the proportions of species in each of the categories (Figs. 4.3 and 4.4). Obligate seeders and fire ephemerals were less prominent in the firebreak and hygrophilous communities, but differences were not great. Similarly, the relative composition in terms of vital attributes was similar in all communities.

A total of 197 species were encountered on the ten quadrats that were surveyed pre-fire (the two quadrats in hygrophilous communities were not enumerated pre-fire). Of these, 134 occurred pre-fire, and 193 post-fire. Changes in the composition of the vegetation after the fire were not great, and similarity of pre- and post-fire vegetation ranged from 72 to 89% (Table 4.3) on the ten quadrats surveyed. Most of this difference is explained by the addition of new species post-fire. While 63 species were added to the list, only 4 species disappeared.

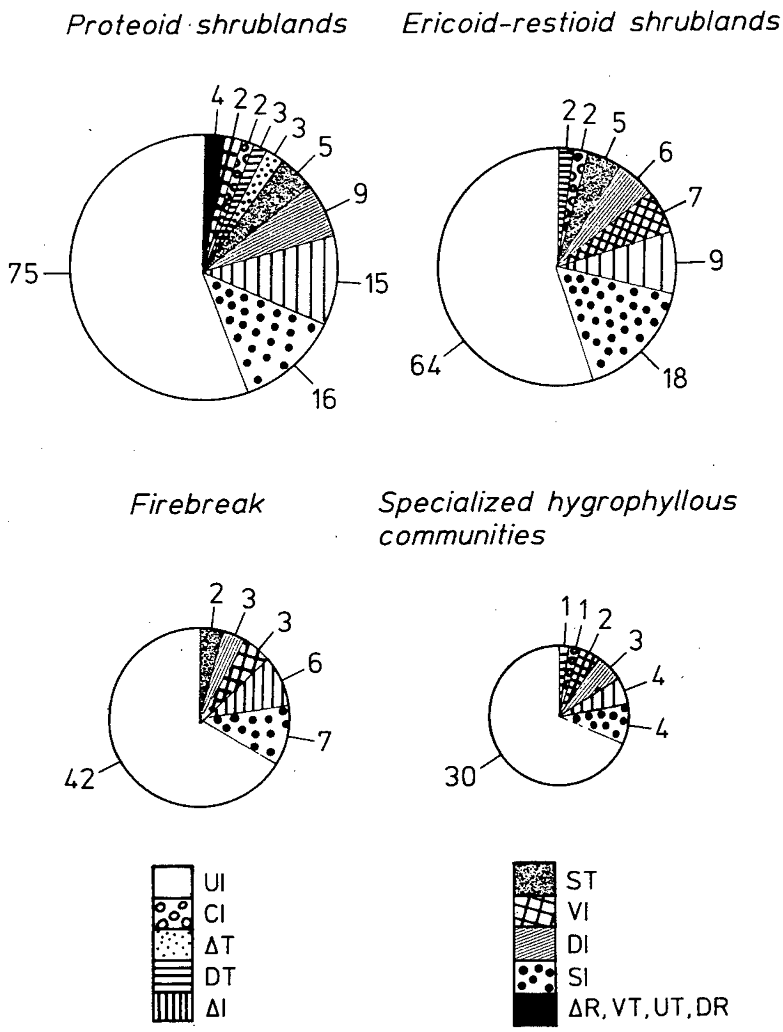

Fig. 4.3. The relative contribution of species, in terms of vital attributes, to four vegetation communities in Swartboskloof. The size of the circle reflects the total number of species encountered. The number of species in each category is indicated on the diagrams; abbreviations as in Fig. 4.2

Table 4.3. An analysis of the pre- and post-fire species composition on 10 × 10 m quadrats in three vegetation communities subjected to fire in Swartboskloof

Community	Number of species pre-fire	Number of species post-fire	Species lost after fire	Species gained after fire	Total species	Pre- to post-fire similarity (Sorenson's index)
Proteoid shrublands	88	131	3	46	134	77.6
Ericoid shrublands	67	109	4	46	113	71.6
Firebreak	53	60	3	10	63	88.5
Entire survey	134	193	4	63	197	81.7

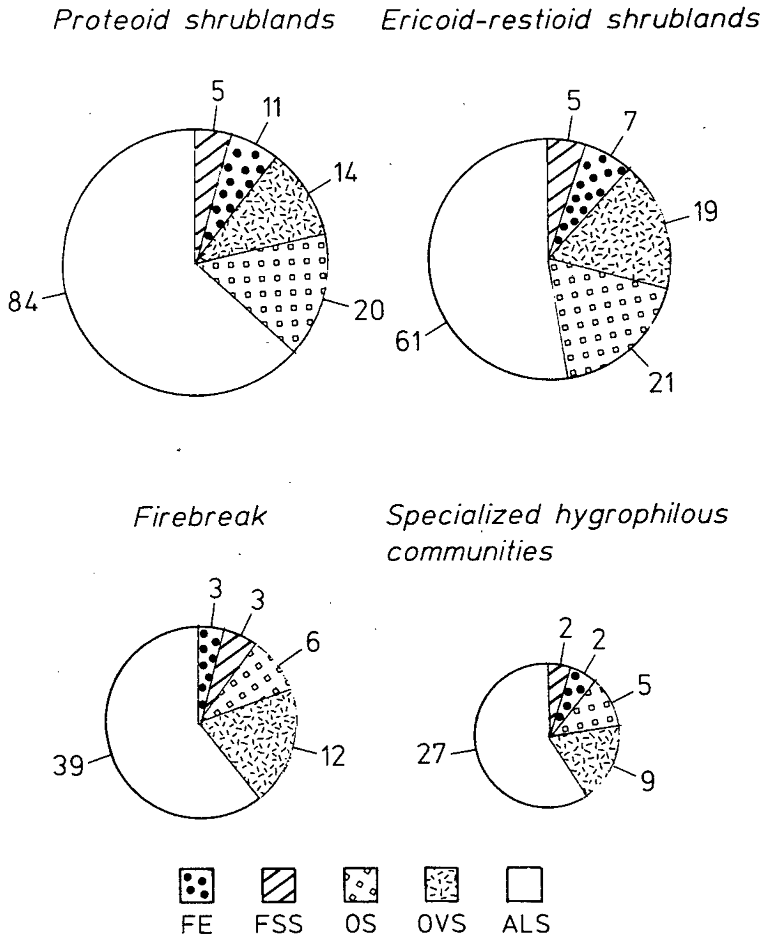

Fig. 4.4. The relative contribution of species, in terms of fire-response types, to four vegetation communities in Swartboskloof. The size of the circle reflects the total number of species encountered. The number of species in each category is indicated on the diagrams; abbreviations as in
Fig. 4.1

All of the communities examined had more species after fire than before fire. The species that appeared after the fire were either fire ephemerals (regenerating from widely dispersed or soil-stored seed banks), geophytes (which were probably present as dormant bulbs but were undetected pre-fire), species that were present as soil-stored seed pools, or species with the ability to colonize the site by means of soil-stored seed banks (Table 4.4). Examples of the dispersed species include fire ephemerals such as *Ursinia pinnata*, *Solanum tomentosum* and *Senecio pubigerus*. Examples of species regenerating from seed pools includes all species of *Thesium*, *Roella ciliata* and *Aspalathus ciliaris*. Many geophytes, such as *Bulbine tuberosa*, *Cyrtanthus ventricosus*, *Ornithogalum hispidum* and *Urginea dregei*, flowered after the fire, but were either dormant, or remained undetected as they were inconspicuous before the fire. Some species that were added to the list were classified as long-lived sprouters, and should have been present before the fire. These may either have been overlooked in the dense vegetation before the fire, or may have regenerated from seed. Similar numbers of species were added to both the proteoid and ericoid-restioid shrubland communities

Table 4.4. An analysis of the number of species gained after fire on 10 × 10 m quadrats in three vegetation communities in Swartboskloof

Community	Fire ephemerals	Geophytes	Species regenerating from soil seed pools	Widely dispersed species	Long-lived sprouters	Total species gained
Proteoid shrublands	11	20	3	5	7	46
Ericoid-restioid shrublands	7	14	8	9	8	46
Firebreak	2	5	1	0	2	10
Entire survey	12	27	5	8	11	63

(Table 4.4). In proteoid shrublands, geophytes and fire ephemerals contributed 67% to the list of species gained. This proportion was smaller (46%) in ericoid-restioid shrublands, which had a higher proportion of species than soil-stored or widely dispersed seeds. There was little change in the firebreak flora.

Of the four species that were lost, two were trees (*Pinus radiata*, an exotic, and *Maytenus acuminata*), and two others were only present as isolated individuals before the fire. As the latter two species have been observed to establish well after fire in other areas, their loss was not real.

The contribution of various regeneration strategies to the pre- and post-fire biomass of the various communities is shown in Figs. 4.5 and 4.6. The largest change occurred in proteoid shrublands, where CI species, which make up only 1% of the species (Fig. 4.2), account for almost 30% of the pre-fire biomass. After fire, these plants have all but disappeared, and will only return to dominance after 10 years (Table 4.1). In all communities, fire ephemeral species appeared in the post-fire flora, and their contribution in terms of biomass was greatest in the proteoid shrublands. There was very little change in the firebreak community, as fire-sensitive species no longer occurred there.

4.3.6 Fire and the Stability of Community Boundaries

The data were used to examine the theoretical effects of varying the fire frequency on the survival of species (Table 4.5). For the data set as a whole, the highest number of species (195 out of 210) survive fire frequencies of between 10 and 15 years. Only four species are eliminated by frequent (5-yr intervals) fire. These are the two *Protea* species (which would not have time to mature) and the two tree species (*Kiggelaria africana* and *Maytenus*

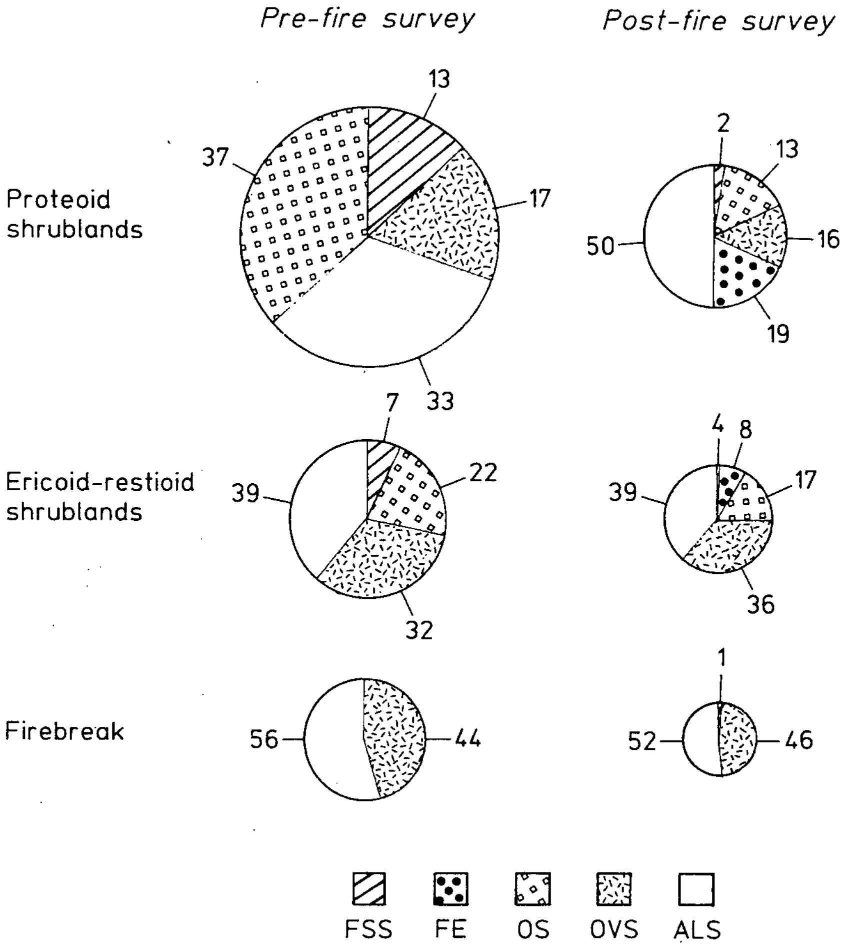

Fig. 4.5. The relative contribution of fire-response types, in terms of biomass, to three vegetation communities immediately before and 30 months after fire in Swartboskloof. The size of the circle reflects the relative biomass. The relative contribution (%) of each category is indicated on the diagrams; abbreviations as in Fig. 4.1

acuminata) which require a mature overstorey to establish. Only the two *Protea* species would be eliminated by long intervals between fires (due to death of adults and loss of seed pools), but up to 16 species were listed as being potentially eliminated. These included many species in the SI class, which face possible elimination should their seed pools not survive the long interfire periods. This analysis is supported by the results of other studies conducted in the Jonkershoek valley (van Wilgen 1981). Non-sprouting *Protea* species were eliminated from a firebreak burnt at 6-year intervals, as well as being almost eliminated through senescence at 37 years post-fire. Tree species were only found in vegetation with a post-fire age of 37 years. Many of the SI species, particularly in the genera *Erica* and *Thesium*, were not found in older vegetation. These were presumably present as seed pools.

The analysis for separate communities (Table 4.5) shows that, in all cases, fire cycles of 10–15 years maintain the highest number of species. In proteoid shrublands, the three species eliminated by certain fire frequencies are the non-sprouting shrubs *Protea repens* and *P. neriifolia*, and the tree *Maytenus acuminata*. The two *Protea* species are also eliminated in ericoid

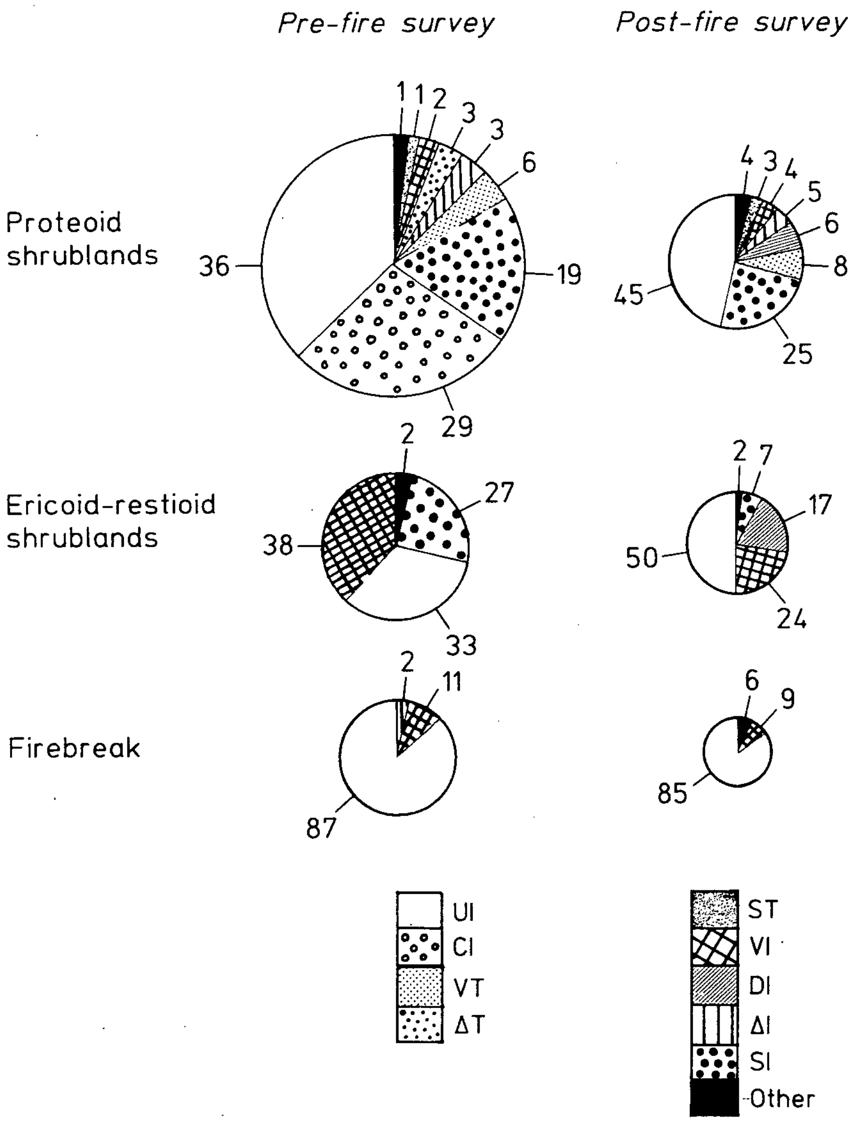

Fig. 4.6. The relative contribution of vital attributes, in terms of biomass, to three vegetation communities immediately before and 30 months after fire in Swartboskloof. The size of the circle reflects the relative biomass. The relative contribution (%) of each category is indicated on the diagrams; abbreviations as in Fig. 4.2

shrublands. The single species eliminated in specialized hygrophilous communities is *Protea neriifolia*, which occurred post-fire as isolated seedlings. None of the species occurring in the frequently burnt firebreak are eliminated by any fire frequency, as sensitive species no longer occur there. In all of the communities, some species are listed as potentially eliminated by long interfire periods. These are species with a longevity less than the fire frequency concerned, which rely on soil-stored seed pools for regeneration after fire. In the absence of data on seed pool longevity, these species can only be considered as potential losses from the community.

The hypothesis that a given fire frequency would favour one community over another is not supported by the above data. All communities are maintained by fire frequencies between 10 and 20 years, and no community is favoured over another by a given fire regime, so that other factors must

Table 4.5. The fate of species in four vegetation communities subjected to fire at different frequencies. Data show the number of species in each category. The species listed as potentially eliminated represent species for which data on seed bank longevity are not available

Fire frequency (yr)	5	10	15	20	25	30	35	40	45	50
Proteoid shrublands										
Species eliminated	3	1	1	1	0	0	0	2	2	2
Species potentially eliminated	0	0	7	8	8	8	8	9	12	12
Species surviving	131	133	126	125	126	126	126	123	120	120
Ericoid-restioid shrublands										
Species eliminated	2	0	0	0	0	0	0	3	3	3
Species potentially eliminated	0	0	5	5	5	6	6	8	12	12
Species surviving	111	113	108	108	108	107	107	105	101	101
Specialized hygrophilous communities										
Species eliminated	1	0	0	0	0	0	0	1	1	1
Species potentially eliminated	0	0	1	1	1	1	1	2	2	2
Species surviving	44	45	44	44	44	44	44	43	43	43
Firebreak										
Species eliminated	0	0	0	0	0	0	0	0	0	0
Species potentially eliminated	0	0	1	2	2	3	3	4	4	4
Species surviving	63	63	62	61	61	60	60	59	59	59
Entire survey										
Species eliminated	4	2	2	2	0	0	0	2	2	2
Species potentially eliminated	0	0	9	10	10	11	11	13	17	17
Species surviving	206	208	199	198	200	199	199	195	193	193

govern the extent of communities. While vegetation structure can be radically altered by changes in fire frequency through the elimination of non-sprouting *Protea* shrubs, it is only in the case of long intervals between fire that, for proteoid shrublands at least, a transition to forest is possible. This question is addressed in more detail in Chapter 5.

4.3.7 Comparison to Other Fire-Prone Shrublands

The flora of the Mediterranean Basin, and the Chilean mattorral, differs from the fynbos in the almost complete absence of non-sprouting plants (Keeley 1986; see also Chap. 7). Californian chaparral differs from fynbos in having an abundant annual flora, a paucity of sprouting herbaceous perennials, and very few non-sprouters that rely on canopy-stored seeds for survival (Keeley 1986). Unlike fynbos, chaparral non-sprouting shrubs are largely resilient to extended fire-free intervals of 100 years or more. Keeley

Table 4.6. The number of plant species in five fire-response categories in Swartboskloof, Australian kwongan (Bell et al. 1984) and Scottish heathland (Hobbs et al. 1984)

Fire-response category	Swartboskloof	Kwongan	Heathland
Fire ephemerals	13	20	0
Obligate seeders	29	31	2
Facultative sprouter-seeders	9	15	2
Autoregenerating long-lived sprouters	130	67	20
Obligate vegetative reproducing sprouters	29	18	3
Total species	210	151	27

(1986) also compared the range of post-fire regeneration characteristics for shrublands in mediterranean-climate regions of California, the Mediterranean Basin, Chile, South Africa and Australia. He rated the relative abundance of plants with soil-stored seeds as low, and those with seed storage on the plant as very abundant in fynbos shrublands. The data for Swartboskloof show that, in terms of the number of species present, soil-stored seed is the more important strategy. Fynbos does not necessarily have an abundance of species which store seeds on the plant, but the vegetation is often dominated by a few species which employ this strategy. Keeley also lists seeding herbaceous perennials as absent in fynbos, but the data for Swartboskloof show that some perennial re-seeding grasses (*Pentaschistis* and *Pentameris* species) do occur.

Data sets suitable for direct comparison with the data from Swartboskloof are rare, but two examples from Australian kwongan shrublands and Scottish heathlands are given in Table 4.6. The proportion of plants that sprout is higher in fynbos than in kwongan, and the proportion of non-sprouting plants and ephemerals is correspondingly lower in fynbos. The diversity of fynbos and kwongan, both in terms of the number of species and the range of fire-response types, is high in comparison to the depauperate Scottish heathlands. The heathlands also lack ephemerals, and have a very high proportion (85%) of sprouting plants.

4.3.8 Fire, Resilience and Dynamics in Fynbos

The resilience (i.e. the ability to return to the pre-fire equilibrium state) of vegetation is a function of species-specific mechanisms (Keeley 1986). Frequent perturbation often selects for species which specialize, and even become dependent on, the relevant disturbance regime. How resilient is fynbos, and how is this reflected in the spectrum of survival types? Most fynbos species are able to sprout. Sprouters can tolerate large deviations from normal fire frequencies, as they are long-lived and basically unaffected by fire. Fire ephemerals and other non-sprouters that rely on soil-stored seed banks may be vulnerable to long interfire periods that exceed the life span of the seeds. The two non-sprouting *Protea* species are vulnerable to both short and long interfire periods, and are therefore the least resilient component of the vegetation. The genera *Protea* and *Leucadendron* often employ the remarkably tenuous CI method of persistence and establishment after fire, and are frequently dominant in fynbos. This indicates evolution in an environment subjected to a narrow range of fire frequency between 10 and 30 years.

Data on the vital attributes of species can be used to predict the presence or absence of species given different frequencies of disturbance. However, the relative abundance of species within a community cannot be predicted from this knowledge. In addition, variation in the season and intensity of fires can have different effects on plant species under similar fire frequencies. The dynamics of fynbos ecosystems in relation to fire is currently best understood in the case of the Proteaceae, where it has been shown that fire frequency alone cannot explain the variation in recruitment observed after fires in different seasons (Bond et al. 1984), or of different intensities (Bond et al. 1990). In addition, the size of the seed bank varies considerably at different stages within the "mature" period (Kruger and Bigalke 1984), and this will affect the relative size of post-fire populations. Models of the factors controlling species coexistence are currently being developed for the Proteaceae, and these offer a substantial advancement in understanding the dynamics of populations of fynbos plants in relation to fire (Cowling and Gxaba 1990; Yeaton and Bond 1991). However, for many other groups of plants, little or nothing is known of the factors controlling their dynamics in relation to fire. For example, the genus *Erica* has many species which rely on soil-stored seed banks for regeneration, but there are no data on the seed production rates or seed bank dynamics of members of this genus. Data on the range of regeneration strategies, as presented here, represent a starting point from which the dynamics of the vegetation in relation to fire can be examined. However, the data are at best rudimentary for the provision of a sound understanding of vegetation dynamics. Future research should concentrate on selected species within the major fire response patterns (Table 4.2) in order to improve the understanding of fynbos dynamics in relation to fire.

Acknowledgements. We thank Adnaan Abrahams, Clare Jones and Gerard Mostert for help with fieldwork and data analysis. Many colleagues assisted in allocating species to species types. We are particularly grateful to Pat Brown, Roger Ellis, Dave Le Maitre, Dave McDonald, Hugh Taylor and Jan Vlok.

Appendix 4.1. Life-forms, fire survival types and vital attributes for 210 species in Swartboskloof. Seed longevity is only given for species which rely on soil-stored seed banks for survival

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
SCHIZAEACEAE						
Schizaea pectinata	H	ALS	ΔI	1	>50	–
DENNSTAEDTIACEAE						
Pteridium aquilinum	H	ALS	ΔT	1	>50	–
ADIANTACEAE						
Pellaea pteroides	H	ALS	ΔT	1	>50	–
CUPRESSACEAE						
Widdringtonia nodiflora	P	ALS	VI	5	>50	–
PINACEAE						
Pinus radiata (*)	P	OS	DT	5	>50	–
ALLIACEAE						
Agapanthus africanus	EG	ALS	UI	1	>50	–
AMARYLLIDACEAE						
Cyrtanthus ventricosus	DG	ALS	UI	1	>50	–
Haemanthus coccineus	DG	ALS	UI	1	>50	–
ASPARAGACEAE						
Protasparagus rubicundus	DG	ALS	UT	1	>50	–
ASPHODELACEAE						
Bulbine tuberosa	DG	ALS	UI	1	>50	–
Caesia contorta	H	ALS	UI	1	>50	–
Trachyandra hirsutiflora	DG	ALS	UI	1	>50	–
Trachyandra hirsuta	DG	ALS	UI	1	>50	–
Trachyandra tabularis	DG	ALS	UI	1	>50	–
CYPERACEAE						
Ficinia deusta	H	ALS	UI	1	>50	–
Ficinia filiformis	H	ALS	UI	1	>50	–

Ficinia nigrescens	H	ALS	UI	1	>50	–
Macrochaetum hexandrum	H	ALS	UI	1	>50	–
Neesenbeckia punctoria	H	OVS	UI	1	>50	–
Tetraria bromoides	H	ALS	VI	2	>50	–
Tetraria burmanii	H	ALS	UI	1	>50	–
Tetraria capillacea	H	ALS	UI	1	>50	–
Tetraria compar	H	ALS	UI	1	>50	–
Tetraria crassa	H	ALS	UI	1	>50	–
Tetraria cuspidata	H	ALS	UI	1	>50	–
Tetraria fasciata	H	ALS	UI	1	>50	–
Tetraria fimbriolata	H	ALS	UI	1	>50	–
Tetraria ustulata	H	ALS	UI	1	>50	–
HAEMODORACEAE						
Dilatris pillansii	EG	ALS	UI	1	>50	–
Wachendorfia paniculata	DG	ALS	UI	1	>50	–
HYACINTHACEAE						
Albuca canadensis	DG	ALS	UI	1	>50	–
Lachenalia orchioides	DG	ALS	UI	1	>50	–
Ornithogalum hispidum	DG	ALS	UI	1	>50	–
Urginea dregei	DG	ALS	UI	1	>50	–
HYPOXIDACEAE						
Spiloxene capensis	DG	ALS	UI	1	>50	–
IRIDACEAE						
Anapalina triticea	DG	ALS	UI	1	>50	–
Aristea africana	MiCh	OS	SI	1	15	>35
Aristea major	EG	ALS	UI	1	>50	–
Aristea spiralis	EG	ALS	UI	1	>50	–
Bobartia gladiata	EG	ALS	UI	1	>50	–
Bobartia indica	EG	ALS	UI	1	>50	–
Geissorhiza aspera	DG	ALS	UI	1	>50	–
Gladiolus blommesteinii	DG	ALS	ΔI	1	>50	–
Gladiolus carneus	DG	ALS	ΔI	1	>50	–
Micranthus alopecuroides	DG	ALS	UI	1	>50	–
Moraea bituminosa	DG	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Moraea tricuspidata	DG	ALS	UI	1	>50	–
Thereianthus spicatus	DG	ALS	UI	1	>50	–
Tritonia crispa	DG	ALS	UI	1	>50	–
Watsonia borbonica	DG	ALS	UI	1	>50	–
ORCHIDACEAE						
Acrolophia capensis	EG	OVS	UI	1	>50	–
Schizodium obliquum	DG	ALS	ΔI	1	>50	–
POACEAE						
Cymbopogon marginatus	H	ALS	UI	1	>50	–
Ehrharta bulbosa	EG	ALS	UI	1	>50	–
Ehrharta dura	H	ALS	UI	1	>50	–
Ehrharta ramosa	H	FSS	SI	1	>50	–
Festuca scabra	EG	ALS	UI	1	>50	–
Merxmuellera cincta	H	ALS	UI	1	>50	–
Merxmuellera rufa	EG	ALS	UI	1	>50	–
Merxmuellera stricta	H	ALS	UI	1	>50	–
Pentameris macrocalycina	H	ALS	UI	1	>50	–
Pentameris thuarii	H	FSS	SI	2	>50	–
Pentaschistis aristidoides	EG	ALS	UI	1	>50	–
Pentaschistis colorata	H	ALS	UI	1	>50	–
Pentaschistis curvifolia	H	FSS	SI	1	>50	–
Pentaschistis malouinensis	H	FSS	SI	1	25	>25
Pentaschistis pallescens	H	ALS	UI	1	>50	–
Themeda triandra	H	ALS	UI	1	>50	–
RESTIONACEAE						
Calopsis membranaceus	H	OVS	VI	2	>50	–
Cannomois virgata	H	OVS	UI	1	>50	–
Elegia asperiflora	H	OVS	UI	1	>50	–
Elegia juncea	H	OVS	UI	1	>50	–
Hypodiscus albo-aristatus	H	OVS	UI	1	>50	–

Hypodiscus aristatus	H	OVS	UI	1	>50	–
Hypodiscus willdenowia	H	OVS	UI	1	>50	–
Ischyrolepis capensis	H	OVS	UI	1	>50	–
Ischyrolepis gaudichaudiana	H	OVS	UI	1	>50	–
Ischyrolepis sieberi	H	OVS	VI	2	>50	–
Platycaulos depauperatus	H	ALS	UI	1	>50	–
Restio filiformis	H	OVS	UI	1	>50	–
Restio triticeus	H	OVS	UI	1	>50	–
Staberoha cernua	H	OVS	UI	1	>50	–
Thamnochortus fruticosus	H	OVS	UI	1	>50	–
Thamnochortus gracilis	H	OVS	UI	1	>50	–
Willdenowia sulcata	H	OVS	UI	1	>50	–
TECOPHILAEACEAE						
Cyanella hyacinthoides	DG	ALS	UI	1	>50	–
ANACARDIACEAE						
Heeria argentea	P	OVS	UR	1	>50	–
Rhus angustifolia	P	ALS	UI	1	>50	–
Rhus rosmarinifolia	P	ALS	UI	1	>50	–
Rhus tomentosa	P	ALS	UI	1	>50	–
APIACEAE						
Annesorhiza inebrians	H	ALS	UI	1	>50	–
Centella glabrata	MiCh	ALS	UI	1	>50	–
Lichtensteinia lacera	DG	ALS	UI	1	>50	–
Peucedanum sieberianum	EG	ALS	UI	1	>50	–
ASTERACEAE						
Anaxeton asperum	NaCh	OS	DI	2	20	–
Arctotis semipapposa	MeCh	ALS	UI	1	>50	–
Athrixia heterophylla	MeCh	OVS	UI	1	>50	–
Berkheya herbacea	H	ALS	ΔI	1	>50	–
Chrysanthemoides monilifera	P	OS	ST	2	10	–
Conyza bonariensis (*)	MeCh	FE	DI	1	3	–
Corymbium glabrum	H	ALS	ΔI	1	>50	–
Corymbium scabrum	H	ALS	ΔI	1	>50	–
Corymbium villosum	H	ALS	ΔI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Disparago ericoides	MeCh	OVS	UI	1	>50	–
Elytropappus glandulosus	MeCh	ALS	UI	1	>50	–
Gazania serrata	MiCh	ALS	ΔI	1	>50	–
Gerbera crocea	H	ALS	ΔI	1	>50	–
Haplocarpha lanata	H	ALS	UI	1	>50	–
Helichrysum cymosum	MeCh	OS	DI	1	30	–
Helichrysum nudifolium	MeCh	ALS	ΔI	1	>50	–
Helichrysum teretifolium	MeCh	ALS	ΔI	1	>50	–
Helichrysum zeyheri	MeCh	ALS	ΔI	1	>50	–
Hypochoeris radicata (*)	H	FE	DI	1	5	–
Mairea lasiocarpa	NaCh	OS	SI	1	35	>15
Metalasia muricata	P	OS	DI	2	>50	–
Osmitopsis afra	MeCh	OVS	UI	1	>50	–
Osmitopsis asteriscoides	P	ALS	UI	1	>50	–
Osteospermum junceum	P	ALS	UI	1	>50	–
Osteospermum tomentosum	NaCh	OVS	UI	1	>50	–
Senecio grandiflorus	P	OS	DI	1	25	–
Senecio paniculatus	P	OS	DI	1	25	–
Senecio pinifolius	MeCh	ALS	UI	1	>50	–
Senecio pubigerus	P	FE	DI	1	5	–
Stoebe plumosa	MeCh	FSS	DI	2	>50	–
Ursinia paleacea	P	FE	DI	1	5	–
Ursinia pinnata	P	FE	DI	1	5	–
BRUNIACEAE						
Berzelia lanuginosa	P	ALS	UI	1	>50	–
Brunia nodiflora	P	ALS	VI	3	>50	–
Nebelia paleacea	P	ALS	VI	3	>50	–
CAMPANULACEAE						
Cyphia bulbosa	DG	ALS	UI	1	>50	–
Cyphia volubilis	DG	ALS	UI	1	>50	–

Lobelia coronopifolia	MeCh	ALS	UI	1	>50	–
Prismatocarpus diffusus	MeCh	ALS	UI	1	>50	–
Roella ciliata	MeCh	FE	SI	1	5	>45
CELASTRACEAE						
Hartogiella schinoides	P	ALS	ΔR	1	>50	–
Maytenus acuminata	P	FSS	DR	5	>50	–
Maytenus oleoides	P	ALS	ΔT	1	>50	–
CRASSULACEAE						
Crassula capensis	EG	ALS	UI	1	>50	–
Crassula fascicularis	MeCh	OS	ST	1	20	–
DIPSACACEAE						
Scabiosa columbaria	MeCh	ALS	ΔI	1	>50	–
DROSERACEAE						
Drosera aliciae	EG	ALS	ΔI	1	>50	–
Drosera capensis	EG	ALS	ΔI	1	>50	–
EBENACEAE						
Diospyros glabra	P	ALS	ΔI	1	>50	–
ERICACEAE						
Blaeria dumosa	NaCh	OS	SI	4	35	>15
Eremia totta	NaCh	OS	SI	3	>50	–
Erica articularis	MeCh	ALS	UI	1	>50	–
Erica coccinea	P	ALS	VI	3	>50	–
Erica hispidula	P	OS	SI	3	>50	–
Erica longifolia	P	OS	SI	3	>50	–
Erica sphaeroidea	MeCh	OS	SI	2	>50	–
EUPHORBIACEAE						
Clutia alaternoides	P	ALS	UI	1	>50	–
Clutia rubricaulis	MeCh	OVS	UI	1	>50	–
Euphorbia genistoides	NaCh	OVS	UI	1	>50	–
FABACEAE						
Aspalathus ciliaris	P	FE	SI	2	6	>44
Cyclopia genistoides	P	ALS	UI	1	>50	–
Indigofera alopecuroides	NaCh	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
Otholobium fruticans	P	ALS	UI	1	>50	–
Otholobium obliquum	P	OVS	UI	1	>50	–
Podalyria montana	P	ALS	UI	1	>50	–
Psoralea aculeata	P	ALS	UI	1	>50	–
Rafnia capensis	MeCh	ALS	UI	1	>50	–
Rhynchosia totta	L	ALS	UI	1	>50	–
FLACOURTIACEAE						
Kiggelaria africana	P	FSS	DR	5	>50	–
GENTIANACEAE						
Chironia baccifera	MeCh	OS	DT	1	10	–
Sebaea exacoides	T	OS	ST	1	1	–
GERANIACEAE						
Pelargonium cucullatum	P	ALS	ΔI	1	>50	–
Pelargonium elongatum	MeCh	OS	DI	1	35	–
Pelargonium longifolium	EG	ALS	ΔI	1	>50	–
Pelargonium myrrhifolium	MeCh	ALS	ΔI	1	>50	–
Pelargonium tabulare	MeCh	ALS	ΔI	1	>50	–
LAURACEAE						
Cassytha ciliolata	VP	OS	DT	1	>50	–
LINACEAE						
Linum africanum	MeCh	ALS	UI	1	>50	–
MESEMBRYANTHEMACEAE						
Erepsia anceps	NaCh	FE	SI	1	5	>45
MONTINIACEAE						
Montinia caryophyllacea	P	ALS	UI	1	>50	–
MYRSINACEAE						
Myrsine africana	P	ALS	ΔR	1	>50	–

OXALIDACEAE						
Oxalis bifida	DG	ALS	UI	1	>50	–
Oxalis lanata	DG	ALS	UI	1	>50	–
Oxalis purpurea	DG	ALS	UI	1	>50	–
Oxalis strigosa	DG	ALS	UI	1	>50	–
Oxalis tenuifolia	DG	ALS	UI	1	>50	–
PENAEACEAE						
Penaea mucronata	P	ALS	UI	1	>50	–
POLYGALACEAE						
Muraltia alopecuroides	MeCh	ALS	UI	1	>50	–
Muraltia heisteria	P	ALS	UI	1	>50	–
Polygala bracteolata	MeCh	FE	SI	1	8	>42
PROTEACEAE						
Aulax pallasia	P	OVS	VI	2	>50	–
Leucadendron salignum	P	ALS	UI	1	>50	–
Protea acaulos	H	OVS	UI	1	>50	–
Protea neriifolia	P	OS	CI	4	35	<1
Protea nitida	P	ALS	VT	2	>50	–
Protea repens	P	OS	CI	3	35	<1
RHAMNACEAE						
Phylica imberbis	MeCh	ALS	UI	1	>50	–
Phylica pubescens	P	OS	SI	3	40	>10
ROSACEAE						
Cliffortia cuneata	P	OS	SI	2	40	>10
Cliffortia polygonifolia	P	OS	SI	3	40	>10
Cliffortia ruscifolia	P	FSS	SI	2	40	>10
RUBIACEAE						
Anthospermum aethiopicum	P	OS	ST	1	8	–
Anthospermum galioides	MiCh	OS	ST	1	8	–
Carpacoce vaginellata	MeCh	ALS	UI	1	>50	–
RUTACEAE						
Coleonema juniperinum	MeCh	FSS	SI	2	>50	–
Diosma hirsuta	MeCh	ALS	UI	1	>50	–

Appendix 4.1 (continued)

Species[a]	Life-form[b]	Fire survival type[c]	Vital attributes[c]	Age to maturity (yrs)	Longevity (yrs)	Seed longevity (yrs)
SANTALACEAE						
Thesium capitatum	MeCh	FE	SI	1	5	>45
Thesium strictum	P	FE	SI	1	5	>45
Thesium virgatum	MeCh	FE	SI	1	5	>45
SCROPHULARIACEAE						
Agathelpis dubia	MeCh	OS	ST	1	8	–
Halleria elliptica	P	OVS	UI	1	>50	–
Oftia africana	P	ALS	UI	1	>50	–
Selago spuria	MeCh	FE	SI	1	5	>45
SOLANACEAE						
Solanum tomentosum	P	OS	DT	1	5	–
THYMELAEACEAE						
Gnidia oppositifolia	P	ALS	UI	1	>50	–
Struthiola ciliata	MeCh	OS	SI	1	35	>15

[a] Species marked (*) are exotics.

[b] Life-forms follow the system of Raunkiaer (1934) and modifications thereof (Pate et al. 1984). The abbreviations are: H = hemicryptophytes (renewal buds close to the ground); MiCh = microchamaephytes (renewal buds within 100 mm of the ground); NaCh = nanochamaephytes (renewal buds 100–200 mm from the ground); MeCh = megachamaephytes (renewal buds 200–800 mm from the ground); P = phanerophytes (renewal buds 800 mm or greater from the ground); EG = evergreen geophytes (shoots buried in the ground); DG = deciduous geophytes (shoots buried in the ground); L = lianas (phanerophytes fully supported on other plants); VP = vascular parasites (plants which grow on other living plants); and Th = therophytes (annuals which complete their whole life cycle in 1 year).

[c] Abbreviations are explained in the text.

Fourth paper: Ecosystem management. *The Ecology of Fynbos: Nutrients, Fire and diversity*. Oxford University Press, Cape Town, (1992).

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Ecosystem management

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INTRODUCTION

The Cape fynbos is one of the world's richest temperate floras crammed into 4.4% of South Africa's land surface. How much do we need to know to manage such a diverse biota, and will we ever know enough? There are substantial difficulties. Too many species exist in fynbos for all their management requirements to be known. Even the management of a single, well-studied species, (e.g. *Pinus radiata*), is fraught with uncertainties in management. Despite its small area, fynbos is renowned for the rapid species turnover from one habitat to the next and from one geographic region to the next (Cowling et al. this volume). We do not understand the reasons for this turnover. Thus, even though we do have a few well-studied examples, there are inadequate guidelines on how widely to generalize results from studies in one habitat and one region to the rest of the fynbos biome.

Despite the apparent immensity of the problem, substantial progress has been made in ecological research relevant to management. This chapter reviews the scientific basis for the current management of fynbos biome vegetation, and examines these in the light of scenarios of likely changes within the biome. We do not attempt to prescribe management methods, since management objectives may change according to land ownership and changing public perceptions. Instead, we discuss current principles, the evidence on which they are based, and their generality in different regions and scales of management. There are no absolutes in fynbos — we hope this chapter will be read not as a recipe but as a review which will indicate our understanding and expose our ignorance.

Researchers often have highly inflated notions on the ability of 'managers and decision makers' to take note of the results of their research. Regardless of the quality of technical knowledge, management is constrained by the size of the area managed and the available finance. In practice, a simple hierarchy of management intensity for fynbos landscapes can be recognized:

- no management — more remote or arid areas;
- 'natural burning zones' — area encircled by fire-breaks but, besides alien removal, with no management intervention. Mostly isolated mountain ranges with relatively low fire hazard from adjacent properties;
- 'block burning' — active management involving the control of invasive plants and prescribed burning at predetermined frequencies — many farms, nature reserves, and catchment areas. The scale can vary from blocks of 500–1 500 ha in catchments to patches of 2–3 ha in farms or nature reserves; and
- 'intensive management' including seed additions, translocations, seed harvesting, pest management, and fire.

Management for the most important goals (Table 14.1) centres largely on the application (or exclusion) of fire, and the control of alien invasive plants. Hence, much research has concerned the response of plants to the fire regime (see below). Most ecological research has been directed at level 3, some at level 2 and very little at level 4. Thus, the flower farmer and the manager of the small nature reserve have been least well served by research. Substantial horticultural research has been conducted on fynbos plants, especially those cultivated for the flower trade or by gardening enthusiasts. There is still much to be done to integrate horticultural insights into veld management at the more extensive scale, but we do not attempt to do so here. Instead, we review how a knowledge of the biology of plants and animals can

TABLE 14.1 Important management objectives and practices in the fynbos biome.

Sphere	Major objectives	Management practices
Nature conservation	Maintenance of species diversity	Prescribed burning to allow seed regeneration; control of invasive organisms
Water conservation	Maintain sustained flow of high quality water	Prescribed burning to increase water yield; control of alien woody plants
Fire management	Reduce fire hazard	Prescribed burning to reduce fuel loads; maintenance of fire breaks; control alien woody plants
Flower harvesting	Sustained yields for profit	Harvesting; prescribed burning to allow seed regeneration; re-seeding depleted areas; pest control
Grazing	Provide additional pasture for domestic livestock	Frequent burning to eliminate shrubs and encourage grasses
Recreation and tourism	Provide facilities for hiking and other outdoor activities	Establishment of trails and other infrastructure

be used to arrive at rational management decisions. In addition, we examine scenarios of habitat fragmentation, funding levels, and climate change for the biome. Managers will need to plan for, or at least understand, the consequences of such changes.

MANAGEMENT PRACTICES

The use of fire in fynbos biome ecosystems

The application of fire is the major management practice in fynbos biome ecosystems. Research into the effects of fire on fynbos has followed a demographic approach (Gill 1981). Most management prescriptions are based on an understanding of the population biology of important species, or even of a single species. Studies at the systems level (e.g. the effects of fire on nutrient cycles) have not been instrumental in deciding appropriate fire regimes for fynbos ecosystems. Burning operations are prescribed in terms of the fire regime (the frequency, season, and intensity at which fires occur), and are based on a knowledge of the effects of these three components on the vegetation.

FIRE FREQUENCY

There are physical limits to the frequencies of fire that can be applied in fynbos. Some fynbos communities accumulate enough fuel to sustain a fire under suitable conditions at a post-fire age of four years, and may burn at three years under extreme hot and dry weather conditions (Kruger 1977a). Fire cycles of less than four years are seldom possible. On the other hand, most attempts to exclude fire for longer than 45 years have met with failure, indicating that the exclusion of fire for longer than this should not be considered feasible.

Although fires in fynbos can burn at any time between four and 45 years, a narrower range of fire frequencies would be needed to ensure that many component species survive repeated fire. The only 'rule of thumb' for determining minimum fire frequencies in fynbos is given by Kruger and Lamb (1978). They suggest that prescribed burns should only take place once 50% of the population of the slowest maturing species in a given area has flowered for at least three successive seasons. This rule is usually applied to shrubs in the family Proteaceae, since these are generally the slowest to mature in fynbos. The time to reach maturity may vary geographically; for example a species may mature quickly in mesic areas, but take much longer to do so in drier areas. Minimum prescribed fire frequencies should take account of this. At the other end of the scale, several arguments have been put forward as important in determining maximum fire intervals. These include senescence in the Proteaceae (see below); lower vegetative cover and greater patchiness in regeneration following the inevitable fire in old fynbos, leading to increased erosion (Bond 1980); and the suppression of understorey species with long intervals between fire (Campbell and Van der Meulen 1980; Esler and Cowling 1990; Cowling et al. this volume). Fire frequencies greater than 25–30 years are seldom recommended due to these considerations.

A useful way to generalize the response of plant communities to different fire frequencies is the vital attributes' scheme proposed by Noble and Slatyer (1980). Although data for most fynbos species are lacking, several indicator species can be examined in this context. Serotinous Proteaceae, dominant shrubs in many fynbos areas, fall into Noble and Slatyer's class CI. These species are killed by fire and regenerate from seed stored in the canopy. CI species are 'intolerant' and recruitment is virtually confined to the period immediately after fire. The seed is short-lived after release and no effective seed reserves persist after the death of the parent and the opening of the cone. Populations of CI species may become locally extinct either as a result of fire before they are reproductively mature (no seed reserves) or if the interval between fires exceeds the lifespan of the individuals in the even-aged population. Frequent fires are a well-known cause of local extinction of slow maturing Proteaceae populations (Kruger 1977a; Van Wilgen and Kruger 1981). Old stands of fynbos are rare but Bond (1980), who has reported poor regeneration of CI Proteaceae after long (40–50 year) intervals between fires, suggested that such poor regeneration may be due to the depletion of seed reserves with senescence of the parents. For species of *Protea* at least, fire intervals of between 8 and 30 years are needed to ensure survival.

Populations of shrubs of the genus *Mimetes* (Proteaceae), found in many fynbos areas, are classed as GI species. GI species build up considerable seed stores in the soil, with longevities exceeding the lifespan of adult plants (> 12 years in the case of *Mimetes splendidus*, A J Lamb unpublished data). *M. splendidus* is an intolerant species and establishes only after fire, at which time the seed pool is exhausted. Data on the longevity of the soil-stored seed pool would be necessary to determine maximum periods between fires. Minimum periods are set by the age at which the species attain maturity and shed seed (about 5–6 years for *M. splendidus*). The seed banks of some non-Proteaceous, non-sprouting GI species (*Agathosma* and *Muraltia*) are small and largely dependent on the current year's input for maintenance (Pierce and Cowling 1991). Seeds of these species do lose viability in the soil (Pierce 1991), indicating that the seed bank is not long-lived. Furthermore, individual plant longevity of these species seldom exceeds 30 years in south-eastern Cape dune fynbos (Pierce and Cowling 1991). Like non-sprouting serotinous Proteaceae, these species would be vulnerable to drastic population reduction or even local extinction under certain fire frequencies.

Most species in fynbos are able to sprout (Noble and Slatyer's groups V, U, and W; see Van der Merwe 1966; Kruger 1987). Such species are less affected by fire frequency as they do not have to reach maturity to survive fires; they are also generally longer lived than non-sprouters. As stated above, non-sprouters are far more sensitive to changes in fire frequency and such plants therefore dictate the fire frequencies required to maintain species diversity.

The approaches described above would indicate that fire frequencies should be between 10 and 25 years to maintain species richness, and this is the most common approach adopted by managers (Van Wilgen et al. 1990a). However, in some cases the aims of management call for short fire frequencies. Fire-breaks, for example, are burnt frequently to reduce biomass (Van Wilgen 1982). Another example concerns areas managed for grazing. Some of the earliest research into the effects of fire on fynbos was directed at the eradication of Afromontane fynbos (see Cowling and Holmes this volume) in the grazing areas of the eastern Cape mountains (Trollope 1971, 1973). In order to eradicate shrubs such as *Erica brownleeae*, *Cliffortia linearifolia*, and *C. paucistaminea*, fires at frequencies of between two and four years were recommended. This effectively destroyed seedlings before they matured and resulted in a 'complete recovery' of the grass sward (Trollope 1973). Similar principles are applied in the management of the Bontebok National Park (Novellie 1984) and could be applied to reduce shrub densities of *Elytropappus rhinocerotis* and *Metalasia muricata*, and increase the cover of grasses in renoster shrublands (Cowling et al. 1986).

Paradoxically, it is sometimes argued that short fire frequencies may be appropriate for the management of fire-sensitive species. The Clanwilliam cedar (*Widdringtonia cedarbergensis*) is a case in point. Cedars are killed by fire and regenerate from seed only. Due to over-exploitation, the species has declined markedly (Manders 1986). The mortality of adult trees is high following intense summer fires, but seedling recruitment is good. Despite this, managers feel that adult mortality after long inter-fire periods (with resultant fires in old, dense vegetation) is unacceptably high. Some areas are therefore deliberately subjected to a regime of short frequency (four year), low intensity winter burns to reduce adult mortality. The drawback of this approach is that seedling recruitment following winter fires is poor (Manders 1987). In addition, the surrounding fynbos is subjected to the most unsuitable regime, both in terms of frequency, and of season (see below).

FIRE SEASON

The time of year at which fires occur is determined by climate and seasonal variations in the fuel properties of the vegetation, given that ignition sources are always available. Seasonal curing of the vegetation is not a feature of fynbos vegetation (Van Wilgen 1984) and fire season therefore depends largely on climatic factors. Owing to the mediterranean-type climate over much of the fynbos biome, fires occur mainly in the summer, but can occur in all months under suitable weather conditions (Van Wilgen 1987).

Fires in different seasons can have marked effects on elements of the vegetation and these can be nearly as pronounced as frequency effects. Shrubs (serotinous Proteaceae) and trees (the Clanwilliam cedar) that are killed by fire show maximum seedling recruitment after late summer and early autumn fires (Jordaan 1949, 1965, 1981; Bond et al. 1984; Manders 1985; Van Wilgen and Viviers 1985; Botha 1989; Midgley 1989). This has been attributed to seed predation by small mammals (see Johnson this volume). Regular prescribed burning outside the late summer-early autumn period could result in the local extinction of species (Bond et al. 1984) and is not usually applied where species conservation is an objective.

There is, however, much variation in the response of plants to fire season which is poorly understood. Autumn fires do not always guarantee good recruitment, just as spring fires do not always ensure poor recruitment (Figure 14.1). Other factors may play a role. Serotinous Proteaceae, for example, show a more marked sensitivity to season of burn on north than on south slopes in the Swartberg (Bond et al. 1984). There has been substantial research on the causes of Proteaceae sensitivity to fire season (Bond 1984; Coetzee and Giliomee 1987; Midgley and Vlok 1986; Midgley 1989; Johnson this volume). An understanding of the causes of this variation would be of considerable value in refining fire prescriptions in different areas, and may allow more flexibility in the approach to fire season in fynbos.

The response of other species in the fynbos biome to variations in fire season supports the contention that the late summer-early autumn period is the best time to burn (Figure 14.2). Seedling regeneration of the fynbos geophyte *Watsonia borbonica* is absent following fires between April and October, and occurs only after summer and autumn burns (Le Maitre 1984). The maximum flowering activity of most fynbos plants occurs in late winter and spring (Kruger 1981) which implies that the maximum seed loads will be available after fires in late summer or early autumn. Proteaceae with soil-stored seed show greatest recruitment following autumn burns, after the current seed crop has matured and been released (Le Maitre 1988). In the case of the shrubs *Paranomus bracteolaris* and *Leucadendron pubescens* growing in the Cederberg, this would mean that burning should take place after early December (Le Maitre 1988). Even

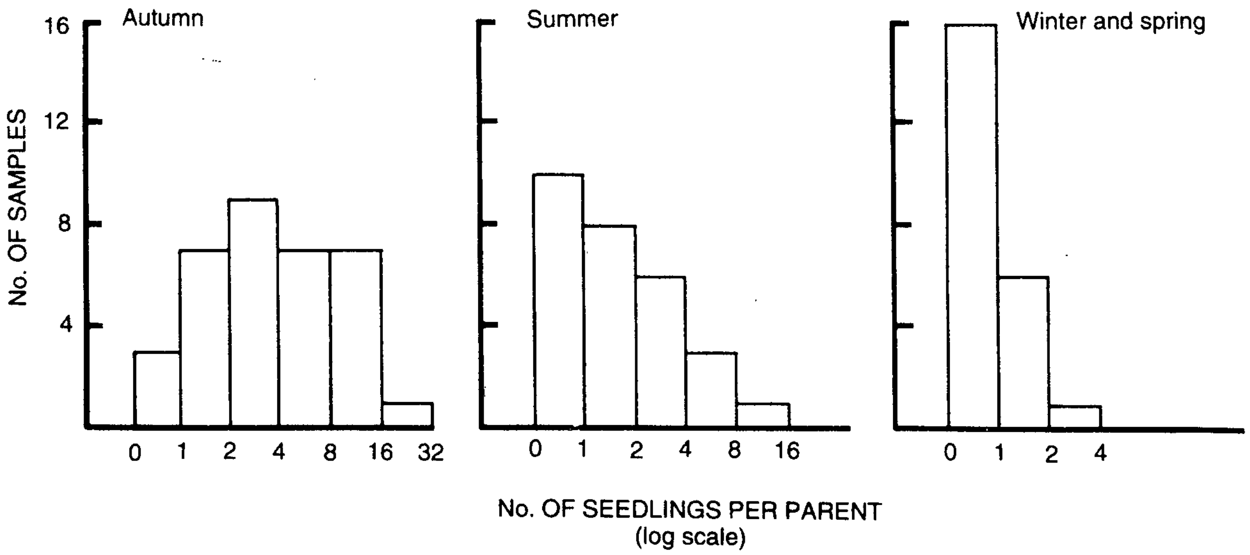

FIGURE 14.1 Regeneration success (number of seedlings per parent) censused after different fire seasons in the southern Cape mountains. Seedling numbers and pre-burn densities were censused after 30 fires with up to four replicate grids each of 65 1x1 m quadrats in each burn. Better recruitment follows autumn and summer fires, but much variation occurs, with poor recruitment (< 1 seedling per parent) after fires in all seasons. Reprinted from Bond et al. (1984) with the permission of Blackwell Scientific Publications.

some animals, such as the geometric tortoise (see below), show traits that reveal a susceptibility to winter or spring burns.

Cowling et al. (1986) have argued for autumn burns (February to April) in south coast renoster shrubland to promote grasses at the expense of shrubs. This recommendation was based on a knowledge of the life histories of the grass *Themeda triandra* and the shrubs *Metalasia muricata* and *Elytropappus rhinocerotis*. At this time of the year, stored carbohydrates in the roots of *Themeda triandra* are high; in addition, germination is promoted by autumn fires. Under frequent burns, to which the grasses are very resistant, the shrubs could be eliminated.

Although fires in summer and autumn are beneficial for most fynbos plant species, fires in autumn and winter may promote certain species over others. For example, *Stoebe plumosa* and *Metalasia* species (shrubs in the family Asteraceae) may benefit from winter burns (M Viviers personal communication). Their shallow soil-stored seed banks are apparently destroyed by intense summer fires, but are favoured by cool winter fires. These species also germinate before most others (Musil and De Witt 1990), giving them an advantage following winter burns. Such variation may not always be viewed as favourable. For example, frequent winter fires, applied to protect cedars (see above) may in fact endanger them, as *Stoebe plumosa* provides a fast-growing fuel bed that will increase, rather than decrease, the intensity of subsequent fires.

FIRE INTENSITY

Fire intensity depends on fuel loads, and the rate at which they burn. Fuel loads in fynbos vary from < 500 gm^{-2} to > 4 000 gm^{-2} (Van Wilgen 1982). The intensity at which a given fuel load will burn can vary by several orders of magnitude (Van Wilgen et al. 1985). Fire intensity can be manipulated either by reducing fuel loads (for example by burning more often) or by selecting the conditions that will lead to the desired type of fire (see below).

It is known that high intensity fires can have adverse effects on sprouting species (Van Wilgen 1982). However, very few studies have been done on the biological effects of intensity. The late summer-early autumn period usually has weather associated with high intensity fires, and indications are that at least some elements of the fynbos biota require high intensity fires for survival. The shrubs *Mimetes fimbriifolius* and *Leucospermum conocarpodendron* regenerate well after high inten-

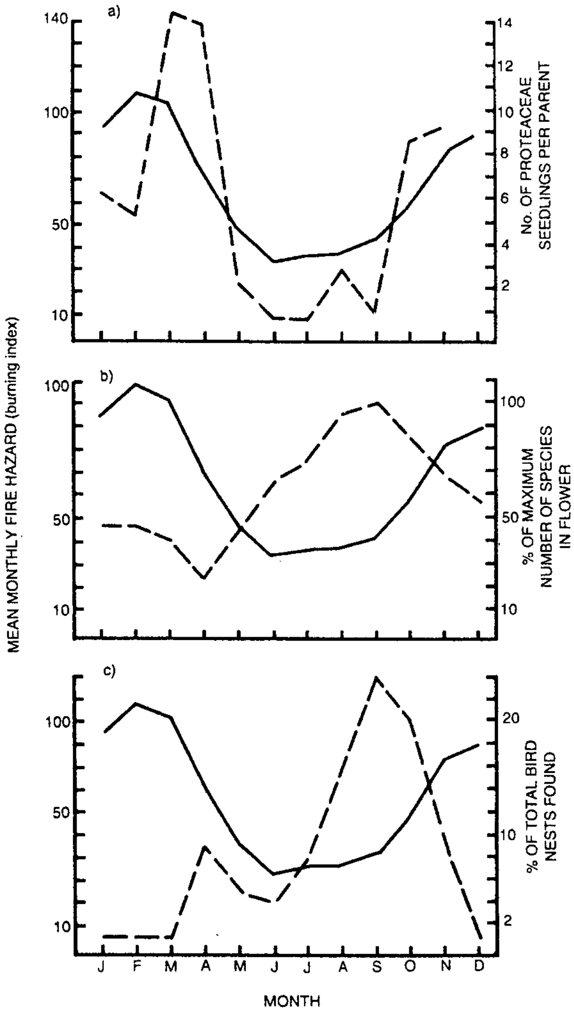

FIGURE 14.2 Seasonal cycles (- - - -) in the fynbos biome in relation to fire hazard (———) at a weather station in the south-western Cape (from Van Wilgen 1985). The graphs show (a) fire survival of Proteaceae (Van Wilgen and Viviers 1985); (b) phenology (Kruger 1981); and (c) nesting activity in birds (Winterbottom 1968). The most likely time for fires (late summer to early autumn) coincides with the period best suited to each cycle.

sity fires, but poorly after low intensity fires (Bond et al. 1990; Figure 14.3). Similar patterns have been observed in *Mimetes splendidus* (A J Lamb personal communication). Such findings present problems for managers, as the desired biological response requires high intensity fires, while safety factors require the opposite.

The relative abundance of species that regenerate from soil-stored seed banks after fire may be affected by fire intensity. For example, lower fire intensities may favour species with shallow seed banks (e.g. the Asteraceae) above those with deeper seed banks (e.g. the Proteaceae) (Musil and De Witt 1990). This is obviously an area that needs more research.

A somewhat different problem arises in areas where the felling of alien trees leads to large accumulations of dead fuel, and results in abnormally intense fires which have severe adverse effects on soil, vegetation, and fauna (Breytenbach 1989; Richardson and Van Wilgen 1986a). In such cases, steps need to be taken to reduce the intensity of fires. This can be done by selecting conditions that will lead to acceptable intensities (Figure 14.4) or by dispersing or physically removing fuel loads.

THE PRACTICAL APPLICATION OF APPROPRIATE FIRE REGIMES

Prescribed burning in the summer months (November to February) is seldom attempted in much of the biome, since the risk of runaway fires is too great. Burning is usually only feasible in March and April; but only about 12 days on average in these two months have suitable weather for prescribed burning in the western Cape. The fire danger during the remaining days is too high to meet the prescribed conditions, or too low to ensure that fires will burn (Van Wilgen and Richardson 1985a). Managers often opt for burning after mid-April to complete burning programmes, but should take into account the consequences in terms of adverse ecological effects. The problems faced by managers who have to complete burning programmes under rarely suitable conditions could be alleviated by the use of systems designed to select conditions that will lead to acceptable fire behaviour.

The adoption of fire danger rating systems, and fire behaviour prediction models, has received considerable attention in the fynbos biome (Van Wilgen 1984; Van Wilgen and Burgan 1984; Van Wilgen and Richardson 1985b; Juhnke and Fuggle 1987; Van Wilgen et al. 1990b). Fire behaviour prediction models developed in the United States of America (Rothermel 1972; Burgan and Rothermel 1984) have been adapted for use in fynbos, using appropriate fuel and weather inputs (Van Wilgen et al. 1985). With this system, it is possible to select environmental conditions that will lead to the desired type of fire. Examples are provided in Table 14.2 and in Figure 14.4. However, the practical application of these techniques has not been successful (Van Wilgen and Manders 1990). In cases where managers have used the technology, a considerable improvement in the ability to make appropriate and informed decisions has been achieved (R H Andrag, G Ruddock personal communication), and the approach holds promise for the future.

Expert systems offer considerable potential for applications where expertise is needed either quickly (as in disaster management), or across a wide range of ecological disciplines (such as in land management decisions, Noble 1987). Little information has been made available on how to apply expert systems to solve problems in ecology (Mentis and Walker 1989), but the approach deserves attention from land managers.

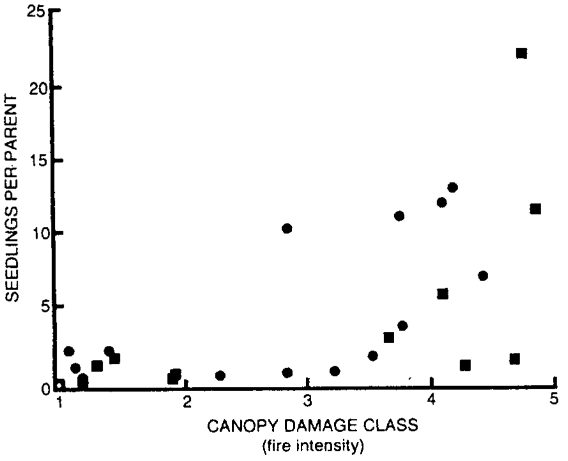

FIGURE 14.3 The relationship between fire intensity (represented by canopy damage classes) and seedling regeneration in two fynbos species with soil-stored seeds. Canopy damage class 1 represents low intensity fires, class 5 represents high intensity fires. The species are *Mimetes fimbriifolius* (solid circles) and *Leucospermum conocarpodendron* (solid squares). High success in germination only occurs after fires have reached an apparent threshold intensity. From Bond et al. (1990).

Flower harvesting

Fynbos plants are harvested for the cut flower trade along the southern lowlands, southern mountain foothills, and as far as the Langkloof in the east. In 1989 the total trade turnover was estimated at R29 million (Greyling and Davis 1989). Between 10 000 and 15 000 people derive their income from the wild flower industry in what are otherwise very poor agricultural conditions. The wild flower trade has thus added value to otherwise marginal agricultural land. A simple measure of this is the recent flurry of claims for compensation, running into millions of rand, for lost income after runaway fires (I Bell personal communication; B W van Wilgen and W J Bond personal observation).

Most of the income from the wild flower trade is derived from export. The market is based on Proteaceae which are now cultivated in several other parts of the world. The market has become highly competitive and the response of local growers and horticultural researchers has been to call for improved quality and new cultivars (Brits et al. 1983). These can best be obtained under cultivation. Almost all of the research on the wild flower trade has dealt with horticultural aspects of cultivating Proteaceae and breeding new varieties. Very few studies have been made on veld harvesting, apparently because this is seen as detrimental to the development of a competitive export market (e.g. Brits et al. 1983). Nevertheless, more than 75% of flowers are still harvested from the veld, mainly in a small area between Cape Hangklip and Mossel Bay (Cowling 1990). Managing veld for cut flowers requires the manipulation of fynbos succession for regeneration, the maintenance of healthy plants for flower production, the maintenance of adequate seed reserves to regenerate populations despite flower removal, and pest control to improve flower quality. Each of these is discussed separately.

MANIPULATION OF SUCCESSION

It is not possible to sustain flower harvesting without fire, despite a contrary belief among many farmers. Many species require fire as a direct or indirect cue for seed germination (e.g. Blommaert 1972; Brits 1986, 1987; Jeffery et al. 1988; Pierce 1990) and even the longer lived Proteaceae senesce and die after 30 to 50 years without fire (Bond 1980; Van Wilgen 1981). Because of life history differences between species, marketable flowers change in abundance after fire. Some species appear only after fire, persist a few years, and then die. The most important commercial examples are the 'everlastings' such as *Helichrysum vestitum*. Others flower within a year or two after fire (e.g. *Erica perspicua*) and continue to flower for many years. Finally, some species are relatively slow to mature and only produce marketable flowers some 5–6 years after fire (e.g. *Protea* and *Leucadendron* species). Thus, the farmer will have a shifting availability of different flower species as the veld ages. Depending on veld composition and the market, farmers may choose to burn on short rotations (e.g. for *Helichrysum*), or in blocks for a mix of different ages, thus providing a cross-section of species from all successional stages.

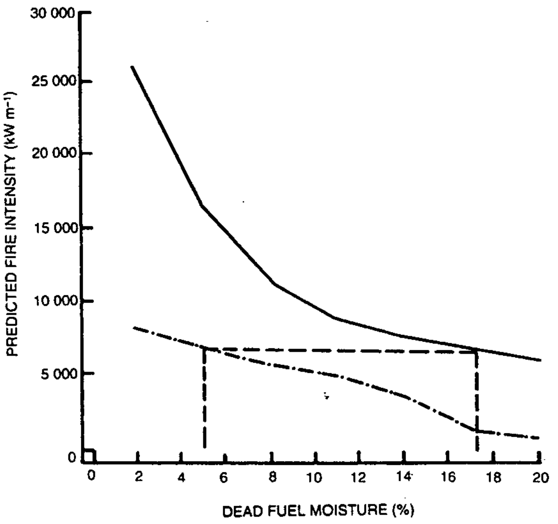

FIGURE 14.4 The effect of dead fuel moisture on predicted fire intensity (using Rothermel's fire model) for two fuel complexes. The upper curve (———) is for felled hakea, and the lower curve (•—•—•—) is for fynbos. The dashed line (– – –) indicates the moisture contents required to achieve similar fire intensities for the two fuel complexes. Reprinted from Richardson and Van Wilgen (1986a) with the permission of The Southern African Institute of Forestry.

The implications of different fire regimes have been discussed earlier. In practice, most veld is burnt after 12 to 15 years when the vigour of *Protea* shrubs declines and stem lengths become too short for the trade. The favourite fire season varies from region to region and appears to be determined mostly by safety factors. On the south-western and southern Cape lowlands (Gansbaai to Stilbaai), late summer and early autumn burns are common. Fires later in the season may be preferred further west in the Bot River area. The effects of fire season on marketable crops in the flower picking areas require further study.

MAINTENANCE OF HEALTHY PLANTS

Cutting methods in the field can have a substantial effect on the ability of a plant to produce subsequent harvestable flowers. The cutting of wood older than two years in the Proteaceae results in reduced shoot formation or the death of the branch, and incorrect pruning can lead to unproductive shrubs which are more susceptible to disease (Brits et al. 1986). Long stems are, however, required in the trade, and poor management of harvesting operations can lead to a decline in flower production.

Many species in fynbos have long stems unprotected by leaves. If stems are cut in these older sections below the leaves, the whole plant can die (Rebelo 1987). Poor harvesting procedures in the veld can thus lead to serious dieback of sensitive species including *Brunia albiflora*, *Erica pinea*, *Protea compacta*, and *Paranomus capitatus* (Rebelo 1987; Rebelo and Holmes 1988). There has been no research on determining the best methods for harvesting non-Proteaceous stems in the veld.

ADEQUATE SEED RESERVES

Clearly, the removal of flower heads or fruiting structures for the dried flower trade can influence the regeneration capacity of the veld. Indiscriminate harvesting of everlastings (*Helichrysum* and *Helipterum* spp.) has probably lead to their demise in the veld (Malan 1988). Many farmers are aware of the problem and harvest seeds from the veld, storing them for later broadcasting. However, the longevity of fynbos seed in storage may often be little more than a year (Eloff and Liede 1987; Pierce 1990). In addition, some species require burial by ants, germination cues can be complex and may require fire stimuli, while others are readily eaten by rodents or other seed predators. In general, seeds could be disseminated in the veld during the first autumn after a fire to ensure rapid germination at a time when vertebrate seed predators are scarce (Bond 1984; Midgley and Clayton 1990). However, the efficacy of seed harvesting and subsequent broadcasting in maintaining populations clearly need investigation.

For veld-harvested Proteaceae, a common alternative has been to limit harvesting to some fraction of the available flowers (Van Wilgen and Lamb 1986). For serotinous Proteaceae, state management agencies restricted picking to not more than half of the blooms or foliage each year with no picking at all for a full year before a prescribed fire. In fact, different species will have different sensitivities to picking intensity. Harvesting at levels in excess of 75% of blooms of the non-sprouting shrub *Phylica ericoides* diminishes the subsequent year's flower crop significantly compared to non-harvested controls; a harvesting intensity of 25% or less had little effect (D J Killian and R M Cowling unpublished data). Sprouting species, such as *Protea cynaroides*, are known to be resilient to heavy utilization (Vogts 1982). Non-sprouting species vary in their seed retention patterns. Some species hold seeds in cones for little more than a year, others retain a substantial fraction of seeds for three or four years (Bond 1985; Van Wilgen and Lamb 1986; Le Maitre 1990). Species with short-lived seed banks are more vulnerable and should be lightly harvested. Mustart and Cowling (submitted) suggest that seed bank sizes should not be decreased by more than 50% in seroti-

TABLE 14.2 **Predictions of flame length (m) for different wind speeds and moisture contents of the dead fraction of the vegetation, using Rothermel's (1972) fire model and a fynbos fuel model (Van Wilgen 1984). Conditions that will lead to a fire with flame lengths of between 2 and 5 m are blocked off, to illustrate how the predictions can be used to select combinations of wind speed and fuel moisture that will result in a fire with these characteristics.**

Moisture content of fine dead fuel (%)	Wind speed (km/hr) 0	5	10	15	20	25	30
2	1.1	3.4	5.3	7.0	8.4	9.8	11.1
5	1.0	3.0	4.8	6.3	7.6	8.8	10.0
8	0.9	2.7	4.2	5.6	6.8	7.9	8.9
11	0.7	2.2	3.5	4.6	5.5	6.4	7.3
14	0.4	1.2	1.8	2.4	2.9	3.4	3.8
17	0.3	1.1	1.7	2.2	2.7	3.1	3.5
20	0.3	1.0	1.6	2.1	2.6	3.0	3.4

nous Cape Proteaceae. This approximates the maximum degree (22 to 51%) by which unharvested seed banks would be reduced in the event of an unseasonable fire in late spring or early summer, before the current seed has matured. The harvesting of not more than 50% of current inflorescences or cones is recommended. Since there is lowered cone production in the post-harvest year, stem harvesting should only take place on alternate years. This would allow some measure of vegetative and subsequent reproductive restoration (Mustart and Cowling submitted).

There is, of course, little use in controlling harvesting without having full control over other aspects of management such as the timing of fires (see above). The rule regarding no harvesting before prescribed fires, for example, is difficult to apply because uncontrolled fires are still very common (Van Wilgen and Lamb 1986). One way of balancing this particular risk would be to reduce harvesting levels in older veld, since it has a greater probability of burning.

All work on the effects of harvesting on regeneration potential assume a strong relationship between pre-burn seed reserves and the eventual size of post-burn mature populations. This assumption has not been adequately tested. In lowland fynbos, for example, conditions for seedling survival after fire may be more important than seed bank size since seedling numbers are grouped in clumps vastly in excess of adult numbers (W J Bond and R M Cowling unpublished data).

PEST CONTROL

Pre-harvest pest control appears to be very limited in veld harvesting. However, there have been reports of the poisoning of sunbirds and sugarbirds which are said to damage inflorescences (Rebelo 1987). There seems little justification for this practice and it is hardly consistent with suggestions that veld harvesting will help conserve the fynbos ecosystem (Cowling 1990).

HARVESTING OF THATCHING REED

The fynbos restioid, *Thamnochortus insignis* ('dekriet'), is harvested locally in the sandveld of the southern Cape (Albertinia area) for use as thatching material. Linder (1990) provides an account of the biology and utilization of the species. Dekriet is much in demand because of its hard-wearing qualities and is sold as far afield as the Transvaal. The annual value of the crop is between R5–10 million (Linder 1990). Dekriet does not require fire for regeneration. Management is based on cutting good quality culms at a frequency (2–5 years) and season (early winter) which will ensure continued productivity of the plants. Competing shrubs are often removed leaving a relatively pure stand of dekriet. Should the market expand, there seems great potential for the cultivation of this plant.

The control of alien plants and animals

Invasive plants are a major problem in the fynbos biome (Richardson et al. this volume). The control of invasive trees and shrubs is the largest single task facing managers of most natural areas in the biome. In this section, we address the various control options briefly. These may be placed in three groups:

- biological control (hereafter bio-control);
- mechanical control; and
- chemical control.

We include all methods that involve the use of mechanical tools and/or fire under mechanical control: cut-and-burn, cut-and-leave, and burn standing.

CONTROL OPTIONS FOR PLANTS

A number of bio-control agents have been established in the biome (Table 14.3) and several other control options are available (Table 14.4). Clearly, some options are suitable for certain species but inappropriate for others. The effectiveness of any control option depends primarily on the life history attributes of the target species. In many cases, a combination of one or more control options (integrated control) produces the best results (Kluge et al. 1986). The situation is complicated when more than one weed species is present at a site, especially if the species differ markedly in their life history attributes. Other important constraints include managing control options within the confines of prescribed burning schedules. Wildfires often disrupt control operations. An expert system approach may offer the best way of selecting the best control option, but no such system has yet been developed.

TABLE 14.3 **Biological control agents (both intentional and accidental introductions) for the major invasive alien plants in the fynbos.**

Target species	Principal bio-control agents	Mode of operation	References
Acacia cyclops	Indigenous seed-feeding insects *Zulubius acaciaphagus* and *Remiptevans* sp. (Alydidae). No Australian bio-control agents introduced yet	*Z. acaciaphagus* destroys up to 84% seed crop	D Donnelly and M J Morris (unpublished data); Holmes and Rebelo (1988)
Acacia longifolia	Bud-galling wasp *Trichilogaster acaciaelongifoliae* Snout beetle *Melanterius ventralis*	*T. acaciaelongifoliae* reduces seeding and also causes growth suppression; *M. ventralis* attacks green developing seeds; the two agents together reduce seed production by about 99%	Dennill (1985) D Donnelly (unpublished data)
Acacia mearnsii	Several *Melanterius* species are potential bio-control agents; none have yet been released because of the perceived threat to commercial plantings of *A. mearnsii*	*Melanterius* spp. attack green developing seeds	Donnelly (1990)
Acacia melanoxylon	Snout beetle *Melanterius acaciae*	Attacks green developing seeds	D Donnelly (unpublished data)
Acacia saligna	Gall rust *Uromycladium tepperianum*	Galls reduce seed production and general vigour; heavily galled plants die	Morris (1987)
Hakea sericea	Snout beetle *Erytenna consputa* Moth *Carposina autologa* Fungus *Colletotrichum gloeosporioides*	Larvae destroy developing (*E. consputa*) and accumulated mature (*C. autologa*) fruits; the fungus reduces vigour and causes mortality	Morris (1982, 1989); Neser and Kluge (1985)
Leptospermum laevigatum	Seed-affecting organisms available, including a specialized nematode and a fly (Sphaerulariidae, Fergusoninidae) but not yet introduced	Not known	Neser and Kluge (1986)
Paraserianthus lophantha	Snout beetle *Melanterius servulus*	*M. servulus* attacks green developing seeds	D Donnelly (unpublished data)
Pinus pinaster	Pine woolly aphid *Pineus pini* (Homoptera: Adelgidae) (accidental introduction)	Causes cone deformation and stunting leading to reduced seed production	Zwolinski et al. (1989)
Pinus radiata	*Pineus pini* (accidental introduction)	Causes cone deformation and stunting leading to reduced seed production	Bruzas (1981)
Sesbania punicea	Snout weevils *Trichapion lativentre, Rhyssomatus marginatus* and *Neodiplogrammus quadrivittatus*	*T. lativentre* adults feed on leaves, flowers, and young pods and larvae develop in young flower buds; *R. marginatus* develops in immature pods; *N. quadrivittatus* larvae bore through mature branches and stems	Harris and Hoffmann (1985); Hoffmann and Moran (1988)

TABLE 14.4 **The currently available options for the control of some important alien invasive plants in the fynbos biome. Specific information of bio-control agents is given in Table 14.3.**

Species and salient life history attributes	Options	Focus of control measure	Comments / Constraints
Acacia cyclops — does not resprout — relatively short-lived seed bank stored in soil — seeds not stimulated to germinate by fire	a) Bio-control		Not available at present.
	b) Cut-and-leave	Adult mortality and seed bank depletion	This species does not sprout and seed banks are relatively short-lived (Holmes 1989).
	c) Cut-and-burn	Adult mortality and seed bank depletion	Fire destroys seeds near the soil surface.
	d) Burn standing	Adult mortality and seed bank depletion	Adult plants are killed. Follow-up weeding required; this is feasible because recruitment is not fire-coupled and because seed pools are relatively short-lived.
	e) Chemical	Chiefly seeding mortality	Non-target species adversely affected.
	f) Integrated	Long-term control	Use b, c, or d in combination with e where germination is prolific.
Acacia longifolia — does not resprout — relatively long-lived seed bank stored in soil — seeds stimulated to germinate by fire	a) Bio-control	Reduced seed production and vigour	Highly effective. Invasive potential greatly reduced.
	b) Cut-and-leave	Adult mortality	Adults killed but soil-stored seeds stimulated; follow-up weeding of seedlings necessary.
	c) Cut-and-burn	Adult mortality and seed bank depletion	Adults killed but soil-stored seeds stimulated; follow-up weeding of seedlings necessary.
	d) Burn standing	Adult mortality and seed bank depletion	
	e) Chemical	Seedling mortality	Non-target species adversely affected.
	f) Integrated	Long-term control	Use b and a.
Acacia mearnsii — resprouts — relatively long-lived seed bank stored in soil — seeds stimulated to germinate by fire	a) Bio-control	Reduced seed production	Effectiveness untested. Other forms of bio-control not considered due to commercial importance of species.
	b) Cut-and-leave	Adult mortality	Ineffective; plant resprouts.
	c) Cut-and-burn	Adult mortality	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
	d) Burn standing	Adult mortality	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
	e) Chemical	Chiefly seedling mortality	Non-target species adversely affected.
	f) Integrated	Long-term control	Combine b, c, or d with e and a.

TABLE 14.4 continued.

Species and salient life history attributes	Options	Focus of control measure	Comments / Constraints
Acacia melanoxylon	a) Bio-control	—	Nothing available at present.
	b) Cut-and-leave	Adult mortality	Ineffective; plant resprouts.
— resprouts	c) Cut-and-burn	Adult mortality and seed bank depletion	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
— relatively long-lived seed bank stored in soil	d) Burn standing	Adult mortality and seed bank depletion	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
— seeds stimulated to germinate by fire	e) Chemical	Chiefly seeding mortality	Non-target species adversely affected.
	f) Integrated	Long-term control	Combine b, c, or d with e and a.
Acacia saligna	a) Bio-control	Reduced vigour	Introduced fungus slow to establish. Overall effectiveness unknown but potentially very effective.
— resprouts	b) Cut-and-leave	—	Inappropriate. Adults resprout after felling and seed bank persists.
— relatively long-lived seed bank stored in soil	c) Cut-and-burn	Adult mortality and seed bank depletion	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
— seeds stimulated to germinate by fire	d) Burn standing	Adult mortality and seed bank depletion	Ineffective. Adults resprout and germination of soil-stored seed stimulated.
	e) Chemical	Chiefly seedling mortality	Non-target species adversely affected.
	f) Integrated	Long-term control	Combine b, c, or d with e and a.
Hakea gibbosa	a) Bio-control	Reduced seed production and vigour	Not highly effective.
— does not resprout	b) Cut-and-leave	Adult mortality	Ineffective; fire is needed to kill seedlings.
— seeds stored in heat-resistant follicles in the canopy	c) Cut-and-burn	Adult and seedling mortality	Adults felled, seeds germinate and are killed by fire. Highly effective but expensive.
— seed release stimulated by fire or felling	d) Burn standing	Adult mortality	Effective in some cases but usually results in dense stands of seedlings; standing dead trees make manual eradication of seedlings difficult. Seeds are released from standing shrubs and are dispersed to new sites by wind.
	e) Chemical	Adult mortality	Effective in low-density stands for selective control.
	f) Integrated	Long-term control	Combine c with a or e.
Hakea sericea	a) Bio-control	Seed production and vigour	Reduces invasion potential significantly in the long-term but existing stands need to be cleared.
— does not resprout	b) Cut-and-leave	Adult mortality	Fire is needed to kill seedlings.
— seeds stored in heat-resistant follicles in the canopy	c) Cut-and-burn	Adult and seedling mortality	As for *Hakea gibbosa*.
— seed release stimulated by fire or felling	d) Burn standing	Adult mortality	As for *Hakea gibbosa*.
	e) Chemical	Seedling mortality	Ineffective.
	f) Integrated	Long-term control	Combine c with a.

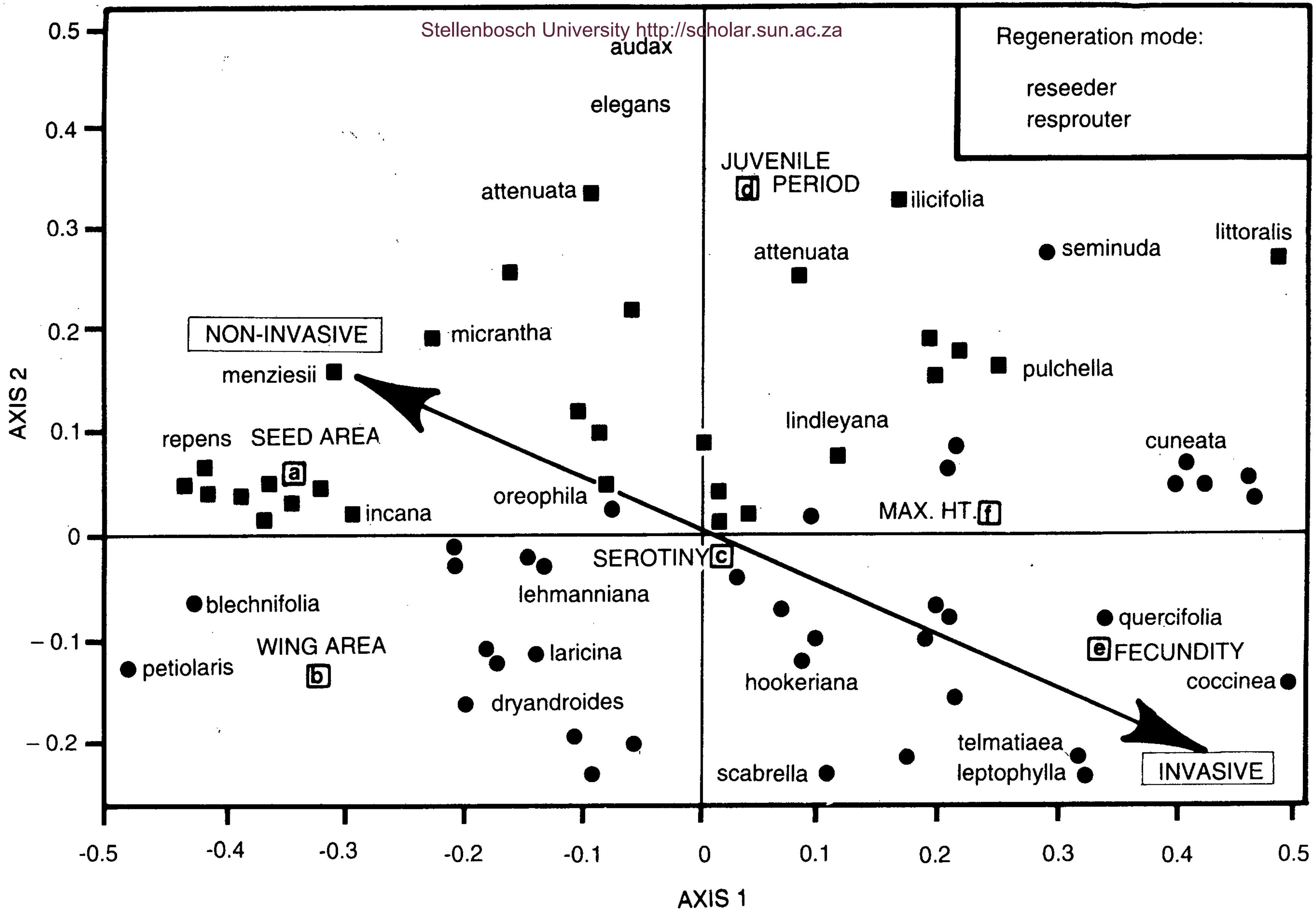

FIGURE 14.5 A simplified plot of the first two axes from a correspondence analysis of a matrix of six life history attributes (a to f) of 69 western Australian *Banksia* taxa. A trend of potential for invading mountain fynbos is defined (modified from Richardson et al. 1990). Tall serotinous shrubs with many small seeds per plant, short juvenile periods, and low fire tolerance (e.g. *B. coccinea*) were identified as high risk introductions. Low sprouting shrubs with few large seeds per plant and long juvenile periods (e.g. *B. menziesii*) are unlikely to become invasive in mountain fynbos. The model can be used for screening species that have good potential for the cut flower market.

SCREENING FUTURE INTRODUCTIONS

Because of the current socio-political situation, funding for alien control programmes will probably decrease (see below), accentuating the need for innovative control strategies. Besides controlling current invaders, attention should be given to screening future introductions for potentially invasive species. Meaningful priorities for the control of current invaders should also be set. Richardson et al. (1990) described invasion windows (conditions suitable for the establishment, growth, and proliferation of invaders) in mountain fynbos and defined attributes that characterize invaders. The scheme was tested using 60 *Pinus* taxa, including several species that have invaded fynbos. Most of the invasive taxa belonged to the 'high risk' group. The model was then applied in screening the potential invasiveness of western Australian *Banksia* species, some of which are likely to be increasingly cultivated in the fynbos biome for the cut flower market. A number of species were identified as 'high risk' introductions (Figure 14.5) and these could be avoided when selecting species for local cultivation.

CONTROL OPTIONS FOR ANIMALS

Animals are not important invaders in the fynbos biome, but it has proved difficult to control the few species that do invade. Among the faunal invaders (Richardson et al. this volume), the American grey squirrel (*Sciurus carolinensis*) and the Himalayan thar (*Hemitragus jemlahicus*) have been the subjects of control programmes. In the case of the squirrel, the imposition of a bounty system did little to contain its spread (Millar 1980). Thars on Table Mountain increased from an estimated 330 to 403 between 1972 and 1980, despite the culling of 629 animals (Brooke et al. 1986). Culling has been relaxed since 1981, with an average take-off of 2.8% which is way below the estimated population growth rate of 23% per annum. The most recent (1988) estimate of population size is 1 635 (P H Lloyd unpublished data). Options for the control of the Argentine ant have not been examined in detail but, considering the failure of control programmes elsewhere in the world, the chances of achieving significant control of this species in the fynbos appear very remote. Experience from other regions (Erhlich 1989) also suggests that the control of the European starling or other introduced birds in the fynbos biome is very unlikely to succeed. Managers should concentrate on preventing the introduction of other notorious invaders, and containing those that are introduced before they undergo large range expansions.

The management of fynbos for fauna

The faunal component of fynbos ecosystems is not often a subject of concern to managers. Traditionally, fynbos is regarded as poor grazing. Limited work has shown that there are numerous nutritional deficiencies in fynbos (Joubert and Stindt 1979a, b; Stindt and Joubert 1978). The Department of Agriculture does no research on the grazing potential of fynbos ecosystems, as they are not considered as suitable for grazing. What work has been done has been aimed at eradicating encroaching fynbos elements from grasslands (Trollope 1971, 1973). Nonetheless, fynbos is frequently used for grazing by domestic livestock, especially in the eastern part of the biome (Cowling 1983). In addition, some fynbos ecosystems are managed specifically for endemic faunal elements. We will not attempt to develop general principles for faunal management, but rather show by means of examples (the endemic geometric tortoise and the bontebok) how the biological requirements of a species can be used to determine management prescriptions.

The geometric tortoise (*Psammobates geometricus*) is endemic to the few remaining patches of renoster shrublands on the western Cape lowlands. Some salient features of its life history (E Baard unpublished data) determine the management actions taken to ensure its survival. The species subsists on a diet of soft herbaceous plants, and is not found in old, dense vegetation. It reaches sexual maturity at five to six years; eggs are laid from October to December and they hatch between April and May. Geometric tortoise reserves are managed by burning on a cycle greater than six years, but less than 12 years to ensure that adults are mature when fires take place, and that food plants are always available. Fires are timed to occur when eggs are underground (January to

March). The fire regime applied to ensure the survival of geometric tortoises is remarkably similar to that needed for serotinous *Protea* species. Grazing by domestic stock is sometimes considered as an alternative to burning as it opens up the vegetation (thus providing conditions favouring the tortoises' food plants) and does not kill any adults.

The bontebok (*Damaliscus dorcas* subsp. *dorcas*) occurred historically in renoster shrubland, most of which is now under cultivation. It is preserved in a few patches of fynbos, not its favoured habitat. Bontebok consume grasses (Beukes 1987) which are seldom a major component in fynbos in the western part of the biome (Cowling and Holmes this volume). In the Bontebok National Park, the vegetation is burnt on a short (four year) cycle to favour grass at the expense of shrubby elements (Novellie 1984; Verster 1989). The relatively frequent fire cycles applied to provide bontebok with food will undoubtedly lead to the loss of plant species. In addition, the application of grazing pressure far in excess of that under which the plants evolved will probably cause further attrition. For this reason, parts of the park are managed for floral conservation and are burnt on longer (10–12 year) cycles (Novellie 1984). However, the preservation of Africa's rarest antelope (Smithers 1983) is seen as justification for relatively frequent burning in limited areas of fynbos. Similar conflicts may potentially exist in the case of the Cape Mountain Zebra (*Equus zebra* subsp. *zebra*).

SCENARIOS

In previous sections we addressed management in fynbos ecosystems and attempted to clarify the scientific basis for thes e actions. But what of the future? It is clear that the biome faces increasing fragmentation of the natural landscape, invasion of these fragments by alien plants, a decline in funds for management, and climatic change. How can managers make rational decisions faced with such uncertainty? In this section we examine some scenarios in the biome and explore the implications for the management of fynbos.

Fragmentation

Although large areas of mountain fynbos remain intact, lowland fynbos has become fragmented into small remnants by agriculture, urbanization, and forestry (Rebelo this volume). This poses problems for conservation and management (Kruger 1977b). Biologists have become aware that the survival of species is linked to the area of habitat (Bond et al. 1988). Consequently, if large extensive areas of habitat become fragmented into small isolated parts, the local extinction of species may follow. Bond et al. (1988) showed that more than 75% of plant species had become extinct on isolated islands of fynbos in the Knysna Forest. The most vulnerable species were those most dependent on fire (sprouters and small, early successional shrubs). To reduce the level of extinctions, managers can either increase the area of natural land conserved, or ensure that isolated areas experience regular fires. The minimum area needed for plant conservation may vary greatly depending on circumstances, but some guidelines are beginning to emerge (Bond et al. 1988; Cowling and Bond 1991). Appro-priate fire regimes are of more immediate importance but there are often logistical and legal problems in burning small reserves, particularly near urban areas.

Besides changes in fire regime, other processes can also be influenced by habitat fragmentation. Some of these are ecological in nature. Few have been documented. Our own observations suggest that vertebrate densities are sometimes very high in refugia of natural veld leading to intense seed predation or herbivory; Argentine ants may invade more readily from cultivated land into small patches of veld; and pesticides blown or washed in from farm lands may disrupt plant-animal interactions.

Studies on extinction risks for specific taxa are still in their infancy. One demographic study (Bond 1989) predicts, surprisingly, that the species most vulnerable to extinction because of habitat fragmentation may also be the most common ones (e.g. *Protea repens* and *P. neriifolia*). Genetic processes are also influenced by population size as determined by habitat area (Franklin 1980; Lande 1988). In theory, managers can reduce the genetic effects of small population size by translocation. Although the problem has been recognized for fynbos (e.g. Hall 1987a), there is almost no work on the topic. Besides maintaining an awareness of the problem (see also Rebelo this volume), there is little the manager can do at present.

The inverse of fragmentation is that new corridors of habitat are opened up. With human-induced alteration of habitats, the fynbos biome has become less insular and many species have migrated into the fynbos from adjacent biomes. For example, 120 species of birds (35% of the current avifauna) have invaded the biome since 1850 (Macdonald 1991). We should expect more 'invaders' from adjacent regions as changes become more pervasive. For example, habitats such as forest patches, formally isolated in a 'sea' of fynbos, are now joined by corridors (plantations of alien trees) that permit diffusion of biota (e.g. Richardson 1989).

Funding

The management of fynbos ecosystems for nature conservation is currently dependent on state funding. As an example, the current (1990) level of funding for catchment conservation in the Western Cape Region is R7.5 million. The budget was increased by only R7 000 (0.1%) from the previous year — this with an annual inflation rate of around 15%. The money must also be used for additional tasks other than the prescribed burning and weed control programmes for which it was originally budgeted. There is an increased demand for recreational facilities, and as farming activities encroach further into mountain land, the demand for fire protection increases. Social upliftment is a priority in the region, and labour costs have increased at a rate several times greater than inflation. Eight years ago, managers were of the opinion that the alien weed problem would be brought under control within 15 years (Kluge and Richardson 1983); they no longer hold this view (R H Andrag personal communication). Changes in the levels of funding for weed control will affect the ultimate condition of fynbos ecosystems.

Four scenarios of funding, and their implication, provide a framework within which changes can be examined. In real terms, current levels of funding will allow prescribed burning to take place once every 15 years, but the cost of weed control programmes would mean that each management unit could only be cleared every second fire cycle (Scenario 1). Using the known rates of proliferation for *Pinus radiata* (Richardson and Brown 1986), alien cover would reach 34% in the second fire cycle. It would return to low levels again following clearing. In order to keep areas clear of invasives, funding would have to be increased to a level where clearing would be possible in conjunction with every prescribed fire (Scenario 2). Under such a scenario, it would be possible to keep the cover of aliens down to < 1%. A more likely scenario would be that funding would decrease in real terms, so that clearing would only be possible every third fire cycle (Scenario 3). Here, cover of aliens would increase to 34% in the second cycle, and to 90% in the third cycle. Should clearing of these infestations be attempted, they would be extremely costly compared to Scenario 1 or 2, due to the dense nature of the stands. Under a worst-case scenario (Scenario 4), no funding for the clearing of aliens would be provided. Alien invasions would increase to 100% cover after about four fire cycles, and would remain at these levels thereafter. The implications of these scenarios for species diversity, water yield, and fire hazard (Table 14.5) are discussed below. Such implications should be weighed carefully when decisions to cut back on alien control programmes are considered.

IMPLICATIONS FOR SPECIES DIVERSITY

In the fynbos biome, invasion by alien plants has resulted in a maximum of 26 extinctions (Hall and Veldhuis 1985). Whereas none of these extinctions can be attributed exclusively to alien plants (Richardson et al. 1989), a cascade of extinctions is virtually inevitable in the next few decades should Scenarios 3, 4, or probably even Scenario 1 prevail. Approximately 750 fynbos plant species (nine per cent of the flora) are currently at risk (Hall 1987b; Macdonald et al. 1989; Richardson et al. this volume). The list of extinct species will grow rapidly as an increasing number of communities are disrupted by invasions and, probably more importantly, as the time since the establishment of thickets of alien species increases, with concomitant attrition of seed banks of suppressed endemic species. Serotinous Proteaceae, small-leaved sprouting and myrmeco-

TABLE 14.5 **The outcome of various funding scenarios and the implications for species diversity, water yields, and fire hazard in fynbos ecosystems. The projections for species diversity are based on data in Richardson et al. (1989), those for water yield on data in Van Wyk (1987), and those for fire hazard on data in Versfeld and Van Wilgen (1986).**

Funding level	Outcome	Implications for species diversity	Effect on water yield	Effect on fire hazard
I Unchanged	Cover of aliens never exceeds 50%	Local extinction of sensitive species could occur	Reduced by 9%	Fuel loads increased by 50%
II Increased	Cover of aliens remains low (< 1%)	Current species diversity maintained	Little or no reduction	Little or no increase
III Decreased	Cover of aliens becomes dense (> 90%) at times	Local extinction of sensitive species likely; population sizes of common species reduced	Reduced by 21%	Fuel loads increased by 140%
IV Curtailed	Aliens form closed stands over large areas	Local extinction of most indigenous species	Reduced by 50%	Fuel loads increased by 330%

chorous woody shrubs, and large-leaved sprouting shrubs are especially susceptible to extinction (Richardson and Van Wilgen 1986b). A major effort and expenditure of funds are clearly required to prevent extinctions.

Control measures aimed at reducing the detrimental effects of alien plants on biotic diversity must:

- remove the existing dense stands with the least possible additional damage to surviving vegetation and soil-stored seed banks; and
- prevent the establishment of new dense stands.

Alien weed species that have commercial value are the largest problem, as continued propagation and dispersal will mean that control programmes can never be scaled down. We pose the question of whether agencies responsible for the cultivation of these species should not help to offset the costs incurred elsewhere in controlling the resultant invasions?

IMPLICATIONS FOR WATER YIELD

The conversion of fynbos shrublands to closed-canopy pine forests reduces stream flow by almost 50% (Van Wyk 1987). Similar reductions are likely for self-sown stands of pines and other species. For the various scenarios examined, reductions in stream flow will range from almost nothing (Scenario 2) to 50% (Scenario 4). The real costs of this, in terms of reduced water supplies to cities, industries, and agriculture are probably enormous. The question of whether we can afford to allow this to happen (through allowing funding to decrease) needs to be addressed urgently.

IMPLICATIONS FOR FIRE BEHAVIOUR

Fuel loads are greater in dense stands of aliens than in fynbos, but fires are generally more easily ignited in fynbos where there is an abundance of fine material in the herbaceous layer. Dense stands of alien plants burn only under extreme weather conditions, although such fires will be of much higher intensity than fires in uninvaded fynbos. Fires under these conditions are more difficult to contain and are potentially more damaging to ecosystems than fires in indigenous vegetation (Van Wilgen and Richardson 1985b). Under the scenarios examined here, the increase in fuel loads would range from almost nothing to more than 300% (Table 14.5). Fires that occur in stands with vastly increased fuel loads would be uncontrollable, and would result in damage both to the soil and to adjacent properties and crops.

Climatic change

Global climate change as a result of increases in carbon dioxide and other greenhouse gasses will affect all of the earth's ecosystems. Although the predictions for change are crude, they may have important implications for fynbos. Again, we can only examine potential scenarios of climatic change, and attempt to quantify their effects.

CHANGES TO THE FIRE REGIME

We selected some scenarios of likely climatic change (Table 14.6) and used these, together with a 10 year weather record from Swartboskloof (33°57'S, 18°55'E), to generate fire danger indices from the United States National Fire Danger Rating System (Deeming et al. 1978). The results are shown in Figure 14.6. Increases in temperature alone (Scenario 2), or in temperature and rainfall (Scenario 4) do not affect the likelihood of fires markedly. However, a seasonal shift in rainfall patterns will change the seasonal distribution of fires (Scenario 3). Exactly how plants will respond to these changes is not known. Scenario 3 shows that fires will most likely occur between March and July. Fynbos plants reach a minimum flowering activity in April, and this increases steadily through to a maximum in September (Kruger 1981). At times of active flowering (e.g. June and July), fires will destroy unripe seed crops and therefore reduce recruitment. Furthermore, for serotinous Proteaceae, the time between seed release after fire and germination could lengthen, causing high levels of seed predation (Johnson this volume). This could result in individual species becoming extinct (Figure 14.7).

CLIMATE AND PLANT SPECIES DISTRIBUTION

It is difficult to predict the effect of climate change on the distribution of plant species (Bond and Richardson 1990). We can, how-

TABLE 14.6 Scenarios of climatic change used to simulate changes to seasonal fire potential in the fynbos biome.

Climate change scenario	Temperature	Rainfall
1	No change	No change
2	Increase of 2°C in daily maximum temp	No change
3	Increase of 2°C in daily maximum temp	Seasonal shift forward by 4 months
4	Increase of 2°C in daily maximum and minimum temperature in summer and 3°C in winter	Increase of 15% in daily rainfall figures

ever, speculate on the primary influence of factors such as changed seasonal distribution of rainfall and changed mean annual temperatures on community structure. According to some predictions (R E Schulze personal communication), the western Cape will receive more rain in summer and annual mean temperatures will increase. This might favour invasion by summer-growing C_4 grasses from the east, at least in the lowlands where nutrients are not severely limiting (Cowling and Holmes this volume; Stock this volume). This could have a massive impact on community structure, directly if the grasses suppress geophytes and shrub seedlings in the vulnerable post-fire period, and indirectly by facilitating shorter fire rotations. Fire intensity would decline, reducing the abundance of species which require hot fires for regeneration (Bond et al. 1990). Since natural areas in the lowlands are already fragmented, extinction would probably exceed immigration, at least for woody elements, and the result would be reduced richness of fynbos components. Increased summer rain would alleviate soil moisture deficits and possibly favour the invasion of fynbos by forest species that are currently confined to riparian zones, although the increased abundance of grasses and the shorter fire rotations may counter such invasions (Cowling and Holmes this volume).

Plant responses to climate change are likely to be individualistic, especially in their reproduction. Increased temperatures, for example, could inhibit germination in several important fynbos taxa, with seeds stimulated by cold temperatures. For example, *Leucospermum cordifolium* has soil-stored seeds which germinate best when maximum temperatures exceed 24°C and minima are less than 9°C. Under current conditions, these temperature combinations occur in burnt, unshaded sites in autumn and spring (Brits 1986; Figure 14.7). Greenhouse warming of 3–4°C could cause delays of months in germination timing or outright germination failure (Figure 14.7), leading to the rapid population decline of this species. However, germination response is quite variable and we do not know the capacity for rapid selective change. An enormous amount of detailed physiological knowledge of reproductive cues would be needed to predict the potential threats to fynbos species. The most sensitive species would be long-lived nonsprouters. More effort is needed in determining the possible effects of climate change on the reproductive biology of such species.

Much more research is required before we can make useful predictions on the distribution of vegetation under different scenarios for climatic change. The problem is made worse by the complex interactions that regulate range limits (Richardson and Bond 1991). The limited information available suggests that

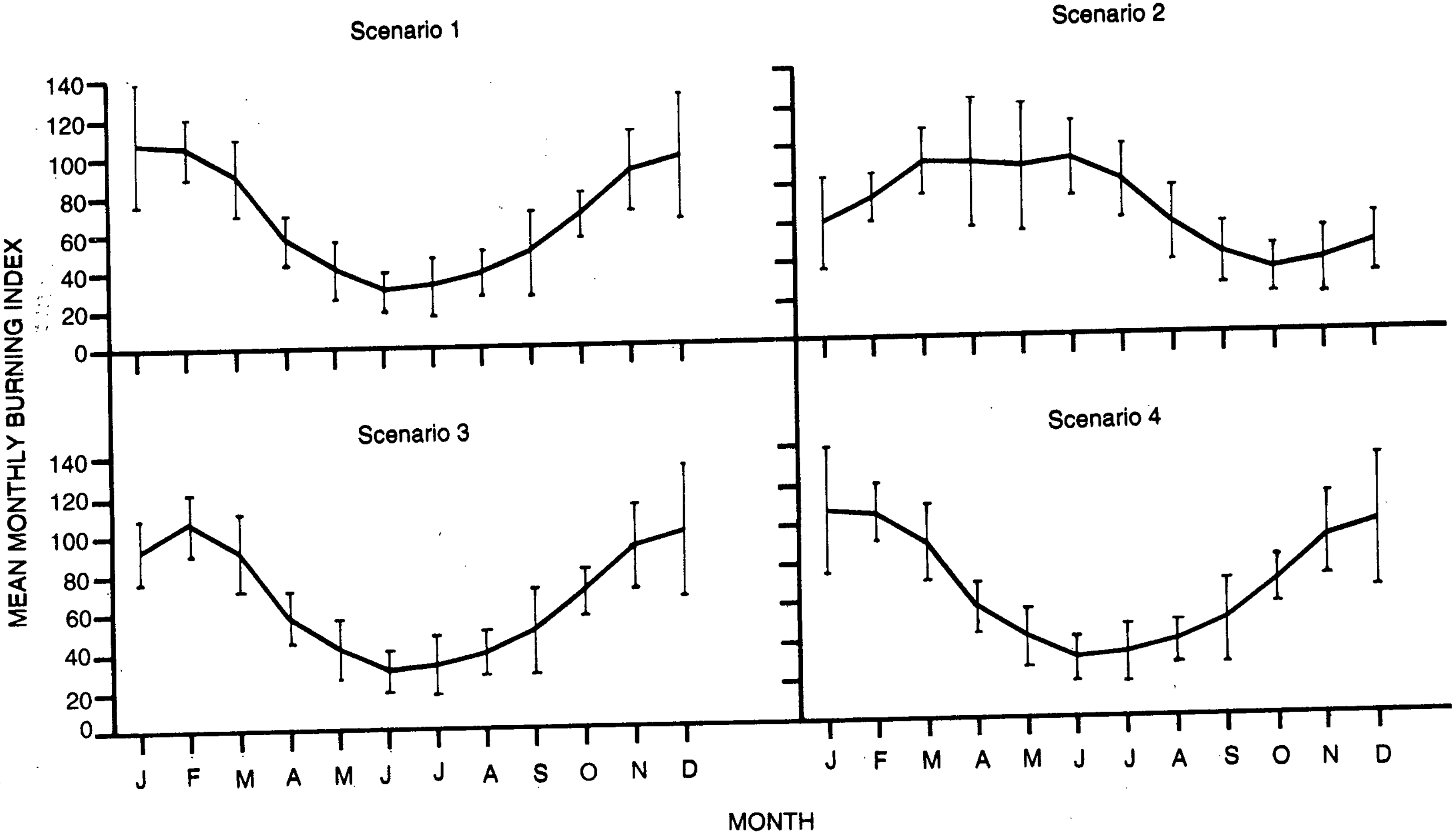

FIGURE 14.6 The annual cycles of mean monthly fire danger (burning index) under four scenarios of climatic change (Table 14.6) at a site in mountain fynbos.

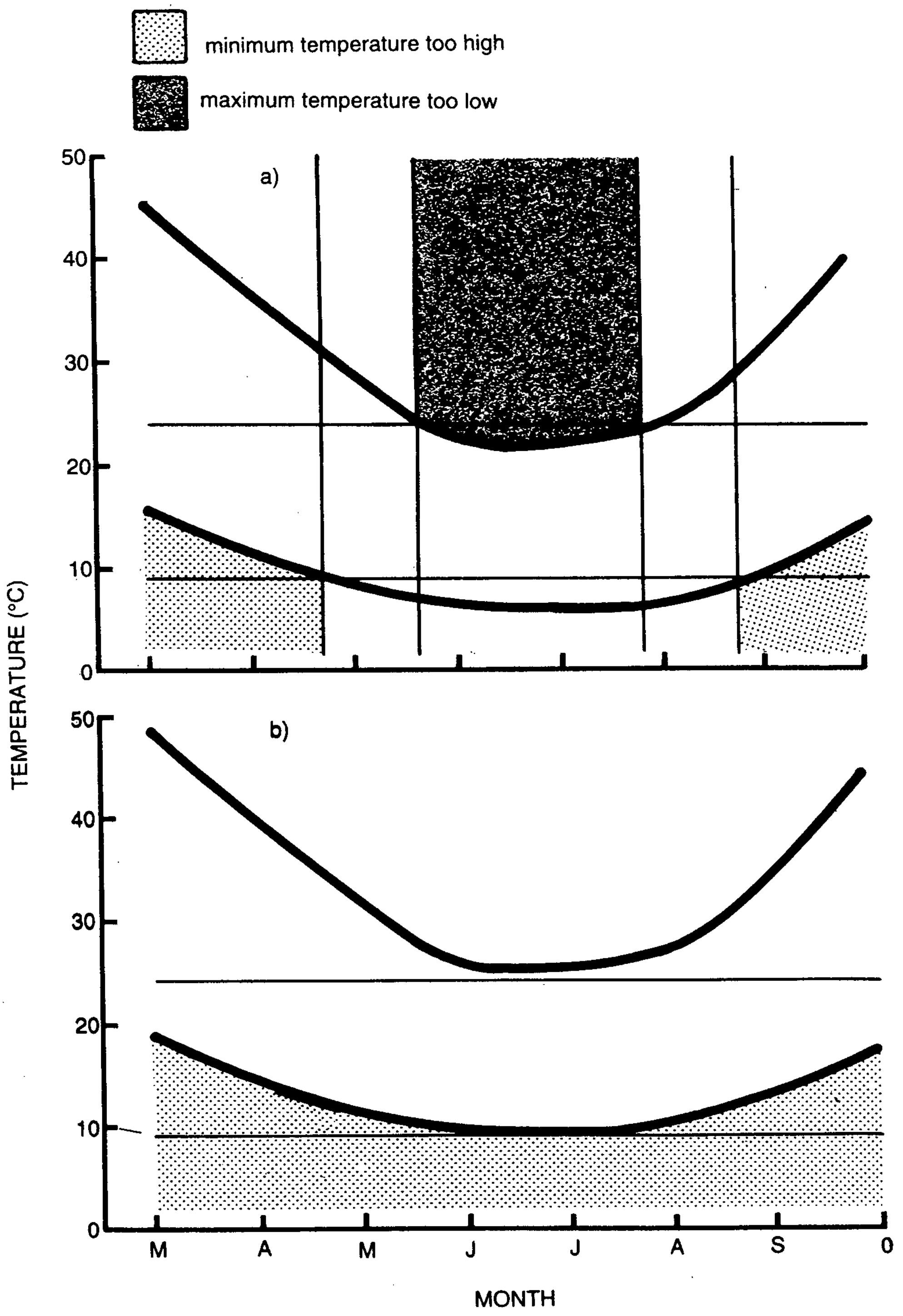

FIGURE 14.7 The potential effects of climatic warming on the seed germination of *Leucospermum cordifolium*, Proteaceae. (a) Optimum germination requires the simultaneous occurrence of minimum temperatures of < 9°C and maximum temperatures of > 24°C (Brits 1986). Under current conditions, these temperature combinations occur only after fire in autumn and spring (shaded areas on the temperature curves indicate periods and causes of inhibition at other times). (b) With a 4°C warming, seeds would not germinate. From data in Brits (1986).

the impact of climate change will be most marked in the lowlands, and that the seed-regenerating shrubs of the Proteaceae will be severely stressed, many to the point of extinction. Changes of this magnitude provide an enormous challenge to researchers and managers.

CONCLUSIONS

Fynbos ecosystems have two major management requirements: a regular fire regime and the need for the eradication of alien plants. Both require practical management solutions, and in both cases there are demanding problems. Many fynbos species need intense fires for persistence, but these are not easy to manage. Alien weed control needs generous funding, and this is not easy to obtain. We have attempted to review the reasons for these needs, and to spell out the consequences should the needs not be met. The chapter has highlighted the need to improve technical skills, such as making use of fire behaviour prediction models, and developing (and making use of) expert systems. A thorough, professional approach to management, through the proper use of such models and systems, is probably the only way in which fynbos managers will be able to cope adequately with the immensity of the task. Much remains to be done to integrate these approaches into management, but such an endeavour is worthwhile. Research should concentrate on improving the understanding of variation over the biome (such as the response of plants to fire season), and should focus on processes likely to be impacted by fragmentation and climatic change. We believe that researchers should form strong partnerships with managers to ensure that appropriate questions are addressed, and that research results are implemented. We cannot afford not to do so.

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Fifth paper: A computer-based system for fire management in the mountains of the Cape Province, South Africa. *International Journal of Wildland Fire* (1994).

Int. J. Wildland Fire 4(1): 17-32, 1994
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A Computer-Based System for Fire Management in the Mountains of the Cape Province, South Africa

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Abstract. This paper describes a Catchment Management System (CMS) that provides objective procedures for managing fire. Prescribed burning is carried out in the mountain catchments of the Cape Province, South Africa, to enhance water yield, to rejuvenate the indigenous shrubland vegetation, to reduce fire hazard and to control invasive alien plants. Fire is the only practical tool for achieving these aims in the mountainous terrain. Recent research has improved understanding of the response of these systems to fire, but managing fire to achieve goals is very difficult. The CMS comprises a central geographical information system for managing and processing spatial data, linked to personal computers with DBase IV data-bases and simple rule-based models for decision-making. Current applications are: prioritization of areas for burning, monitoring the success of fire management, mapping fire hazard for fire control planning, and the production of management summaries and statistics.

This paper presents examples of these applications from three areas in the Cape Province with different management problems and priorities: the Kammanassie in the southern Cape, and the Kogelberg and Table Mountain areas in the western Cape.

Keywords: Fynbos; Catchment management; Geographic information systems; Management systems; Fire

Introduction

There are many problems associated with applying prescribed burning over large areas, particularly in mountainous terrain. Practical problems relate to how and when to set fires within acceptable limits of ecological tolerance of the biota and safety of personnel. Problems are compounded when managed areas are important for recreation or adjoin high-density human settlements. Keeping records of the extent and effects of fires is also problematical. A more fundamental problem arises when managers attempt to translate stated objectives into operational terms. For example, how is the broad policy of conserving genetic diversity in the species-rich Cape Floristic Region translated into management actions? How are the outcomes of these management actions monitored? Ecological studies have advanced our knowledge of the role and effects of fire in ecosystems, but there are few examples of rigorous management systems that seek to apply this knowledge systematically (e.g. Kessell 1990).

Prescribed burning is used extensively in the mountain catchment areas of the Cape Province of South Africa. Fire is used to rejuvenate fynbos (the indigenous shrubland vegetation), to reduce fire hazard, to enhance water yields, and as part of the integrated control of invasive alien trees and shrubs (van Wilgen et al. 1990). The principal aim in most catchments is to maintain a sustained yield of high quality water. Equal weighting is usually given to the aim of conserving biotic diversity. Many areas are managed for multiple objectives, including water, biodiversity, recreation, grazing and the production of wild flowers. Part of the problem of how to use fire is that mountain fynbos ecosystems are extremely complex (Cowling 1992); it will never be possible to know how every organism will respond to a particular management practice. Recent research has improved understanding of ecosystem, community and species response to fire in fynbos (e.g. van Wilgen et al. 1992). This knowledge must now be translated into objective management procedures.

Good records are essential for rational decision-making. Advances in geographical information systems (GIS) and related computer technology have made the

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handling of large quantities of spatial data feasible. In this paper we describe a computer-based system for managing fire in Cape catchments. The system stores, retrieves and processes data, and produces the summaries, statistics and maps required by catchment managers. The Catchment Management System (CMS) also deals with the problem of selecting areas for prescribed burning (a prioritizing problem), and provides a new method for monitoring the progress and success of fire management. Although the system is intended for operational use in the Cape, it should find application in many other ecosystems managed by fire. The conceptual development of the CMS is described in detail elsewhere (Richardson et al. 1992; Le Maitre et al. 1993). Our aim here is to describe the practical application of the system with special reference to the management of fire.

Study Areas

Three mountain areas, the Kammanassie, the Kogelberg and Table Mountain, were selected for development and testing of the system (Figure 1). We chose these areas because they provide fairly typical examples of the range of management problems in the mesic southwestern and xeric southern Cape. They have different vegetation structure and major land-use constraints and different values as water catchments and as reserves for rare and endemic species of plants and animals. Invasive alien trees and shrubs are abundant in the Kogelberg and on Table Mountain, where they are a fundamental management problem, but absent from the remote Kammanassie (Table 1).

Details of the Systems

The two parts of the CMS were designed as separate components to accommodate management requirements (Figure 2). Firstly, managers expressed the need to access data on the personal computers at their remote stations (PCs with DOS using DBASE IV). Secondly, a large centralised data-base was needed to capture, store and manage the spatial data and produce maps (a Sun Sparc workstation with UNIX running Arc/Info Version 6) (Le Maitre et al. 1993).

The system on both computers comprises a set of databases for distinct spatial units. The key databases are those dealing with details of the management units (subdivisions of land, termed compartments), fire records, and land tenure. The systems were designed to allow the manager to access and edit data on a PC, perform queries and produce summary reports. Special routines were implemented to produce summary histograms in DBASE IV (see later). The data can also be transferred, by means of 720 kb 3-inch computer disks, between the two systems using built-in routines. This allows for changes made by the manager to be placed on the central system and vice versa. Data transfer via modem is not yet feasible because of the isolation of the offices from where the catchments are managed (poor telephone links, often without direct dialling).

The centralized spatial database produces summary reports, and processes any spatial data required by the manager. For example, the manager must compile fire reports containing information such as date and duration, cause, point of origin, costs and a brief description of the control operation and a map of the fire boundaries. Estimates must be made of areas burnt for each

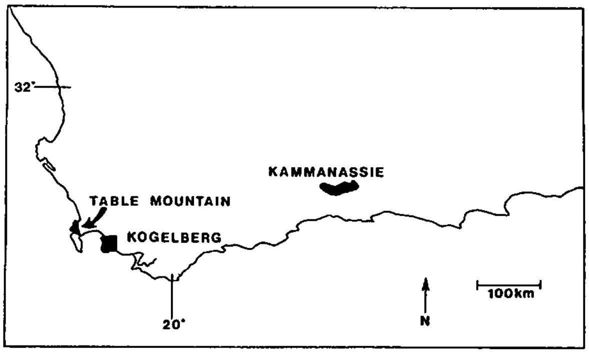


Figure 1. The locations of three study areas chosen for testing the Catchment Management System in the Cape Province, South Africa.

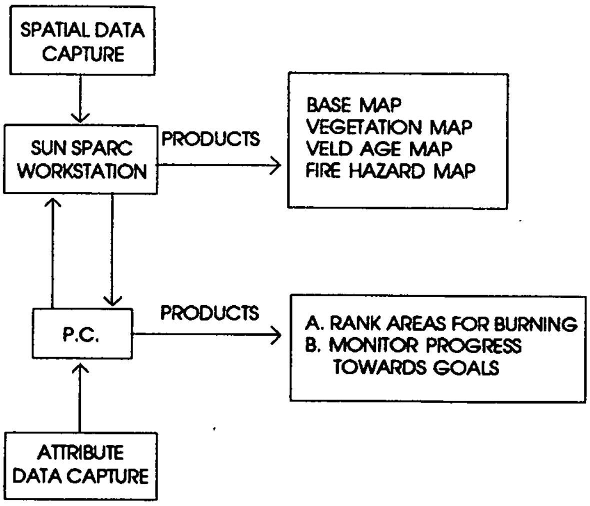


Figure 2. Schematic representation of the Catchment Management System.

Table 1 Details of the Kammanassie, Kogelberg and Table Mountain catchment areas.

Major features	Kammanassie	Kogelberg	Table Mountain
Location	Situated east of Oudtshoorn in the southern Cape (33° 40'S; 22° 45'E).	Centred at 32° 20'S; 19° 03'E in the southwestern Cape 50 km east of Cape Town.	Situated immediately to the south of the centre of Cape Town and bordered by urban areas and the coast (33° 59'S; 18° 25'E).
Size	The Kammanassie State Forest is about 27,989 ha in extent. An additional 21,532 ha of proclaimed mountain catchment is managed in cooperation with the landowners.	The total managed area is about 34,400 ha which includes about 23,700 ha of State Forest and 5,600 ha of Cape Town Municipal land. The remainder is proclaimed Mountain Catchment Area.	The area of Table Mountain that falls within the Cape Peninsula Protected Natural Environment is about 5,700 ha and includes about 2,800 ha of Cape Town Municipal Nature Reserve and 1,300 ha of State Forest Land.
Topography, geology and soils	The topography is broken by deep ravines formed by the major rivers along fault lines. Southern slopes are steeper than northern slopes. The geology is similar to that of the Kogelberg, being dominated by an upper and lower Cape sandstone formation separated by a high-altitude shale band. There is a greater proportion of finer sand in the sandstones than in the other two areas; this gives rise to soils with a higher nutrient content and water holding capacity than those of the Kogelberg.	Topography is rugged with deep ravines and steep south-facing slopes. The geology is dominated by Cape sandstones; the lower and upper formations are separated by a band of tillite and shale. Soils are mostly coarse white sands with very low nutrient levels. Finer soils occur on shale bands, and peaty organic soils are found on the upper south-facing slopes (Boucher 1978).	The topography is dominated by the plateaux of Table Mountain, with Lions Head and Signal Hill extending northwards, Devils Peak on the east, the Twelve Apostles extending south-east and the Newlands-Constantia ridge extending southwards. The slopes on all sides are precipitous with extensive cliff faces, deep and steep talus slopes. The plateaux and upper 300m are Cape Sandstones which overlie Malmesbury Shales in the northern and Cape Granites in the southern part. The soils of the plateaux are sandy and shallow while those of the middle and lower slopes are derived from the granites and shales and vary from clays to loams.
Elevation	Extends from 800 to 1,900 m above sea level; most of the area is between 900 and 1,500 m. The highest peak is Mannetjies Berg (1,955 m).	Extends from sea level to 1,268 m; most of the area is between 800 and 1,000 m.	Extends from sea-level to 1,000 m above sea-level; most of the area is between 500m and 750 m with a high plateau (the front table) at about 1,000 m. The highest point is Maclear's Beacon at 1,045 m.
Precipitation	Rainfall is strongly influenced by orographic effects; northern slopes are in a rain shadow. The rainfall is bimodal with peaks in autumn and spring and ranges from 300 mm yr^{-1} on the lower north-facing slopes to 700 mm yr^{-1} on the crest.	Rainfall ranges from 700 mm yr^{-1} at the coast to 1,200 mm yr^{-1} on higher peaks which are regularly covered with cloud when southeasterly winds blow. 46% of the total annual precipitation falls between June and August, and 77% between May and September (Le Maitre 1984).	Rainfall ranges from about 500 mm yr^{-1} at the coast to about 1,780 mm on the peaks. Rainfall occurs mainly in winter (65% falls from May to September; Anon 1988).
Temperature	On the lower northern slopes January maxima and minima are 39 and 7°C respectively while in July they are 24 and -3°C. On the upper slopes the corresponding values are 32 and 2°C (January) and 18 and -3°C (July).	Temperatures are strongly influenced by the ocean. At one site (elevation 110 m), maximum and minimum temperatures in January and July are 26.5, 16.0 and 21.2, 6.0 °C.	Temperatures are strongly influenced by the ocean. Maximum and minimum temperatures for January are 20.0 and 12.4 on the top and 26.8 and 15.8 °C at the coast. The corresponding figures for July are 12.0, 6.4 and 17.3, 9.6 °C (Anon 1988).

Table 1 (continued)

Major Features	Kammanassie	Kogelberg	Table Mountain
Fire weather	Although rainfall is evenly distributed throughout the year high evapotranspiration in summer generates what is effectively a winter rainfall regime. Most fires therefore occur in summer.	Climatic fire potential is highest in summer but annual fluctuations in mean fire weather are moderate because of proximity to the sea. Large fires are most likely under extreme conditions in summer but can occur under bergwind conditions in winter.	The highest fire danger occurs in mid- to late-summer when the danger of wildfires from open fires outdoors is also greatest. Lighting of open fires is usually prohibited between October and March but the proximity to the urban area results in numerous fires.
Vegetation and flora	Predominant vegetation types are mesic- and dry mountain fynbos and Central Mountain Renosterveld (Moll et al. 1984). The vegetation shows a marked altitudinal zonation mainly due to rainfall. Crest communities are dominated by low fynbos with shrubs of the Ericaceae and Proteaceae. On the upper slopes there is a zone of medium-tall (1 - 1.5 m) proteoid shrubland. Below this there is a tall proteoid shrubland (1.5 - 2.5 m) which is replaced by and open proteoid shrubland ("waboomveld") on talus and on east- and west facing ridge slopes. At lower altitudes (< 1,100 m on south slopes, < 1,400 m on north slopes) there is dry fynbos dominated by ericoid shrubs and restioids which grades into shrubby renosterveld and succulent karoo shrublands (which rarely burn) (Southwood 1983). The Southern Cape mountains have a lower diversity of species than those of the Western Cape (Cowling and Holmes 1992) so there are few endemics. Endemic species include *Leucandendron singulare*, *Bobartia plicata*, *Geissorhiza elsiae*, *Elegeia altigena* and *Romulea vlokii*. The mountain forms an island and appears to have been isolated for a long time so that there are several interesting variants on widespread fynbos species (J. Vlok personal communication 1992). This mountain range also provides one of the last refuges for the rare Cape Mountain Zebra.	Predominant vegetation types are mesic- and dry mountain fynbos and Central Mountain Renosterveld (Moll et al. 1984). Northern and lower slopes are covered with low to mid-high ericoid shrublands with patchy proteoid shrublands. Upper northern slopes carry tall shrublands dominated by Proteaceae and Bruniaceae. Tall shrublands occur on southern slopes, with restioid herblands on peaty soils (Boucher 1978). Upper slope communities have many endemic plant species (notably *Orothamnus zeyheri*, *Mimetes arboreus* and a number of *Erica* species). The vegetation on the shale band at low altitude also has some endemics e.g. *Erica pillansii*, and *E. porteri*. Forests are restricted to small patches and riverine strips. Wynand Louwsbos is the best developed forest, and is very similar in species composition to the extensive forests in the southern Cape (Boucher 1978). About 1 500 plant species have been recorded in the Kogelberg. The area is a centre of diversity for the Cape families Proteaceae, Ericaceae, Restionaceaae (Boucher 1977; Oliver et al. 1983). Many plant species and one reptile and six amphibian species are endemic to the area (CPA 1991).	The predominant vegetation is mesic mountain fynbos, but there are indigenous forests on the southern and south-eastern slopes (Michell 1922; Moll and Campbell 1978). West Coast Renosterveld occurs on the Malmesbury shales of the northern part (Devil's Peak and Signal Hill). The plateaux area on the front and back tables support short to mid-high ericoid shrublands with dense, tall restioids on seepage areas. The cliff ledges and steep slopes support mid-high shrublands. Tall proteoid shrublands formerly dominated the lower slopes but the abundance of the tall proteas has been reduced by frequent fires. The dominant proteas on the northern and western slopes are *Protea lepidocarpodendron* and *P. repens*, while *Leucadendron argenteum* is common on the south-easterly slopes. *Protea nitida* is common in rocky talus areas on all aspects and *Leucospermum conocarpodendron* is common on northern and western aspects. 1,470 plant species have been recorded on Table Mountain, at least three of which are endemic: *Erica pilulifera*, *E. abietina* and *Staavia glutinosa*. Species diversity of larger mammals has been considerably reduced. There are, however, a large number of smaller animals, including the endemic ghost frog, *Heleophryne rosei*.

Table 1 (continued)

Important management considerations:	**Kammanassie**	**Kogelberg**	**Table Mountain**
Current and past fire management	The area is managed as a natural fire zone, i.e. an area which is sufficiently large, free of alien plants, free of fires of human origin, and with safe enough boundaries for a natural fire regime to prevail (van Wilgen et al. in press).	The vegetation has been managed by applying prescribed fires since 1968 (Boucher 1978)	The area has been intensively managed for many years. Prior to 1975 the emphasis was on using firebreaks to control fire spread. Some prescribed burning has been done with the aim of clearing and controlling invasive weed species.
Land-use inside the catchment	Nature conservation, grazing and dry-land agriculture	Important catchment area (proposed site for a major dam), nature conservation, recreation	Extensive recreation and nature conservation, with plantations of exotic species on the south east slopes.
Land-use in adjacent areas	Grazing and dry-land agriculture, irrigated lands and orchards.	Apple orchards, pine plantations, wildflower harvesting	Primarily high-density urban areas with low-density urban areas, parks and a major botanical garden in the south east.
Importance as a water source	Runoff is strongly seasonal, so important in summer.	A key water source for Greater Cape Town and other towns.	Was an important water source for Cape Town and its western and southern suburbs until the early 1900's.
Rare species	Endemic plant species include *Leucadendron singulare* and *Bobartia paniculata*.	178 plant species and 3 subspecies with special conservation status. Of these, 77 species are endemic (35 listed in the Red Data Book) and 101 are not endemic (51 in RDB).	33 plant species found on Table Mountain are listed in the Red Data Book. Of these, 17 species are endemic to the Cape Peninsula.
Alien plants	No alien plants cause management problems.	A major problem. The most abundant species are *Pinus pinaster*, *Acacia cyclops*, *A. longifolia*, *A. saligna* and *Leptospermum laevigatum*.	A major problem. The most abundant species are *Pinus pinaster*, *Acacia mearnsii*, *A. melanoxylon*, *A. saligna*, *A. cyclops* and *Hakea sericea*.

class (state land, proclaimed mountain catchment area, private land). The CMS uses information in the spatial database to derive this information (see Le Maitre et al. (1993) for further details). Applications of the system are described below.

Choosing the Next Area(s) to Burn : the RANK Module

Approach

At the start of each fire season, managers must decide how best to allocate their limited resources towards the major task of prescribed burning. Catchments are divided into management units, termed compartments, that vary in size depending on the topography. Most are between 500 and 1,000 ha in extent — the area that can practically be burnt in one day. Major factors that influence the choice of compartments to burn are: vegetation age, the status of alien plants, and the flammability of the vegetation.

Vegetation age is important because many fynbos species are sensitive to the length of the interval between fires (van Wilgen et al. 1992). Short intervals between fires (<4 yrs) eliminate some shrubs by killing plants before they have produced seeds. Populations of some species, notably the tall serotinous shrubs, may also be reduced significantly if the inter-fire period is too long, since adults die and canopy-stored seed banks are lost. Fire at intervals of 12 - 15 years benefits most fynbos taxa (Richardson and van Wilgen 1992).

Alien plants are a major problem for catchment managers. Invaders such as pines (*Pinus* spp.), *Hakea sericea* and *Acacia* species are fire-adapted (Richardson et al. 1992). Fires through untreated stands result in prolific regeneration and the establishment of dense forests of aliens which suppress indigenous elements, and alter other ecosystem properties (review in Richardson et al. in press). Alien plant control, involving felling of trees and shrubs, is carried out before prescribed burns which then kill alien seedlings (van Wilgen et al. 1992).

The flammability of vegetation, an index of the ease of controlling fires, also influences the allocation of priorities. Other criteria include the status of indicator species, the presence of rare and endangered species, the potential damage if fires spread to adjacent areas, the water needs downstream, and the state of readiness of the compartment for burning (such as the preparation of fire breaks).

The RANK module of the CMS generates a table of all the compartments in a given region (centre), ranked according to their suitability for burning. Ranking is done using vegetation age, the status of alien plants (if applicable), and a flammability index (Figure 3). The other factors listed above are included in the table, but are currently not used for ranking. The system is interactive, and derives information required for ranking from the compartment data-base, from other modules in the CMS, and from data provided by the user in response to prompts.

An application

An example of the ranking of compartments in the Kammanassie is given in Table 2. Because alien plants are absent in this area, ranking is done by vegetation age and the fire hazard class (see the HAZARD module below). Areas with the oldest post-fire age (>28 years) are all flagged for burning, but those with the highest fire hazard are given higher priority. Both indicator species (*Protea lorifolia* and *P. repens*) identified for the area attain reproductive maturity within five years after fire — there is therefore no need to override the generated ranking. No special species have been identified yet for the Kammanassie. As these are recognized and added to the database, managers could decide to advance or postpone burning to accommodate particular requirements of these species.

The output table allows managers to see all the relevant information that may be needed to make a decision on whether or not to burn, at a glance. Although the ranking is subject to the rules outlined in Figure 3, a manager can override the resultant ranking. The important point is that all relevant information can be accessed easily, rapidly, and in a form that is useful.

Monitoring the Success of the Management : the MONITOR Module

Approach

The objectives of catchment management, namely to enhance water yield and maintain biotic diversity, are extremely difficult to measure or monitor. However, these objectives are met by fire, and the progress of a fire management plan can be more easily monitored. We suggested that fire should be applied to fynbos catchments with four goals in mind (Table 3). The monitoring system is based on the assumption that progress towards these goals can be gauged by monitoring patterns in the fire regime (see also van Wilgen et al. in press).

An important aim of the MONITOR module of the CMS is to synthesize data in such way that the manager can assess progress towards management goals rapidly.

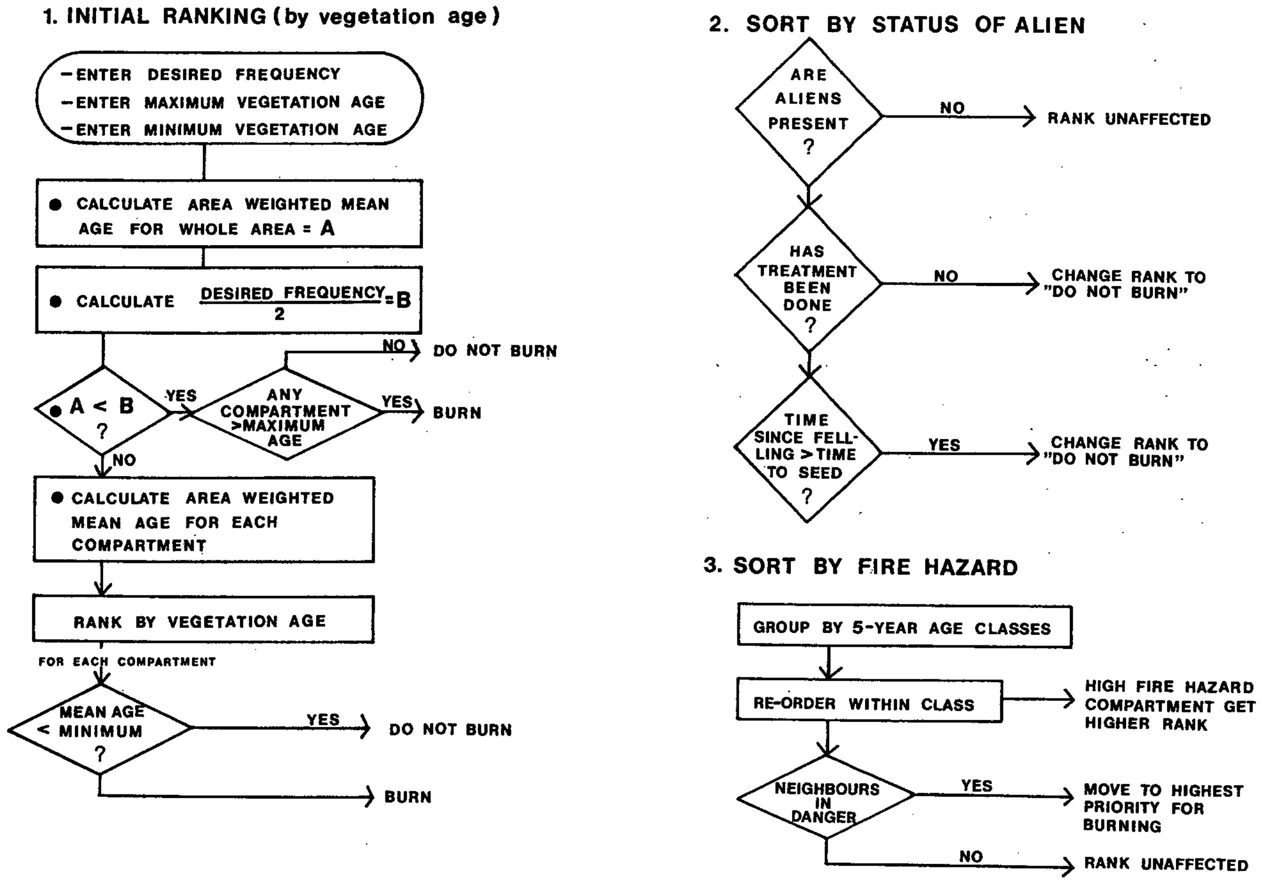


Figure 3. Flow diagram showing simple rules for ranking management areas (compartments) for burning. Data to rank the areas are obtained from a GIS-driven database (modified from van Wilgen et al. in press).

Table 2 Ranking of compartments according to their readiness for burning: an example from the Kammanassie. Compartments are ranked according to vegetation age and flammability only (alien plants are absent from the area). Other criteria are presented to guide decisions.

Centre: Kammanassie Area: 45836 ha Mean Age: 15 yrs Min Age: 3 yrs Max Age: 32 yrs Number of compartments: 88

Comp. num.	Comp. Area (ha)	Indices used for ranking				Burning priority	Additional information		
		Veg. age		Alien status	Hazard Class		Special Species; Vital Attribute	Indicator species	Juvenile period
		mean	range						
A01	415.9	32	32-32	None - ranking unaffected	extreme	BURN	-	*Protea lorifolia*	5.0
A03	163.2	32	32-32	None - ranking unaffected	extreme	BURN	-	*Protea lorifolia*	5.0
A29	236.6	32	7-32	None - ranking unaffected	extreme	BURN	-	*Protea repens*	4.0
A30	1154.0	31	7-32	None - ranking unaffected	extreme	BURN	-	*Protea repens*	4.0
B23	84.7	32	32-32	None - ranking unaffected	slight	BURN	-	*Protea lorifolia*	5.0
B48	273.2	32	32-32	None - ranking unaffected	slight	BURN	-	*Protea lorifolia*	5.0
A02	492.2	28	7-32	None - ranking unaffected	extreme	BURN	-	*Protea lorifolia*	5.0
A04	551.9	26	7-32	None - ranking unaffected	extreme	BURN	-	*Protea lorifolia*	5.0
A05	768.3	27	4-32	None - ranking unaffected	extreme	BURN	-	*Protea repens*	4.0
A33	692.5	28	7-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A09	1458.6	5	4-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A11	479.4	6	4-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea lorifolia*	5.0
A12	394.1	6	4-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea lorifolia*	5.0
A13	702.7	5	3-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A17	1185.6	6	3-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A21	325.3	6	3-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A24	1157.3	6	5-32	None - ranking unaffected	extreme	DO NOT BURN	-	Protea repens	4.0
A31	591.3	7	4-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0
A39	1030.9	7	4-32	None - ranking unaffected	extreme	DO NOT BURN	-	*Protea repens*	4.0

This is done by producing a series of summary tables and graphs showing the current age distribution of the vegetation, the age of the vegetation when it last burned, the percentage of the area burnt in different months in the last year, and a cumulative frequency curve of the fire recurrence interval over the whole fire history available for the area.

Applications

Figures 4 to 7 show the summary histograms and graphs that consolidate information required by managers to judge whether burning programmes for the different areas achieve desired patterns. The histograms showing the distribution of current post-fire age classes (Figure 4) show that all areas have an uneven distribution which is undesirable from a management perspective (the desired distribution is shown by means of a dashed line). Management aims to create a mosaic of different ages, from young to mature, in order to break up continuous fuel beds and spread the load of prescribed burning more evenly. Both very young and very old vegetation are over-represented in the Kammanassie, and vegetation of moderate post-fire age is under-represented. Very young veld predominates in the Kogelberg; about 64% of the area has a post-fire age of 2 years or less, and there is almost no vegetation older than 23 years. This can be ascribed to lightning-induced wildfires which preempted prescribed burns. The vegetation on Table Mountain is largely mature (30% is 20 years old, 27% is 48-92 yrs old), although about 25% of the area has vegetation with a post-fire age of 12 years or less.

Patterns of seasonal distribution of fire occurrence for the three areas (Figure 5) are derived from the date

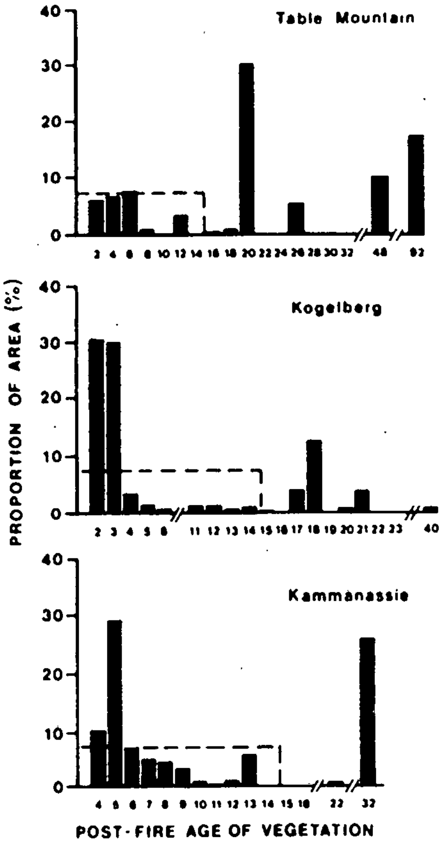


Figure 4. The distribution of post-fire age classes in the Kammanassie, Kogelberg and Table Mountain as on 31 December 1991. The dashed line (- - - -) indicates the desired distribution from a managemet point-of-view, with a fire frequency of 15 years.

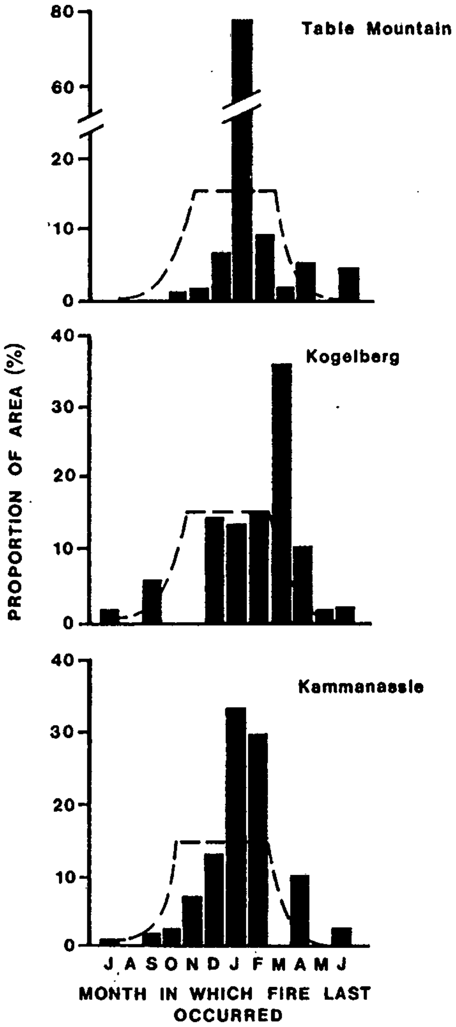


Figure 5. Seasonal distribution of fire occurrence (based on the last fire at each point assessed) in the Kammanassie, Kogelberg and Table Mountain. The dashed line (- - - -) indicates a hypothetical desired distribution from a management point-of-view.

of the last fire. Most fires in the Kammanassie occurred between December and February, and fires between May and August are rare. Since all the fires were started by natural causes in this natural fire zone (see Table 1), the pattern conforms closely with the desired pattern indicated by a dashed line. Most fires in the Kogelberg occurred between December and April, and a large proportion (36%) of the area burnt in a single wild fire in March 1991. Almost all recorded fires on Table Mountain took place in January, and only 5% of the area burnt between May and October.

Analysis of the distribution of vegetation age at the time of the last fire (Figure 6) was problematical for the Kammanassie and Table Mountain, since fire records were incomplete, and the date of the previous fire was unknown for many sites. The fire history of the Kogelberg is relatively well known (66% of the areas had records of two or more fires). In parts for which the date of the previous fire was known, fires occurred in vegetation of between 9 and 21 years post-fire. The CMS will facilitate the keeping of good fire records, and this analysis will become more meaningful in the future as records accumulate.

The graphs of cumulative probability of fire (Figure 7) show at a glance how burning programmes compare with desired patterns. In the Kammanassie the actual interval between fires was less than desired interval. For example, 50% of the vegetation burnt at 12 years or less post-fire, whereas the desired distribution aims at 14 years or less. Vegetation age never exceeded 16 years, but some patches should ideally survive without fire for up to 30 years.

In the case of the Kogelberg, fires in young vegetation (<12 yrs) are over-represented whereas fires in

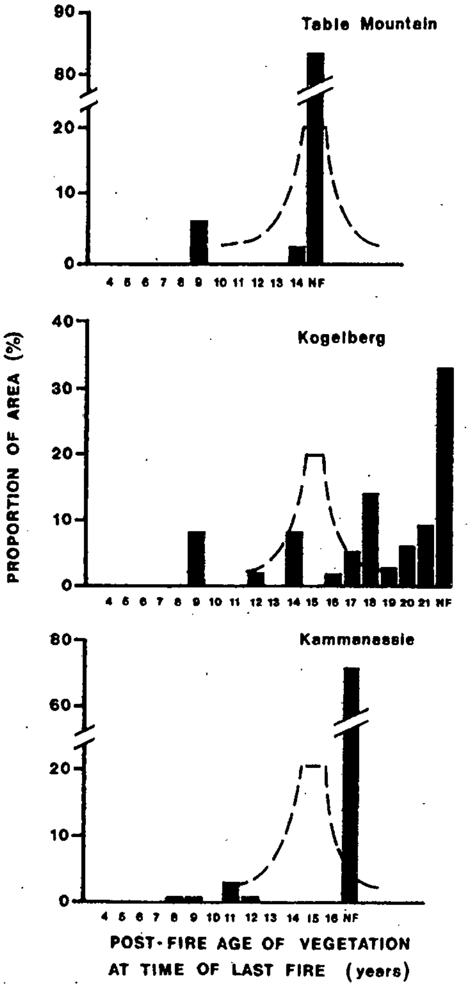


Figure 6. Distribution of vegetation age at the time of the last fire for the Kammanassie, Kogelberg and Table Mountain as on 31 December 1991. The dashed line (- - - -) indicates the desired distribution from a management point-of-view. NF denotes areas where no fire records exist.

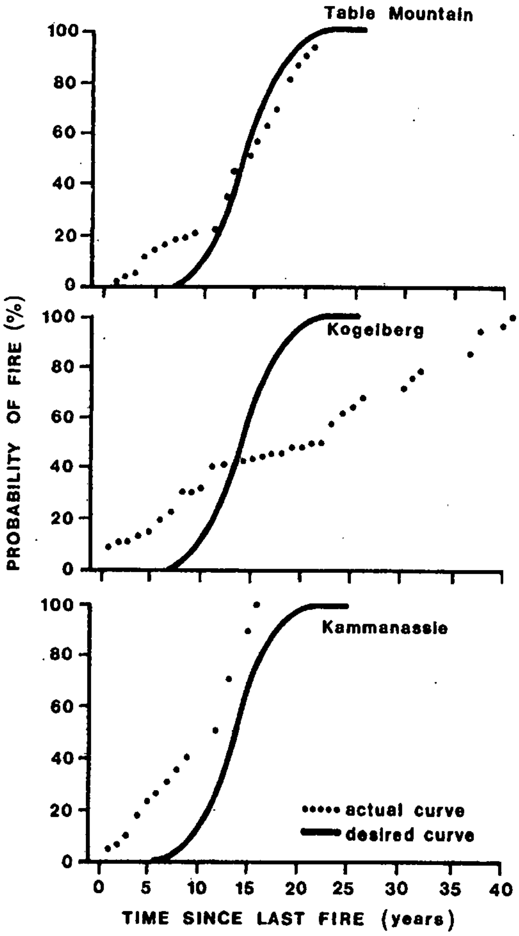


Figure 7. The cumulative probability of fire in the Kammanassie, Kogelberg and Table Mountain as on 31 December 1991. The solid line indicates the desired distribution from a management point-of-view.

older vegetation are under-represented. As a result, patches of vegetation survive for up to 47 years without fire. Fires in younger vegetation are over-represented on Table Mountain. However, the occurrence of fire in vegetation of 15-20 years age follows the desired pattern and there is no build-up of old vegetation.

The above examples are provided to illustrate the principles of the system and to show the way in which the records are interpreted. The shapes of the curves showing the desired distribution (dashed lines in Figures 4 to 6) are not rigid; those in Figures 4, 5, 6 and 7 are based on the rationale set out in Table 3. This is a first approximation, based largely on research in the western part of the region. Different shapes will probably be required for different areas within the fynbos biome. For example, longer intervals between fires may be desirable in more arid areas, and the desired seasonal distribution of fires will differ as one moves from west to east (winter-rainfall to all-year rainfall). Managers should debate these issues and derive their own curves to suit the needs of the area concerned. The CMS provides the means to store, retrieve, and analyze the fire records for an area, and present the data in such a way as to allow for monitoring the progress of the fire management regime towards desired goals.

Mapping Fire Hazard for Fire Control Planning : the HAZARD Module

Approach

Fire hazard is determined by, among other things, the amount of fuel (accumulated biomass) available to burn. An assessment of fire hazard facilitates fire-control planning and the optimal siting of firebreaks. Fire hazard is also a useful measure for deciding which areas should be burnt to break-up large continuous areas of flammable vegetation, thus avoiding unmanageable conflagrations.

Fire hazard in fynbos is determined by post-fire age; old areas (post-fire age > c. 30 years) are usually highly flammable. However, rates of regrowth differ between vegetation communities, and this affects the accumulation of biomass. Fynbos communities therefore differ in their inherent susceptibility to fire. These differences are quantifiable; the HAZARD module of the CMS was developed to map these features.

For mapping fire hazard, we first determined major structural classes in the vegetation of each area using existing maps [Southwood (1983) for the Kammanassie; Boucher (1978) for the Kogelberg; and various published and unpublished maps for Table Mountain]. The

Table 3. The underlying rationale for four operational goals of fire management in mountain fynbos catchments.

Goal		Rationale
1.	To achieve an even distribution of post-fire ages in the area concerned.	If an area is burned, for example, at a mean frequency of 15 years, then the area should contain 15 equal segments from one to 15 years post-fire age. Each year 6.7% (1/15) of the area should be burnt. A predominance of old or young vegetation would be undesirable and could be corrected by burning or not burning as the case may be.
2.	To achieve a target seasonal distribution of burns.	The aim is to approximate a natural distribution of fire with regard to season. Fynbos fires normally occur between December and March, but can occur in any month. Most fires should be in the "natural" fire season, but a small proportion could (or should) also occur in winter. A variable fire regime is considered important for ensuring coexistence of the greatest number of plant species (different taxa are favoured by different regimes; Yeaton and Bond 1991). It is probably undesirable to have fires in only one or two months. Once the desired pattern has been established, the actual distribution can be plotted from the database, and used to determine a suitable season for the next planned fire.
3.	To assure that the age at which vegetation is burned conforms to a predetermined pattern.	Goal 1 assumes that vegetation should always be burnt at the same pre-determined age. This may be undesirable as it does not allow for variation (it is also unattainable in practice). Some areas should be burnt at longer intervals than the desired fire frequency, while others could be burnt at shorter intervals. Once a desired distribution of post-fire ages at the last fire has been established, the actual situation can be plotted against this. Deviations from the actual situation will indicate suitable age classes for the next fire.
4.	To achieve a predetermined fire history pattern in the area.	Fire history can be determined for an area from the entire fire record. A grid representing 100 x 100 m is overlaid on the fire maps, and the interval between fires is assessed at each of the points. The maximum and minimum intervals between fires at any one point provides the limits within which the system is known to function. The cumulative probability of fire can be assessed from the data (see for example Brown et al. 1991), and compared to a pre-determined desired pattern.

rate of biomass accumulation was estimated for each structural class, based on known rates of biomass accumulation (Kruger 1977; van Wilgen 1982; van Wilgen et al. 1985, 1990; van Wilgen and van Hensbergen 1992). These estimates were used to construct sets of fuel models (Deeming and Brown 1975) needed as inputs to models for predicting fire behaviour (Burgan and Rothermel 1984; Andrews 1986). The fuel models estimate the fuel conditions in each vegetation type at 2-yearly intervals after fire. The FIRE1 module of the BEHAVE fire behaviour prediction system (Andrews 1986) was used to predict flame lengths for each fuel model under conditions for a "normal" day in the fire season (fuel moisture contents of 7 and 100% for dead and live fuel respectively, 15 km hr^{1} wind and no slope). Flame length was predicted from fuel models (vegetation type and age; see Table 4 for an example) for the direction of maximum spread. Maps of predicted flame length were then derived by combining overlays of vegetation type and post-fire age. Relevant flame lengths were then plotted from the data-base. Fire hazard classes, rather than actual flame lengths, were mapped to simplify the map. The classes were: low fire hazard (flame length: 0 - 2 m), moderate fire hazard (2 - 4 m), high fire hazard (4 - 7 m) and extreme fire hazard (> 7 m).

Applications

Fire hazard maps for the Kammanassie, Kogelberg and Table Mountain are shown in Figures 8, 9 and 10. The map for the Kammanassie shows a small area of high fire hazard in the extreme western section of the area and large areas of high fire hazard in the eastern section. Since the area is managed as a natural fire zone, has no alien plants, and the chances of fire spreading into or out of the area are remote, no management intervention is required. The map for the Kogelberg shows that most of the area has low fire hazard - the result of a large wildfire in March 1992. No immediate management action is required to protect adjacent areas have high-value crops. Fire hazard prediction is particularly useful for Table Mountain, which is surrounded by the city of Cape Town and epitomizes the problems of fire management on the wildland/urban interface. Recent wildfires in the area have caused considerable damage (e.g. Scott et al. 1991). Figure 10 shows several areas of high fire hazard adjoining urban areas. Management intervention, such as controlled burning under moderate conditions, would be a priority to pre-empt wildfires under adverse conditions that may cause extensive damage in adjacent urban areas.

Discussion

Field trials have shown that applications of the first version of the CMS, such as those presented in this paper, can improve the efficiency of fire management in Cape mountain catchments. The challenge is to convince managers that it is worth their while spending time learning how to use the new system. The adoption of the CMS could be bedeviled by user-apathy. There seems to be an inherent resistance to "high-tech" solutions to environmental management problems in some quarters (e.g. van Wilgen & Manders 1990). We have attempted to pre-empt this by working closely with managers at all stages of development, starting with an extensive survey of the needs of managers through to the ongoing field testing and development of additional modules. Each step was endorsed by a

Table 4. The Kogelberg erica - restio fuel model. The model incorporates communities on limestone and acid sand flats, and dry short fynbos with moist patches, erica - restio vegetation on mesic seaward slopes, and erica - restio vegetation on xeric and mesic upper slopes. Data are estimates for closed stands and were derived from Le Maitre (1986) and van Wilgen et al. (1990) using regression analysis. Similar modules were developed for the short erica - restio, tall moist shrub, seep and marsh, low herb and shrub, and acacia thicket vegetation formations.

Age class (yrs)	Total biomass (g m^{-2})	Fuel loads (g m^{-2})					Fuel bed depth (m)	Fuel model number
		1 hour	10 hour	100 hour	herb	woody		
0-2	224	17.25	0.00	0.00	179.20	16.80	0.30	26
3-5	768	61.44	3.84	0.00	576.00	61.44	0.60	27
6-8	1047	94.23	10.47	5.24	732.90	99.47	0.80	28
9-11	1235	135.85	18.53	12.35	765.70	123.50	1.00	29
12-14	1379	186.17	27.58	16.55	772.24	151.69	1.15	30
15-17	1494	231.57	37.35	22.41	776.88	165.83	1.18	31
18-20	1590	314.82	49.29	30.21	775.92	174.90	1.20	32
21-23	1673	368.06	66.92	41.83	803.04	184.03	1.22	33
24-26	1746	419.04	104.76	47.14	820.62	192.06	1.22	34
27-29	1811	470.86	126.77	54.33	814.95	199.21	1.22	35
30-32	1869	523.32	149.52	61.68	747.60	196.25	1.22	36
≥33	1922	576.60	172.98	67.27	672.70	192.20	1.22	37

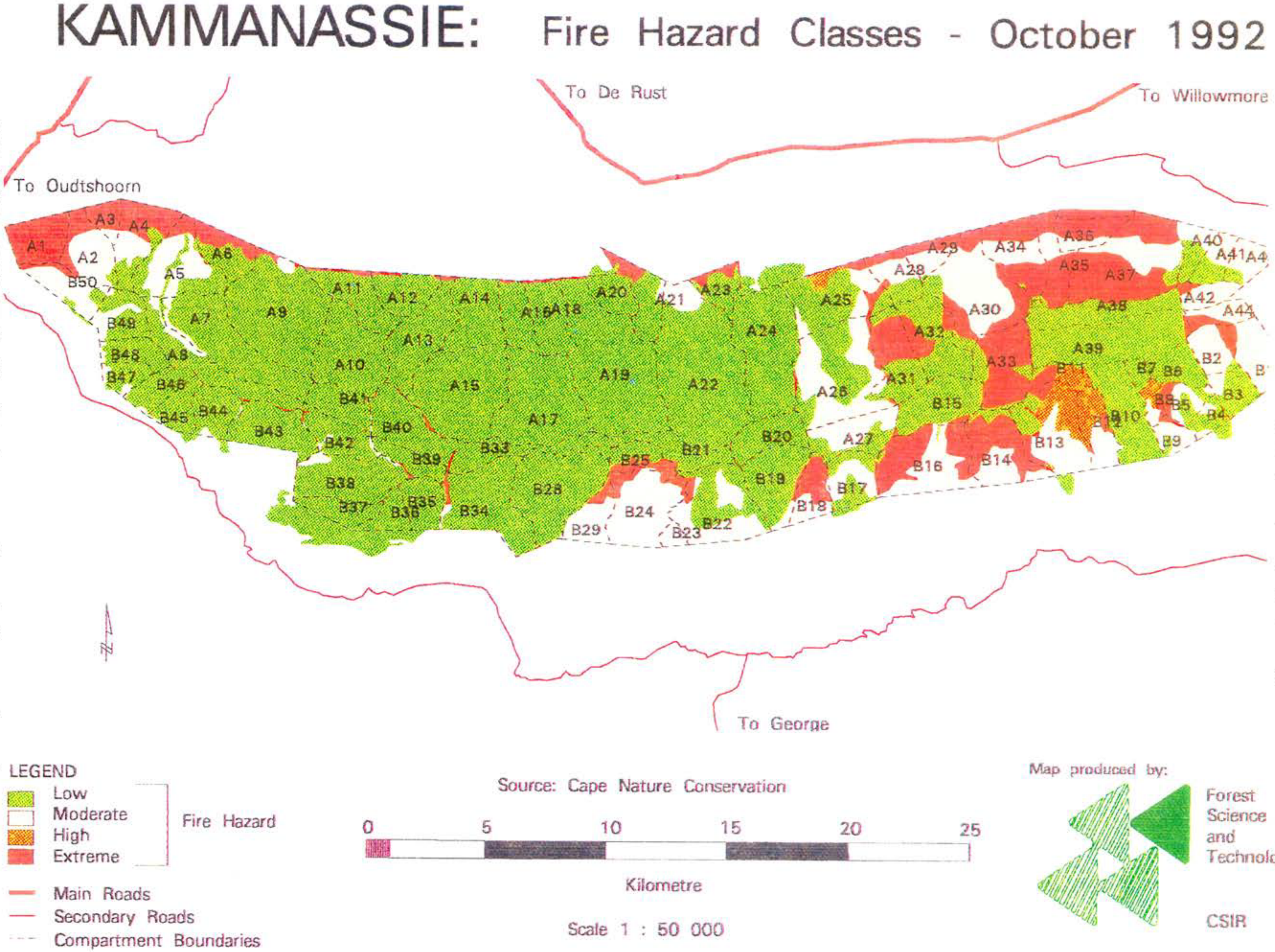
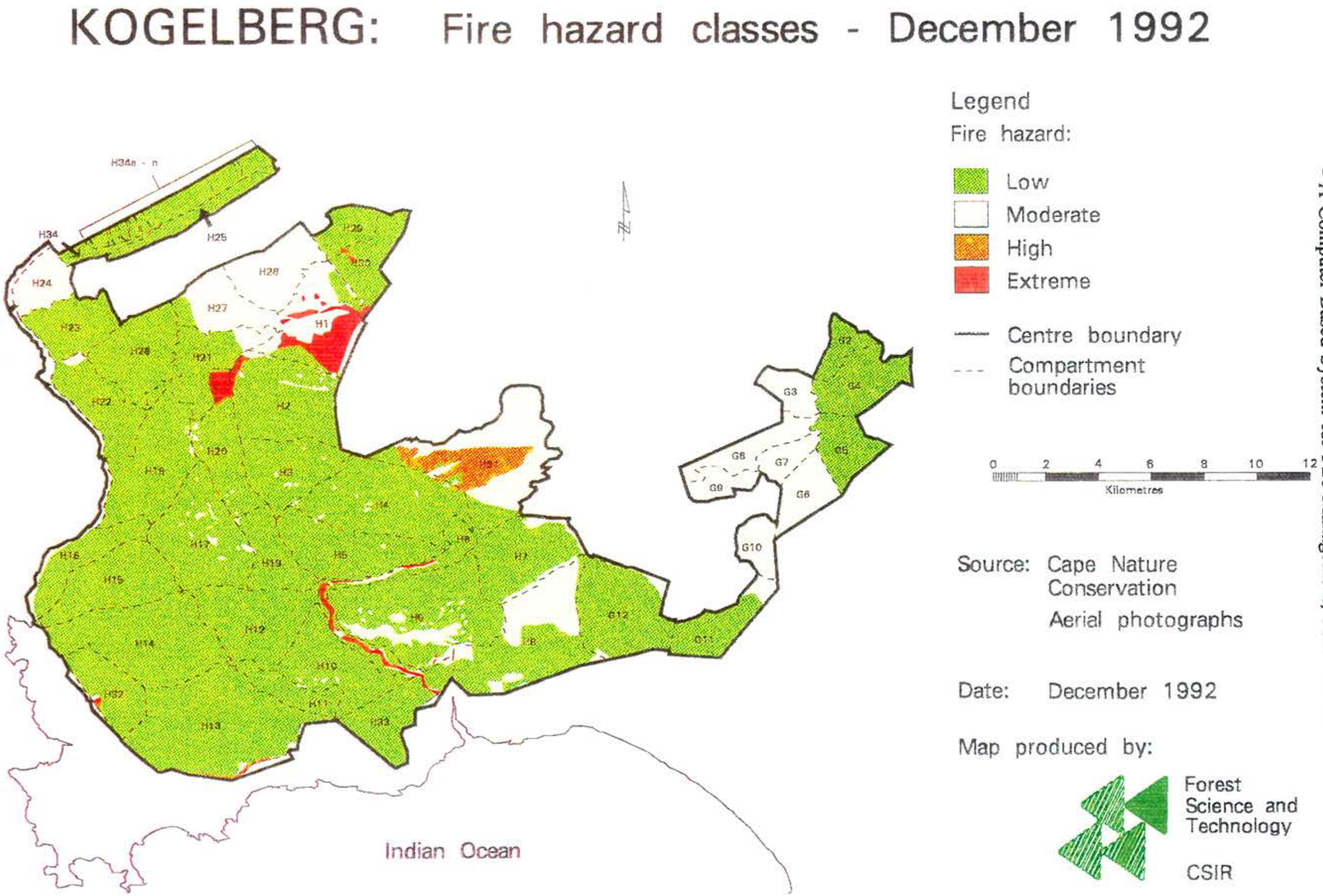


Figure 8. Fire hazard map for the Kammanassie.



Source: Cape Nature Conservation
Aerial photographs

Date: December 1992

Figure 9. Fire hazard map for the Kogelberg.

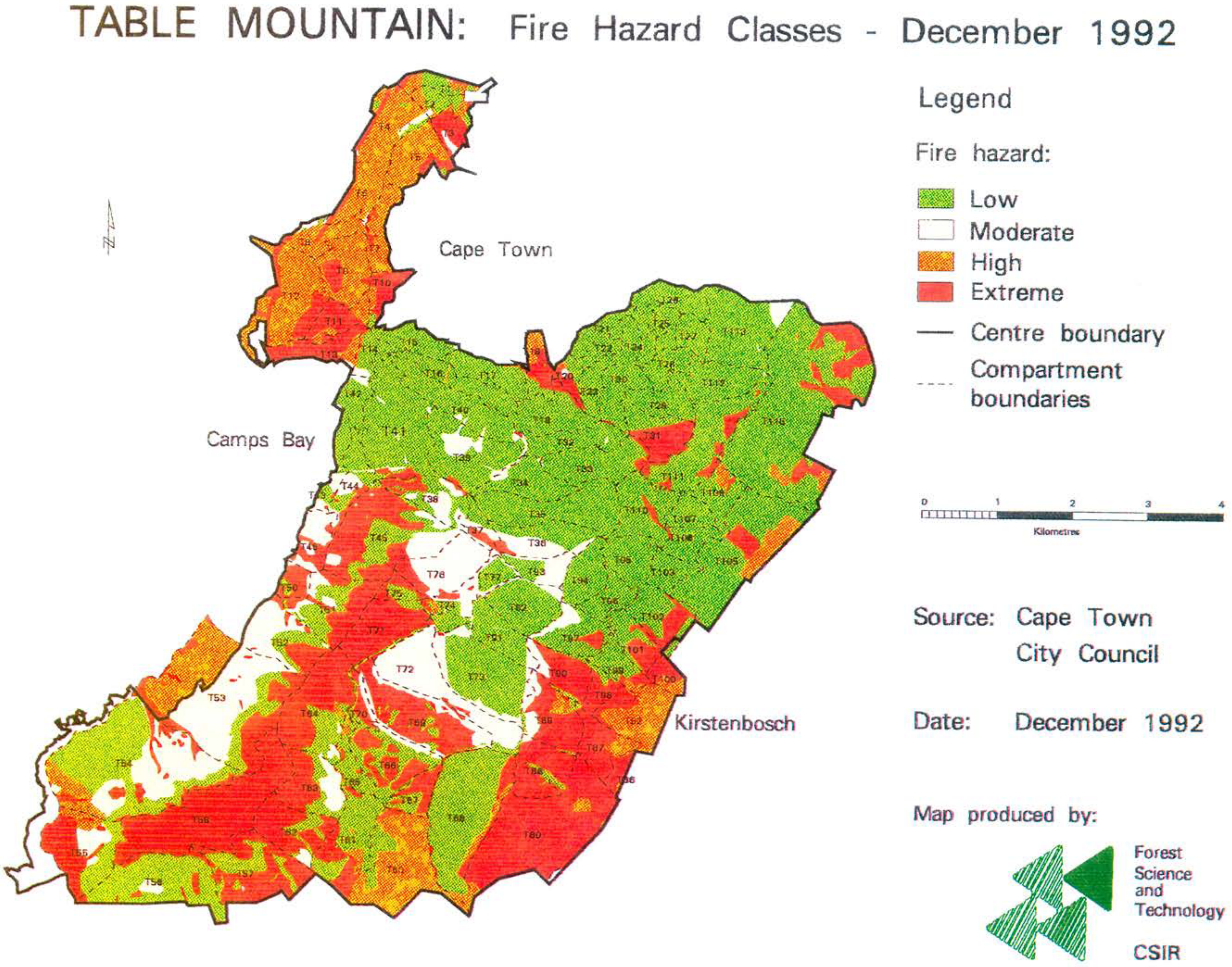


Figure 10. Fire hazard map for Table Mountain.

steering committee, comprising high-level managers of potential user agencies, field managers, academics and ecologists. If the system is accepted for general use, we believe that there will be better management decisions, partly because of the better and more accessible information on which to base the decisions. The CMS interrogates spatial and other data relevant to management units and facilitates the rapid checking against pre-determined rules, some of which are easily overlooked if the manager has to consult numerous files and maps each time a decision must be made. The rule-based models can easily be edited or replaced as new information becomes available, or as priorities for management change. The CMS also provides the much-needed infrastructure for storing and analysing monitoring information relating to catchment areas.

The CMS offers managers and researchers insights into scientific applications through appropriate modelling and analysis of available information. For example, it is possible to model the consequences (e.g. in terms of future costs or benefits) of various feasible courses of action. Two new modules are currently in development to aid in the management of invasive alien plants, this being the single most important facet of management in many Cape catchments. The first module comprises an expert system which draws on the CMS data bases to provide managers with guidelines, based on empirical evidence and ecological theory, for formulating control strategies. The second assesses the impact of invasion by alien plants on streamflow. Experimental evidence from catchment studies is being used to derive models for relating streamflow to vegetation structure (or biomass) for different plant communities. This module incorporates simulations of fire occurrence and alien plant spread.

Fire-spread models, using vegetation structure, topography and weather conditions as inputs are intuitively appealing, and would be very useful for managers. We know of no accurate fire-spread models for terrain with a complex matrix of fuel conditions and rugged topography. For this reason, no fire-spread component will be built into the CMS.

A cost-benefit analysis to compare the old system (compartment register and maps on paper) with the CMS with respect to cost, time and quality of information has just been commissioned. We hope that this study will demonstrate the advantages of the CMS to managers and thus help to establish acceptance of the system.

Acknowledgements. The development of the CMS was funded by the South African Department of Environment Affairs. Members of the CMS steering committee (S. Bekker, J.M. Bosch, R.M. Cowling, G.J. Breytenbach, C.J. Burgers, M. Cohen, A.A. Gubb, D. Laidler, H. Maaren, C. Marais, W. Middleman, E.J. Moll, and N. van Wyk) provided valuable suggestions, comments and criticism. For assistance with data capture and management, we thank L. Cunningham, C. Jones, D. McKelly and R. Robyntjies. Programming on the UNIX system was done by D. McKelly. The enthusiastic support of Cape Nature Conservation is gratefully acknowledged.

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First paper: Fuels and fire behaviour dynamics on large-scale savanna fires in Kruger National Park, South Africa. *Journal of Geophysical Research*.

JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 101, NO. D19, PAGES 23,541–23,550, OCTOBER 30, 1996

Fuels and fire behavior dynamics on large-scale savanna fires in Kruger National Park, South Africa

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Abstract. Biomass characterization and fire behavior documentation were carried out on two large (>2000 ha) experimental fires conducted in arid savanna fuels in Kruger National Park in September 1992. Prefire fuel loads, fuel consumption, spread rates, flame zone characteristics, and in-fire and perimeter wind field dynamics were measured in order to determine overall energy release rates for each fire. Convection column dynamics were also measured in support of airborne trace gas and particulate measurements. Energy release rates varied significantly between the two fires, and this was strongly reflected in convection column development. The lower-intensity fire produced a weak, poorly defined smoke plume, while a well-developed column with a capping cumulus top developed during the higher intensity fire. Further experimental burning studies, in savannas with higher fuel loads, are recommended to further explore the fire behavior–convection column dynamics relationship investigated in this study.

Introduction

In recent years, evidence has begun to accumulate indicating that emissions from some forms of biomass burning are a significant perturbation of atmospheric chemistry, with resultant impacts on the Earth's physical and chemical climate. Under the International Global Atmospheric Chemistry (IGAC) Project, a core project of the International Geosphere-Biosphere Program (IGBP), a group of atmospheric and fire scientists worked together to develop a large-scale experiment to test the hypothesis that biomass burning emissions from southern Africa and South America play an important role in atmospheric chemistry over a large region of the Earth. Entitled STARE (Southern Tropical Atlantic Regional Experiment), this experiment had two major components which were integrated to form an ambitious scientific program: TRACE-A (Transport and Atmospheric Chemistry near the Equator–Atlantic) addressed fire sources (deforestation and savanna burning) in Brazil and the long-range transport of emissions over the south tropical Atlantic; SAFARI (Southern African Fire-Atmosphere Research Initiative) investigated the emissions from savanna fires in southern Africa, their transport across the African continent, and the relationship between fires and savanna ecology.

SAFARI took place during September 1992 and centered around a series of eight experimental fires conducted in savanna fuels in the Kruger National Park, South Africa. Unlike previous investigations into biomass burning emissions, SAFARI contained a major ground component designed to document fire behavior, ecological response to fire, and the ground-based source characterization of fire emissions, as it was recognized that fire emissions and ecological response are strongly dependent on fire behavior. This study was designed to characterize fuels and fire behavior in a manner that would provide accurate baseline data for use by atmospheric scientists involved in investigating the nature and fate of fire emissions under the airborne component of SAFARI. Six small (<7 ha) experimental fires were carried out in the Kruger National Park in September, but this study, which was coordinated by cooperating fire scientists from South Africa and Canada, was conducted on two large experimental fires (>2000 ha) on which extensive airborne (helicopter and fixed-wing) smoke sampling took place.

Savannas in Southern Africa

The term savanna originally described central South American grassland, but is now accepted as describing vegetation with a herbaceous, usually graminoid, layer with an upper layer of woody plants, which can vary from widely spaced to 75% canopy cover [*Edwards*, 1983; *Rutherford and Westfall*, 1986]. The savanna biome in southern Africa, as described by *Rutherford and Westfall* [1986], extends from north of 22°S latitude into central Namibia, Botswana, Mozambique, and various regions of South Africa. Within South Africa, extensive savannas occur in the northern two thirds of the Transvaal, with smaller pockets located in the higher-rainfall areas of the northern Cape Province, lower-altitude areas of the northwestern Orange Free State, central and east Swaziland, lower-altitude areas of Natal, Transkei, and the eastern Cape Province, and certain belts in the eastern Cape Province. The biome is the largest in southern Africa, covering 959,000 km^2 or 46.2% of Africa south of the Zambezi and Cunene Rivers (i.e., South Africa, Namibia, Botswana, Zimbabwe, and Southern Mozambique). Most of this area is in the extensive plains of the

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Paper number 95JD01734.
0148-0227/96/95JD-01734$09.00

Kalahari Basin and the coastal platform of Mozambique/Tongaland.

The herbaceous layer in savannas varies from about 1000 kg/ha in arid areas to 7000 kg/ha on optimum sites. Moist savannas have high levels of herbaceous productivity, with annual production values of up to 4800 kg/ha for central African miombo [*Rutherford*, 1978]. In South African moist savannas the herbaceous production is much less, probably closer to 2200 kg/ha [*Huntley*, 1984]. Above ground (dry) biomass depends to a large extent on the proportion of woody plants present, and varies from 5000 kg/ha in open, shrubby savanna to 45,000–60,000 kg/ha in some savanna woodlands or thickets. Estimates for the biomass of the woody component range from approximately 20,000 kg/ha for *Burkea africana* (red syringa) savanna at Nylsvley to 40,000 kg/ha for *Brachystegia* woodland in Zambia [*Huntley*, 1984]. Herbaceous layer biomass amounts above 2000 kg/ha can readily carry a surface fire. Consequently, annual fires are possible in higher-rainfall areas with woody plant canopy cover usually less than 40%. Fire is a regular phenomenon in moist savannas, annual winter burns being the normal pattern in central Africa. However, in South Africa, fire may be as infrequent as once in 5 years in the Transvaal Waterberg which receives about 600 mm of rainfall per year [*Huntley*, 1984]. Annual fires are rare in arid savannas where productivity is low and insufficient fuel accumulates to sustain fires [*Rutherford and Westfall*, 1986].

Fire has been a natural factor of the environment of African savannas for millenia and, consequently, has become ecologically important to the functioning of these ecosystems. Humans are the primary source of ignition in African savannas, where the extended dry winter season creates a highly flammable grass component of savannas that is very susceptible to fire. However, a primary function of African savannas is to provide adequate forage for domestic livestock and, to a lesser extent, for wild ungulate populations in conservation areas, and this has necessitated a management strategy in which fire is deliberately used for a variety of purposes. Principal among these are the removal of unpalatable and nonnutritious herbaceous grass material, the maintenance of an optimum balance between grass and bush vegetation, the improvement/maintenance of range condition, and the promotion of nutrient cycling [*Stocks and Trollope*, 1993].

Kruger National Park

Past and Present Fire Regimes

The Kruger National Park (KNP) is situated in the low-lying savannas of the eastern Transvaal in South Africa, adjacent to Mozambique in the east and Zimbabwe in the north. More than 2000 plant species, in a range of communities, occur in KNP, along with 122 species of mammals (including most large African species), over 400 species of birds, 55 fish species, and 109 reptile species [*van Wilgen et al.*, 1990]. The primary management aims of KNP [*Joubert*, 1988] are the development and maintenance of maximum biotic diversity through minimum interference in natural ecosystem functioning and the creation of opportunities for tourists to observe this biotic diversity. Fire is fundamental to the achievement of these objectives, and a continually evolving program of prescribed burning has been developed in this regard [*van Wyk*, 1971; *Trollope and Potgieter*, 1985]. Lightning fires are common in KNP [*Gertenbach*, 1979], but prescribed fire has been applied since the establishment of the park in 1926. Prior to 1954, deliberate burning was used to provide green grazing for wildlife regardless of the effect on vegetation, but this practice was abandoned with the initiation of a systematic burning program in 1954. This burning program has undergone many changes over time, evolving into the current prescribed fire practice. Under the present KNP burning program, 456 burning blocks have been grouped into 88 management units. Previous fire history, rainfall data, and the state of the vegetation within the management unit are now considered prior to burning, and the result is a more flexible burning program that more closely simulates a natural fire regime. Toward this end, larger burns are now conducted so that more of each area is burned by a greater range of types of fire. These larger areas burn for days, during which the fire front fragments, further simulating natural fires.

Analysis of KNP fire records for the 1980–1992 period revealed that on average, 253,326 ha (13% of the park) burns annually (W. S. W. Trollope, unpublished data). The prescribed burning program accounted for 47% of the area burned annually, while fires caused by refugees from Mozambique were responsible for 24% of the area burned. Wildfires caused by poachers, tourists, arsonists, accidents, and reasons unknown accounted for 19% of the total area burned. Lightning is not a very significant ignition source, being responsible for only 10% of the area burned annually. The probable reason for this is that other ignition sources preempt lightning fires, so lightning would be more important if there was a reduction in prescribed burning and other ignition sources.

Within KNP most rotational burning takes place in the winter and early spring, with approximately 80% of the area burned under the prescribed burning program occurring during this period. Refugee-caused fires are most significant during the winter and early spring, while the vast majority of lightning fires occur during the late spring and summer seasons. Fires ignited by other causes (poachers, tourists, etc.) are most frequent during the dry winter months. The end result is that although fires occur throughout the year in KNP, almost 75% of the total annual area burned takes place in the winter period between June and October.

Vegetation

The Kruger National Park comprises an area of about 1.9 million ha, of which the major portion is arid savanna. Moist savannas occur in the extreme southwest and northwest of KNP. Savannas in the KNP are locally known as bushveld [*van Wyk*, 1972]. Because there are no noteworthy topographical obstacles, this area forms a continuation of the low-lying areas of Zimbabwe and Mozambique. An exceptional number of tropical elements are thus included in the vegetation. Moreover, the Limpopo Valley probably served as an immigration route for desert plants from Botswana, Namibia, and Angola [*van Wyk*, 1972].

The two large-scale fires carried out during SAFARI took place near Pretoriuskop in the extreme southwest portion of KNP. Vegetation typical of this area (as mapped by *van Wyk* [1972]) extends over 2–3% of the park. It is characterized by very dense grass cover in which *Hyperthelia dissoluta* (thatch grass) appears the most important species; others such as *Elionurus muticus* (lemongrass), *Heteropogon contortus* (spear grass), and *Setaria flabellata* (wild millet) are codominant. The vegetation is open savanna, with occasional impenetrable thickets along drainage courses. Sicklebush (*Dichrostachys cineria* spp. *nyassana*) and *Terminalia sericea* (silver terminalia) are by far the most important species in this area, while *Parinari curatellifolia* (mobola plum), *Sclerocarya caffra* (marula), *Strychnos madagascariensis* (monkey orange), *Maytenus senega-*

Figure 1. Photograph of fuel arrangement typical of blocks 55 and 56 in KNP.

lensis (red spike thorn), and *Euclea divinorum* (ghwarri) are common. Rare species include *Faurea saligna* (boekenhout), *Faurea speciosa* (broadleaf boekenhout), *Acacia sieberiana* var. *woodii* (paper bark thorn), and *Acacia karroo* (sweet thorn). As a consequence of the relatively high rainfall in this region, quite a number of hydrophilic species such as *Syzygium guineense* (water pear), *Syzygium cordatum* (waterberry), *Trichilia emetica* (Natal mahogany), *Albizia versicolor* (large-leaved false thorn), and *Ficus sycomorus* (sycamore fig) occur on the undulations [*van Wyk*, 1972].

Prior to ignition of the two large SAFARI burns (blocks 56 and 55, respectively), vegetation was sampled in order to determine grass and tree species composition. Dominant grasses were similar on both burn areas, with *Setaria flabellata*, *Loudetia simplex*, *Diheteropogon amplectens*, *Hyperthelia dissoluta*, and *Heteropogon contortus* predominating. Predominant tree species on both burning blocks included *Terminalia sericea* (silver terminalia), *Dichrostachys cinerea* (sicklebush), *Strychnos madagascariensis* (monkey orange), *Maytenus senagalensis* (red spike thorn), *Acacia exuvalis* (flaky thorn), and *Combretum zeyheri* (large-fruited bush willow). Figure 1 illustrates grass and shrub fuels typical of both large fires.

Methods

As blocks 55 and 56 were quite large, the approach to quantifying fuels and fire behavior parameters for each block involved a mixture of large-scale and small-scale sampling. Where appropriate, as in the determination of grass fuel loads which could be highly variable depending on location, sampling was carried out throughout each block. On the other hand, numerous measurements of flame temperatures, heights, and residence times were carried out in the vicinity of a small, preselected site within each burning block where most of the ground- and tower-based instrumentation used in this study was located.

Fuel Sampling

As grass is the major carrying fuel in savanna fires, a large effort was made to determine grass fuel loads and overall distribution on blocks 55 and 56. Grass fuel loads were estimated with a disc pasture meter (DPM), as described by *Bransby and Tainton* [1977], and developed and calibrated for anticipated grass fuel loads in KNP by *Trollope and Potgieter* [1986]. This instrument, developed to permit fast and accurate sampling over large areas where fuel variability is an important factor, overcomes the labor-intensive problems associated with clipping and weighing individual samples. The DPM consists of a circular aluminum disc fitted with a measuring rod, and the standing crop of grass fuel is estimated by relating the settling height of the quantity of grass material holding it above the ground. In a reconnaissance of blocks 55 and 56 in July 1992 it was determined that a uniform high fuel load existed over all of block 55, and it was therefore not necessary to divide the block into different homogeneous vegetation units (HVUs) with respect to fuel load. Conversely, block 56 comprised four different HVUs with significantly different grass fuel loads. The arrangement of DPM samples on both blocks is shown in Figure 2.

In block 55, twenty-two preburn surveys, each comprising 100 DPM readings, were conducted at fixed sample sites located around the block perimeter and along two transects through the block. The 100 DPM readings were arranged along two 100-m transects 25 m apart at each sample site, i.e., a reading every 2 m. Postburn surveys were conducted at each of eight perimeter locations used earlier for preburn measurements. In block 56 a similar sampling scheme was followed, with the number of preburn survey sites being increased to 27 in order to adequately address the significantly different grass fuel loads within the block. Postburn surveys were also carried out at eight perimeter locations where preburn surveys were conducted.

The mean disc height was calculated for all preburn and postburn surveys on block 55, and the difference, expressed in kilograms per hectare, was considered to be the average grass fuel consumption during this fire. For block 56 a grass fuel consumption figure was determined for each HVU.

With the realization that woody fuels form an extremely minor component of savanna surface fuels, only a limited sampling of these fuels took place on blocks 55 and 56. Down woody fuels were sampled, in various size classes, using a variation of the line intersect method [*Van Wagner*, 1968] developed by *McRae et al.* [1979]. This sampling took place, before and after both burns, on a small area in the interior of each block where additional ground-based instrumentation was located. Transects 400 m and 300 m in length were sampled on blocks 55 and 56, respectively.

Weather and Fuel Moisture

Daily observations (1400 LT) of temperature, relative humidity, wind speed and direction, and precipitation, recorded at the Pretoriuskop weather station, located 8 km northwest and 3 km west of the centers of blocks 55 and 56, respectively, were used to determine general weather conditions in the months leading up to SAFARI. During the burning of blocks 55 and 56, temperature, relative humidity, and wind speed were recorded at approximately half-hour intervals using hand-held equipment on site. In addition, perimeter anemometer towers continuously recorded wind speed and direction throughout each burn.

Fuel moisture samples were collected from the interior of each block just prior to ignition, for both grass fuels and fine woody material. These samples were stored in airtight jars and subsequently oven-dried at 80°C for 24 hours.

Fire Behavior

An array of five in-fire towers, located in the interior sampling area, and four fire perimeter towers was used in an integrated analysis of whole-fire wind, thermal, and energy field dynamics for each large burn (see Figure 3). All towers

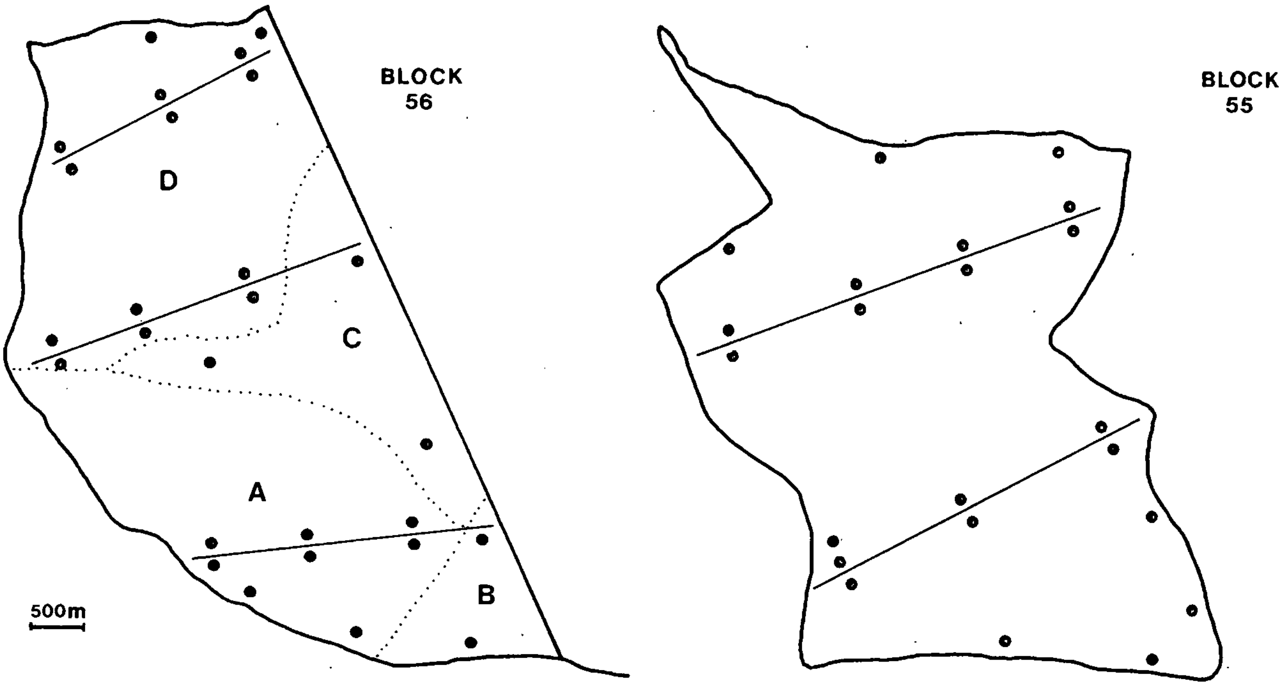

Figure 2. Arrangement of disc pasture meter sampling locations on blocks 55 and 56, showing homogeneous vegetation units within block 56.

recorded horizontal wind speed and direction continuously throughout each burn, while the interior towers were also equipped to measure vertical wind speed and direction. In addition, the interior towers were also equipped with thermocouples to continuously record temperatures at fixed distances above ground. All data recorded at the interior towers were stored on buried data loggers. The arrangement and location of instrumentation on blocks 55 and 56 are shown in Figure 4.

Flame heights were measured at 10 locations within the interior sampling site, using fire retardant–treated strings suspended in a taut fashion from metal tubing 3.5 m above ground [*Ryan*, 1981]. This device was designed in this manner so that the string would burn only during the passage of the flame front and would not burn by smoldering afterward, thus giving a reasonable estimation of flame heights within the interior sampling area. Flame height was then converted to flame length using the angle of the flame relative to the ground [*Ryan*, 1981].

Visually measuring the forward rate of spread of savanna fires, particularly over large areas, is difficult because of the lack of distinguishing geographic features, so a helicopter-mounted global positioning system (GPS), with an external antenna, was used to map the position of the fire front at various times throughout each of the large KNP fires. This was attempted as a backup procedure to visual mapping of the spread rate of both fires from a second helicopter. In addition, electronic timing devices, adapted from *Blank and Simard* [1983] and activated by the passage of the advancing fire front, were used to measure spread rates in and around the heavily instrumented tower location within each burn.

Smoke Column Dynamics

The shape and size of the smoke/convection column over a wildland fire are a function of the rate at which energy is being released at ground level (which depends on the rate and

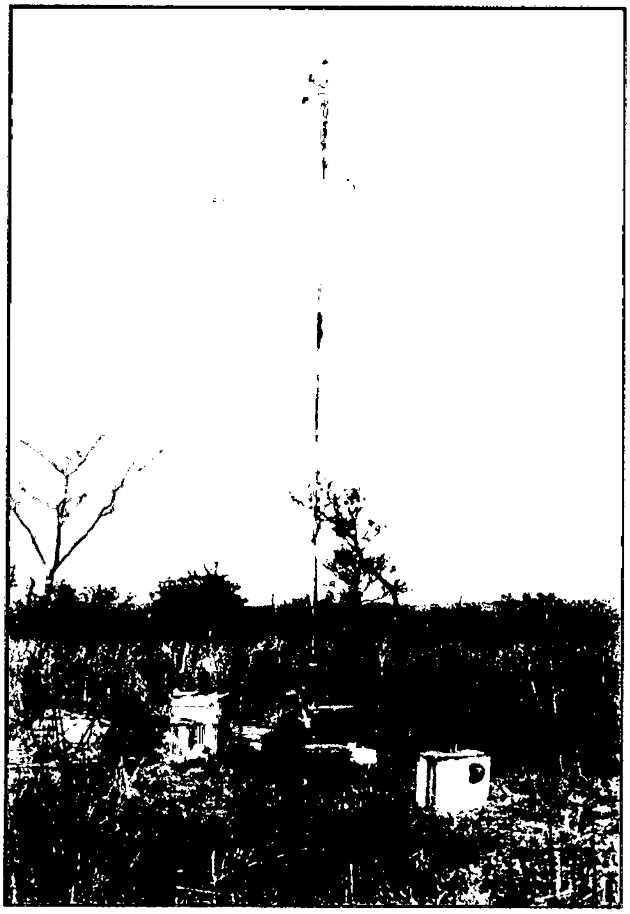

Figure 3. Photo of typical in-fire tower used in measuring wind, thermal, and energy field dynamics during burning of blocks 55 and 56.

amount of fuel consumption and the forward rate of fire spread) and the wind velocity and temperature profile of the atmosphere above the fire. During the two large burns in KNP, an attempt was made to determine the height of the convection column at various times throughout the burn, with the intention of relating that measurement to energy release determinations on the ground and atmospheric wind and temperature data determined through radiosonde ascents. Unfortunately, radiosonde equipment located at Pretoriuskop malfunctioned during SAFARI, and the nearest official stations were not considered close enough to provide data useful to this study.

On each burn, two theodolites were placed some distance from the burn site, at a 90° angle to the direction in which the smoke column was expected to drift during the fire. By turning horizontal and vertical angles with the theodolites, it was possible to record the height and position of the smoke column at various times throughout the burn. Observers at the two theodolite sites were in radio contact to ensure simultaneous measurements. Theodolites were located on nearby hills (kopjes) to provide an unobstructed view of smoke column development. These observation points had to be far enough away from each burn to permit observation of the column top, resulting in the selection of points from 6 to 11 km distant from each KNP block burn.

As a further measure of column dynamics, the two smoke-sampling aircraft working on each fire were asked to observe and record the height of the top of the convection column when possible during their flights.

Results and Discussion

The first large burn was carried out in block 56 (2043 ha) on September 18, and the second burn took place in block 55 (2333 ha) on September 24.

Fuels Inventory and Consumption

Grass fuel loadings, and associated statistics, as determined using the DPM, are presented for both blocks 55 and 56 in Table 1. As block 55 had a relatively homogeneous grass fuel load, all 22 samples were averaged to produce a mean preburn fuel load of 4035 kg/ha. Preburn fuel loads for the three HVUs identified in block 56 were 2437, 959, and 3922 kg/ha for HVUs A, B, and C, respectively. It was subjectively felt that differences in fuel loads between HVUs were primarily a reflection of grazing pressure.

Postburn DPM surveys, conducted around the perimeter of each fire, determined average postburn grass fuel loads of 333 kg/ha for both blocks 55 and 56. This translates into grass consumption figures of 3702 kg/ha for block 55 and 2103 and 3588 kg/ha for HVUs A and C, respectively, in block 56. As HVU B was largely unburned owing to a lack of grass fuel, postburn measurements were not made in this area.

Down woody fuel loads for very fine fuels (<1.0 cm diameter) were extremely low, averaging only 84 and 26 kg/ha on blocks 55 and 56, respectively. For the purpose of intensity calculations, only these fine woody fuels were considered to be consumed during the flaming phase of combustion. Postburn inventories indicated that all woody fuels in this size class were consumed in both fires. In general, larger down woody fuels were consumed in varying amounts, but this was assumed to have occurred during the smoldering phase of combustion.

Total fuel consumption figures for blocks 55 and 56, combining both grass and woody fuel consumption, are therefore 3786 and 3614 kg/ha, respectively. For block 56, fuel consump-

Table 1. Preburn Grass Fuel Loads for Block 55 and Three Homogeneous Vegetation Units (A, B, and C) for Block 56

Sample Number	Fuel Load, kg/ha
Block 55	
1	5130
2	5964
3	4408
4	4678
5	3333
6	2831
7	2918
8	2874
9	3799
10	3373
11	3333
12	3531
13	4477
14	4269
15	2424
16	2831
17	5467
18	5763
19	5763
20	3211
21	4339
22	4056
Mean	4035.1
s.d.	1076.6
Block 56, HVU A	
A1	1735
A2	1819
A3	1943
A4	2392
A5	1281
A6	1287
A7	3232
A8	4374
A9	4374
A10	1929
Mean	2436.6
s.d.	1163.03
Block 56, HVU B	
B1	830
B2	1328
B3	720
Mean	959.3
s.d.	324.0
Block 56, HVU C	
C1	2924
C2	3196
C3	3243
C4	3694
C5	5125
C6	4973
C7	3528
C8	3252
C9	3639
C10	3888
C11	3960
C12	4403
C13	4243
C14	4842
Mean	3921.5
s.d.	704.4

HVU denotes homogeneous vegetation unit; s.d. denotes standard deviation.

Table 2. Pretoriuskop 1400 LT Weather Observations for September 1992

Day in September	Dry Bulb Temperature, °C	Relative Humidity, %	Wind Speed, km/h	Wind Direction, deg	Precipitation, mm
1	27.6	38	7.2	360	0
2	32.0	27	18.0	360	0
3	34.8	22	18.0	360	0
4	33.0	30	calm	360	0
5	31.0	28	28.8	180	0
6	27.6	38	7.2	360	0
7	26.5	47	18.0	90	0
8	30.0	31	18.0	180	1.0
9	31.5	25	25.2	180	1.0
10	29.2	40	calm	360	0
11	27.3	51	calm	360	1.0
12	36.7	16	7.2	180	0
13	20.9	57	21.6	130	0
14	21.9	62	7.2	360	0
15	24.2	77	calm	360	0
16	32.0	38	calm	360	0
17	20.5	68	7.2	130	0.6
18	30.6	41	10.8	360	0.1
19	36.8	24	7.2	360	0
20	37.9	11	21.6	360	0
21	34.5	19	21.6	360	0
22	17.5	61	18.0	90	0
23	15.6	67	3.6	180	0
24	26.8	45	14.4	360	0
25	34.0	28	10.8	90	0
26	28.3	47	7.2	360	0
27	20.3	75	calm	360	1.2

tion figures for HVU C were considered representative of the complete burn, as most of the head fire portion of the fire took place in this area.

Table 2 shows the daily 1400 LT weather observations recorded at Pretoriuskop during the month of September 1992. The most significant aspect of the weather in KNP during the 5 months prior to the SAFARI was the almost complete lack of precipitation, although this is common during the dry season. Aside from one 30-mm rainfall event during August, no appreciable precipitation occurred in the Pretoriuskop area during the fall and winter of 1992. Table 2 presents the daily 1400 LT weather observations at Pretoriuskop during September 1992, reflecting a very dry and relatively warm period. As a result, grass fuels in blocks 55 and 56 were in an extremely dry condition prior to burning. Other SAFARI investigators determined that grass fuels were about 90% cured on these burn sites in late September 1992 [*Kuhlbusch et al.*, this issue].

Table 3 outlines weather observations obtained on site, with hand-held instruments, at periodic intervals during both burns. Generally, temperatures rose throughout the period of each burn, while relative humidity values decreased and wind speeds increased. This was expected, and the backfire portion of each burn was ignited during the morning, with head fire ignition beginning in the early afternoon as conditions became warmer, drier, and somewhat more windy.

Fire Behavior

Hand ignition of both blocks 55 and 56 followed the same general procedure: slow backfire ignition along the downwind sides followed immediately by rapid head fire ignition along the upwind edges. As winds were generally from the north, backfiring took place along the south and west sides of each block. This operation took approximately 4 hours to complete on each burn, as care was taken to prevent escapes because of the extreme drought prevailing over the region. Backfire ignition began at approximately 1100 LT on block 56 and about 0900 LT on block 55. Head fire ignition commenced immediately after completion of the backfire, beginning at 1305 LT on block 55 and 1518 LT on block 56, but the head fire ignition procedure differed between blocks. On block 55, two ignition teams commenced at the northeast corner and began igniting simultaneously west and south from that point. On block 56 each team moved simultaneously eastward across the northern border and southward along the eastern perimeter. The rate of spread maps for blocks 56 and 55, obtained through visual mapping by helicopter, are shown in Figures 4a and 4b, respectively.

In general, block 56 was a very patchy burn, as the head fire became fragmented owing to discontinuous grass fuels and the effect of a number of drainage features. Approximately 1 hour after head fire ignition began, the fire was spreading as two separate lobes which spread to the southwest before being slowed by the patchy fuels and becoming flanking fires. This, in combination with increasing darkness, resulted in much of the remainder of block 56's burning slowly overnight or not burning at all. Approximately 20% of block 56 remained unburned.

Block 55 was a much more uniform fire, spreading as a number of lobes, but still moving rather continuously through the block in slightly over an hour. Generally, weather conditions were similar during both fires, with the exception being cooler temperatures during the block 55 fire. However, this fire spread more quickly and regularly, probably owing to more continuous fuels and the fact that head fire ignition took place simultaneously in two directions from the windward northeast corner. Both fires burned through the in-fire tower array as head fires.

The helicopter-mounted GPS worked quite well during the block 56 fire, producing a computerized map that delineated fire front positions quite similar to those obtained through visual mapping. However, on the more intense block 55 fire, dense smoke and turbulence prevented the GPS helicopter from flying directly over the fire front, and no readings were obtained.

Table 3. On-Site Weather Observations Taken During Block 56 (September 18) and Block 55 (September 24) Fires Using Hand-Held Instruments

Time, LT	Dry Bulb Temperature, °C	Relative Humidity, %	Wind Speed, km/h	Wind Direction, deg
		Block 56		
1125	28.3	44	5.8	360
1204	30.3	41	7.9	45
1234	32.2	34	6.5	45
1310	31.1	35	7.2	45
1401	30.0	37	11.2	45
1513	31.7	31	11.2	45
1604	30.6	35	11.2	45
1702	28.9	38	3.2	45
		Block 55		
0936	23.3	49	4.7	315
1011	23.3	49	1.4	315
1054	25.6	43	9.7	45
1125	26.7	44	7.9	45
1201	26.7	44	6.5	45
1242	27.8	40	9.7	45
1453	28.9	37	11.2	45
1611	26.7	44	1.4	45

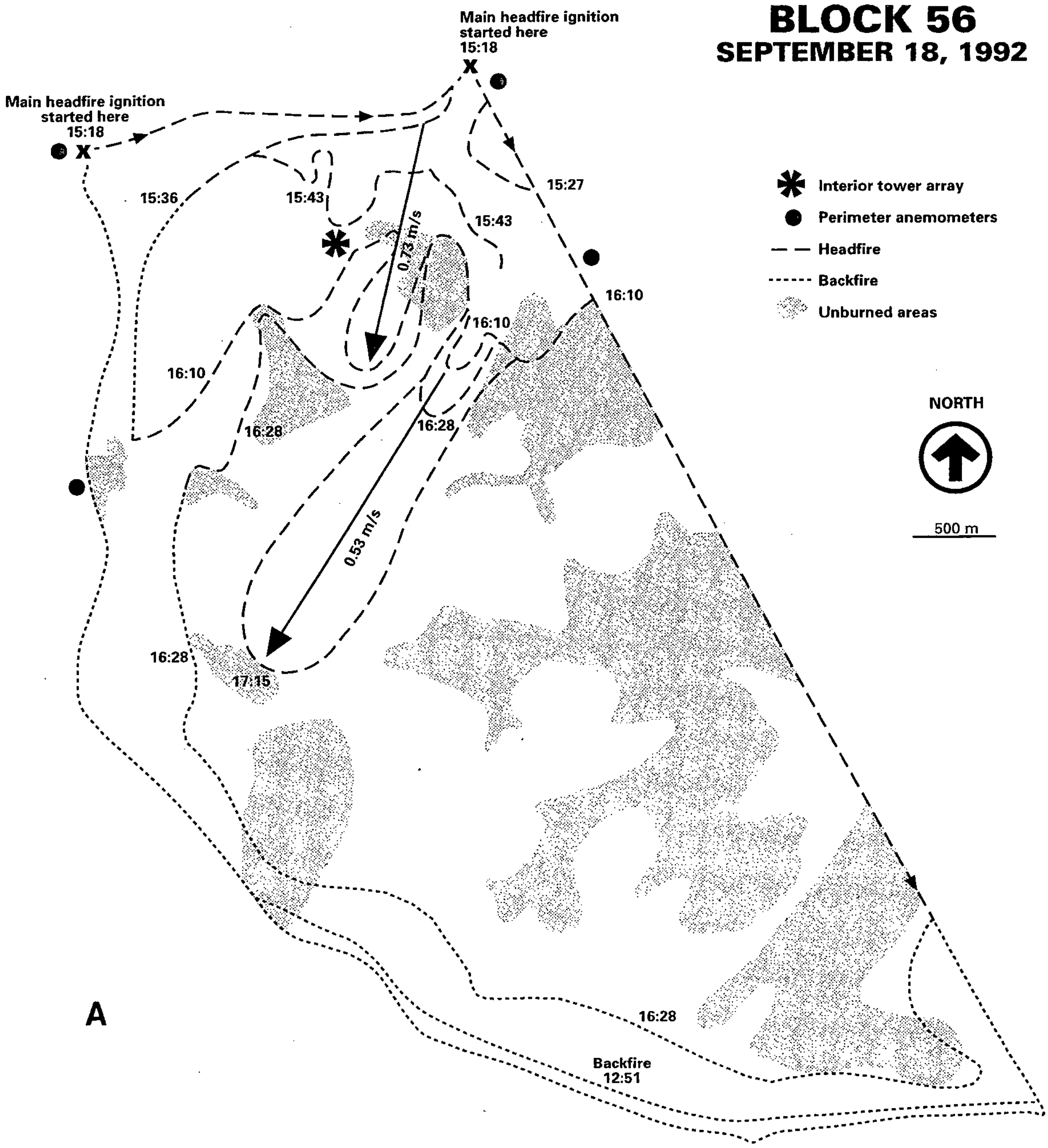

Figure 4. Rate of spread maps for (a) block 56 and (b) block 55, showing ignition patterns, the position of the fire front at various times, and the location of interior and perimeter towers.

Average head fire spread rates, determined over runs of 1.5–3.0 km (Figure 4), were 1.62 m/s (5.83 km/h) for block 55 and 0.63 m/s (2.27 km/h) for block 56. These values were combined with fuel consumption figures of 3786 and 3614 kg/ha for blocks 55 and 56, respectively, and an average heat of combustion for grass of 17,781 kJ/kg [*Trollope*, 1984] to estimate frontal fire intensity using the following equation [*Byram*, 1959]:

$$I = Hwr \tag{1}$$

where I represents frontal fire intensity (kilowatts per meter), H represents the heat of combustion (kilojoules per kilogram), w represents the weight of fuel consumed (kilograms per square meter), and r represents the fire front rate of spread (meters per second). Using this approach, frontal fire intensities of 10,906 and 4048 kW/m were determined for the head fire portions of blocks 55 and 56, respectively.

As another means of determining the amount of energy being released during each burn, the area burned between periods when the fire was mapped was measured and combined with the average fuel consumption and heat of combustion to produce the average heat release (in kilowatts) over that time period. The results, presented for both fires in Table 4, clearly reflect the higher intensity of the block 55 burn.

Flame heights averaged 350 and 169 cm near the interior tower sites in blocks 55 and 56, respectively. Actually, flame heights often exceeded the height of the measuring devices on block 55, but were much more variable (2–346 cm) on block 56. Flame length was calculated from flame height using the flame

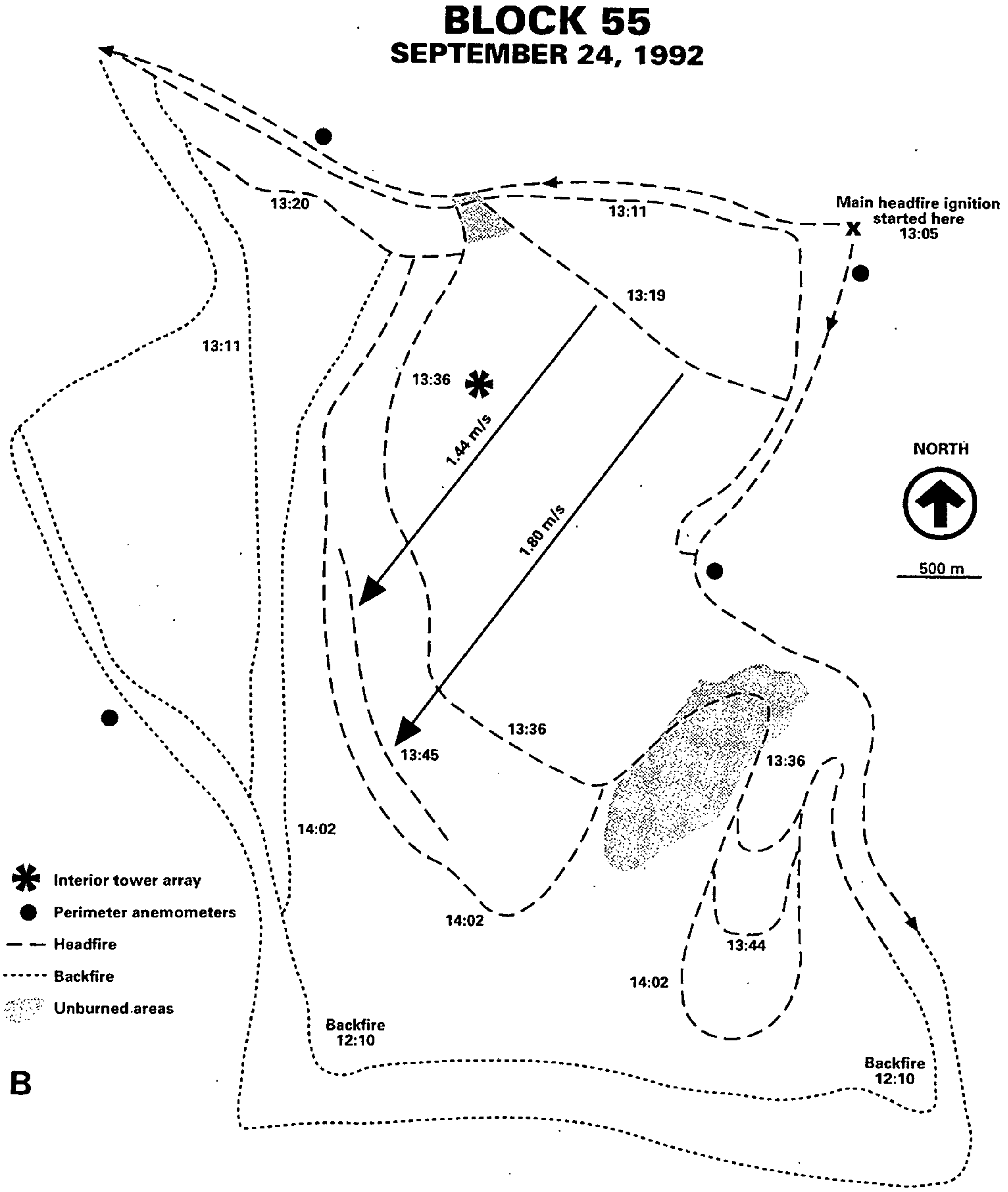

Figure 4. (continued)

tilt [*Ryan*, 1981] obtained from visual observation of low-level aerial photographs taken during each burn (see Figure 5). Using this method, flame lengths on block 55 ranged from 390 to 515 cm in wind gusts, while block 56 flame lengths varied between 173 and 230 cm under the same conditions.

Fire residence times, horizontal wind speeds, and temperature data measured at the interior tower site during both fires are presented in Table 5. The length of time the temperature at ground level remained above 50°C is considered a good indication of the fire's residence time. This translates into an average of 66 and 46 s, respectively, for blocks 55 and 56. This also serves as a rough approximation of the length of the flaming phase of combustion, as smoldering combustion was negligible. Peak interior horizontal winds, obtained during the flame front passage, averaged 47 and 40 km/h for blocks 55 and 56, with updrafts during the same period averaging 20 km/h on block 55 and 11 km/h on block 56. Temperatures at ground level were similar for both burns, averaging above 750°C. Temperatures near the top of each tower (8.5 m) were generally higher on block 55, averaging 164°C, than on block 56, where temperatures averaged 104°C.

From the foregoing results it is obvious that significantly higher energy release rates were attained during the block 55 fire than was the case on block 56, primarily owing to the ignition pattern favoring the development of a long, relatively continuous, fire front. Convection column heights for blocks 55 and 56, based on theodolite measurements, are presented in Table 6. As might be expected when comparing intensity values between the two fires, the column on block 55 was much more significant than on block 56 (see Figure 6). The markedly

Figure 5. Aerial photo of high-intensity fire behavior on block 55 as head fire and backfire zones converge.

higher energy release rates on block 55 resulted in a well-developed column, with a capping cumulus top, during the first hour after head fire ignition began, which reached an estimated maximum height of almost 2500 m above ground. In comparison, the block 56 fire was never intense or continuous enough to produce and/or sustain a well-developed convection column, and the resulting smoke plume was weak and poorly defined, never approaching the production of a capping cumulus top. The theodolite readings in Table 6 are not as precise as anticipated, as slight wind shifts caused the smoke column to drift somewhat, so that it was not at the desired 90° angle to the theodolite locations. However, aircraft observations of the column height on block 55 are in good agreement with the values in Table 6. The Cessna smoke-sampling aircraft reported the capping cumulus top to be approximately 1900 m above ground at 1307 LT and again at 1345 LT (G. Helas, personal communication, 1992). The theodolite readings would appear to be overestimating the column height by 400–500 m during this period, likely owing to poor alignment. By 1353 LT the Cessna reported the top of the smoke column to be at 2200 m above ground and approximately 30 km downwind from block 55.

Conclusions

Large savanna fires present problems in terms of fire behavior documentation, as fragmented burning patterns due to topographic and fuel discontinuities increase fire behavior variability within burns, ultimately affecting convection column dynamics and the fate of emissions from these fires. Savanna fires are also highly variable in terms of fuel loads, weather, and ignition patterns. Despite these limitations, this study has shown that it is possible to quantify fire behavior in savanna fires in a manner directly related to their atmospheric impact. The two large 1992 KNP fires exhibited distinctly different overall fire behavior characteristics, and this was well documented in terms of ground-based energy release measurements and concurrent convection column monitoring.

On the basis of these two KNP fires, it seems that savanna fires, with the limited amount of fuel available to the combustion process, cannot generate the sustained energy release levels necessary to generate convection columns above 3000–4000 m, meaning that savanna fire trace gas and aerosol emissions are released into the lower troposphere. This is in direct contrast to forest fires in the world's boreal and temperate zones which, while exhibiting similar spread rates, consume much larger amounts of fuel, and this is translated into signif-

Table 4. Average Energy Release Rates During Selected Periods of the Block 55 and Block 56 Burns

Time Period, LT	Total Intensity, kW
Block 55	
1319–1336	34, 253, 423
1336–1402	11, 176, 658
Block 56	
1527–1543	3, 146, 089
1543–1610	5, 275, 711
1610–1628	3, 153, 526
1628–1715	2, 620, 553

Table 5. Flame Zone and In-Fire Wind Field Characteristics Measured at the Interior Tower Location on Blocks 55 and 56

Tower	Residence Time, s	Maximum Horizontal Wind,* km/h	Temperature, °C	
			8.5-m Tower	Ground
		Block 55		
1	75	48.6	113	900
2	52	45.4	170	700
3	86	47.9	190	770
4	50	43.9	56	770
Center	···	49.7	290	755
Average	65.8	47.1	164	779
		Block 56		
1	60	35.3	82	820
2	30	33.1	100	700
3	36	42.1	104	795
4	54	38.9	94	700
Center	51	49.3	137	730
Average	46.2	39.7	103	749

*Measured at 9 m above the ground.

Table 6. Convection Column Heights Above Ground Level for Blocks 55 and 56

Block 55 (September 24, 1992)		Block 56 (September 18, 1992)	
Time, LT	Height Above Ground, m	Time, LT	Height Above Ground, m
···	···	1345	49
···	···	1419	423
···	···	1430	1360
···	···	1440	75
1250	730	1450	233
1300*	760	1500*	175
1310	1961	1510	498
1320	1989	1520	993
1330	2348	1530	1308
1340	2717	1540	2137
1346	2477	···	···
1350	2019	1550	1243
1400	1524	1600	1574
1410	1290	1610	1915
···	···	1620	1561
1424	1481	···	···

*Head fire ignition occurred at 1305 and 1518 LT at blocks 55 and 56, respectively. The data have been arranged so that column heights following head fire ignition can be compared between burns.

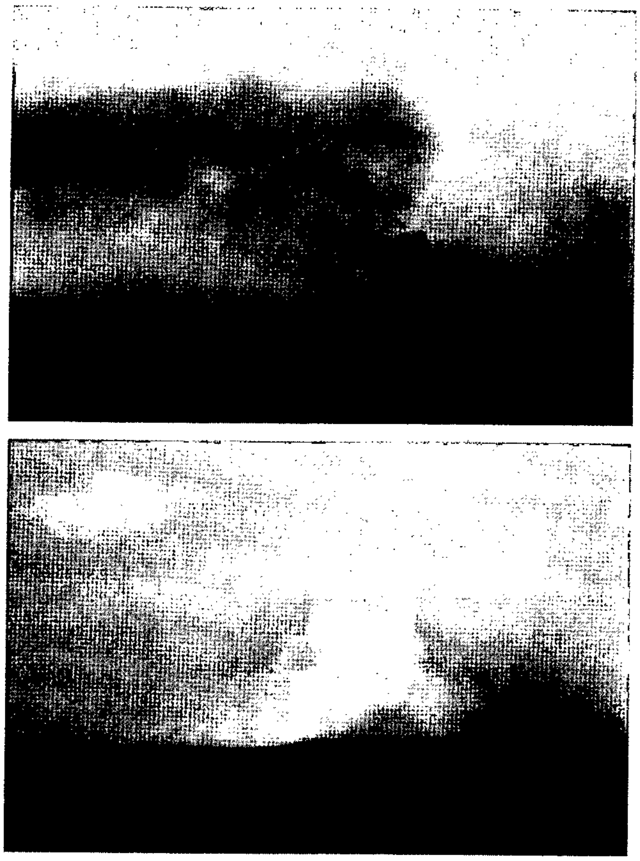

Figure 6. Convection columns on (top) block 56 and (bottom) block 55 fires.

icantly higher energy release rates and convection columns that sometimes reach the stratosphere.

However, these fires were conducted in an arid savanna after a long drought period. Before any definitive conclusions can be drawn on the interrelationship between energy release rates and convection column dynamics in savanna fires, there is a strong need to study large-scale, free-burning savanna fires in nondrought years when higher grass fuel loads would provide greater energy release rates. Future studies would benefit from the use of a dedicated aircraft for convection column measurements and a local rawinsonde operation to provide atmospheric wind and temperature data for correlation with column development. Future experimental fires should be conducted in both subhumid and humid savannas in order to further assess the fire behavior–convection column dynamics–smoke injection height hypothesis presented in this paper.

Acknowledgments. The authors gratefully acknowledge the helpful and capable assistance of Alex and Meryl Weaver of Stellenbosch during the fieldwork portion of this study, and the work of Gary Hartley and Tom Blake (CFS Ontario Region) in graphics design and development. The cooperation of the staff of Kruger National Park, without whose assistance SAFARI would not have been possible, is also acknowledged and very much appreciated.

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(Received July 20, 1994; revised April 4, 1995;
accepted May 5, 1995.)

Second paper: Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern.

Koedoe.

Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern

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Van Wilgen, B.W., H.C. Biggs and A.L.F. Potgieter. 1998. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe* 41(1): 69–87. Pretoria. ISSN 0075-6458.

This paper reviews the options for management of the savanna ecosystems of the Kruger National Park using fire. The major goals of management have shifted from attempts to use fire to achieve a stable vegetation composition, to one of recognising that savanna ecosystems are in constant flux. Fire is a major form of disturbance that helps to maintain a state of flux, and thus to conserve biodiversity. Three candidate approaches for fire management have been put forward—the lightning fire approach, the patch mosaic burning approach, and an approach based on the assessment of ecological criteria. These approaches differ in their underlying philosophies, but not necessarily in their outcomes, although this cannot be predicted with confidence. We propose, therefore, that patterns of fire frequency, season, intensity and spatial distribution be recorded and monitored, and that these patterns should serve as surrogate measures of biodiversity. Guidelines for the definition of thresholds of potential concern with regard to these patterns are discussed. The monitoring of both fire patterns and trends in plant and animal populations can be used to identify interactions between fire and the components of the ecosystem, and these in turn can be used to define a relevant research agenda. The role of management in monitoring and assessing fire patterns (previously regarded as a research responsibility) is emphasised. Convergence in the patterns of fire that result from the different management approaches could also serve as a basis for merging some or all of these approaches in order to simplify management.

Keywords: fire, management, savanna, research, monitoring.

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Introduction

The various approaches to fire management in the 1.9 million ha Kruger National Park over the past 70 years have reflected the evolution of an understanding of the role of fire in savanna ecosystems. The practices since the park's proclamation in 1926 have included the "indiscriminate" application of fire to improve grazing, fire exclusion, prescribed burning on fixed and flexible rotations, and a policy of natural burning (in that order) (Joubert 1986; Van Wilgen *et al.* 1990; Trollope *et al.* 1995). These policies have followed similar trends elsewhere in southern Africa (Mentis & Bailey 1990: Du Plessis 1997). The current policy (introduced in 1992) calls for allowing natural (lighting-ignited) fires to burn freely, but where prescribed burning will not be carried out, and fires of human origin will be suppressed.

The historic fire regime in the Kruger National Park is relatively well known (Trollope 1993; Van Wilgen *et al. in press*). Fires covering 16.79 million ha occurred between 1941 and 1996. Of this area, 5.15 million ha burnt between 1941 and 1957, when limited prescribed burning and protection from fire took place. Between 1957 and 1991, 2213 prescribed burns covering 5.1 million ha (46.3% of the 10.98 million ha burnt during that period) were carried out. Lightning fires burnt 2.5 million ha between 1957 and 1996, or 21.6% of the area burnt during that period. The mean fire return period was 6.3 years, with intervals between fires from 1–40 years. Fires occurred in all months, but prescribed burns were concentrated in early spring (September to November), at the end of the dry season. Lightning fires were later, with 84.7% of the area burning between September and January.

The prior policy of prescribed burning on a three-year cycle was introduced in 1957. The official view at that time called for the policy to continue "until such time that it is proved incorrect" (Joubert 1986). At the same time, a comprehensive burning experiment was initiated to investigate the effects of fire (Van der Schiff 1958). This experiment included the application of annual, biennial and triennial burns in different seasons on plots located in the major landscapes of the park. The experiment was expanded in the late 1970s (Gertenbach & Potgieter 1979), and the application of treatments has continued to the time of writing (1997). The data collected during the course of this experiment have not been analysed, other than in isolated papers of limited scope (Van Wyk 1971; Trollope & Potgieter 1985; Trollope *et al.* 1996a).

The prescribed burning policy remained in place, with some adjustments, until 1992. At that stage, a number of concerns were raised, which resulted in a change in policy from active prescribed burning on a fixed cycle, to one of moving towards a more flexible and variable pattern of burning. This change was in line with the development of non-equilibrium theories of savanna dynamics, which advocate burning under diverse rather than fixed conditions (Mentis & Bailey 1990; Walker 1989). The specific concerns included:

(i) The observation that a dominance of grass species characteristic of poorly managed pastures and overgrazing ("increasers") was a result of "excessively frequent burning" in combination with severe drought (Trollope *et al.* 1995);

(ii) Putative trends in woody vegetation structure (e.g. Viljoen 1988). It would appear (for example, from examining early aerial photographs) that large areas have been homogenised, possibly due to the rigid application of a policy of burning at three-year intervals. The density of larger trees has declined, dramatically for some species, and this decline may be due to a regular fire regime with short-interval fires (in combination with other factors, such as browsing by elephants);

(iii) The practice of 'ringburning" associated with prescribed burning. This refers to the process where fires are ignited around the periphery of management blocks and allowed to burn towards the middle. More natural fires, for example those associated with lightning strikes, would spread out in all directions from a point, allowing the fire to develop a range of intensities as it spread. Ringburning can prevent animals from escaping from fires, and also leads to a disproportionately large area burning as a high-intensity headfire (an effect magnified by the fact that these fires are carried out during the day, and never at night); and

(iv) The lack of variation associated with burning on a fixed cycle. This includes such things as occasional longer periods between fires, or varying the size of fires, on the assumption that such variation will promote the conservation of biodiversity (see, for example, Hansson 1997; Wiens 1997).

In attempting to select an appropriate fire management approach for the Kruger National Park, discussions have focused on the definition and nature of a natural fire regime. This is required by the mission statement, which calls for the maintenance of biodiversity "in all its natural facets and fluxes" (Anon 1997). There has been considerable debate about the best approach to adopt in order to achieve such a regime, which could be expected given the difficulties in defining what qualifies as "natural". Three candidate approaches for fire management have been put forward—these are the lightning fire approach, the patch mosaic burning approach, and an approach based on the assessment of ecological criteria (see below).

This paper explores the essence of the proposed fire management approaches, to examine if, and how, they differ in terms of the outcomes they will deliver. We propose guidelines for developing thresholds of potential concern with regard to the fire patterns that establish themselves in the application of the three management approaches. We provide a brief account of sets of conditions that could guide decisions on whether to discontinue any of the management options, as well as the future of fire-related research in the light of the new management approaches.

The definition of natural fire regimes

The policy of attempting to restore a natural fire regime to the Kruger National Park has been adopted to allow those processes under which the ecosystem evolved to continue operating. Similar attempts have been made elsewhere, particularly in the United States where a strong "wilderness" lobby has driven such policies in a range of National Parks (Kilgore & Heinselman 1990). Parsons & Van Wagtendonk (1996) have defined the goal of such a fire management programme as "to preserve, or where necessary restore, fire as a natural ecosystem process". These authors point out that this goal will be accomplished when fires of similar size burn at similar intervals, intensities and seasons, and thus with similar ecological effects, as fires that burned in the past or that would have occurred today had (modern) humans not intervened.

There are a number of dangers inherent in allowing a system of supposed natural fires to operate unimpeded. The first, and perhaps most obvious, is that the parameters of a natural fire regime are not known and probably not knowable—we therefore cannot be sure that the regime that results is in fact natural. Secondly, processes can only operate naturally when the factors that control them are unaltered from a pristine state (Bonnicksen & Stone 1982). It can be argued that the Kruger National Park is a highly modified environment. It is entirely fenced, restricting the migration of herbivores and thus impacting on the dynamics of both grass fuels and woody plants. Many artificial water points (611 boreholes and 129 dams) have allowed new patterns of herbivory to develop within the boundaries of the park, further impacting fuel loads. Historic programmes of prescribed burning, and culling, have influenced the structure and composition of the ecosystem, and its fuel properties. Development outside of the park has changed the patterns of fires that previously burnt across the (artificial) park borders, while within the park a network of roads and other infrastructure affects fire patterns. Finally, man has played a role in the ecology of Africa, through the use of fire, for a very long time—longer than on any other continent. The degree to which this can be regarded as natural, and the means by which to simulate a mix of lightning and anthropogenic fires, are not known.

Assuming that the characteristics of a natural fire regime could be defined, a number of other questions remain. These include whether a particular management approach would simulate the desired regime, and if it did not, how it would differ in terms of the fire patterns that established themselves. Secondly, the problem of unplanned fires, particularly those started by humans, is so large that any fire management approach has to develop a means of incorporating such unplanned fires into decision processes. The candidate management approaches are outlined in the section below.

The proposed fire management alternatives

Lightning fire approach

This policy, also termed a "wilderness", or *laissez faire* approach by Trollope *et al.* (1995), is aimed at simulating a fire regime that would be similar to the one that existed in the park prior to intervention by modern man, and one to which the biota of the park would be best adapted. The approach calls for allowing natural (lighting-ignited) fires to burn freely, but where prescribed burning will not be carried out, and fires of human origin will be suppressed. Because lightning alone may not ignite sufficient fires to simulate a "natural" regime, some consideration has to be given to allowing additional fires to burn. These would make up for fires that would have been started by early man, or those that would have entered the park from outside, but are not able to do so due to modifications or suppression outside of the park. Managers will be required to suppress fires that are not started by lightning, and it is assumed that the area burnt by these (non-lightning) fires will be sufficient to make up for the additional fires that would have occurred in the past. This approach has been followed for almost 6 years, and has apparently resulted in some shifts away from patterns that characterised the historic fire regime in the park (Van Wilgen *et al.*, *in press*). These include a smaller total area burnt (resulting in longer mean fire return periods), a shift in season to later in the year, and a shift in fire size distribution to include a number of very large fires.

Patch mosaic burning

This approach (B.H. Brockett *pers. comm.*) aims to establish a mosaic of vegetation structural types, by applying a large number of fires over an extended period within each year. The assumption is that the heterogenous mosaic that results from the application of such fires will be the most efficient means of conserving biodiversity. The system is applied by determining the grass biomass in April of each year. The percentage of the area to be burnt is determined as a function of biomass, and ranges from about 5% of the area for a biomass of 1500 kg/ha, to 50% for a biomass of 7000 kg/ha or more. The number of fires in which this area will be burnt is a function of the percentage, and ranges from a target of 6 fires per 50 000 ha in cases where only 1% of the area will be burnt, to a target of 40 fires per 50 000 ha in cases where 50% of the area will be burnt. These fires are then distributed over the available months between April and November. Fires are ignited at random points, and allowed to burn out by themselves. Once the target area allocated to each month falls between defined limits , no further fires are ignited until the next month. Because the initial fires are put in early, before conditions that would lead to extensive fires have begun, initial fires tend to be smaller. Once conditions that would allow for fires to spread over large areas set in, the fires are prevented from becoming too large as they burn out against earlier, smaller burns. The net result is a mosaic of burns of different sizes, burnt under different conditions and in different seasons. This method has been successfully used in the Pilanesberg National Park (50 000 ha) and elsewhere, and could be applied to similar-sized subdivisions within the Kruger National Park (for example, a ranger section).

Ecological criteria assessment

This system was developed in response to the concern that excessively frequent burning and severe drought had led to a deterioration in the grass species composition in many areas of the Kruger National Park (Trollope *et al.* 1995). Under this system, the decision of whether to burn or not is based on an assessment of grass biomass and the species composition of the grass sward, and the area already burnt in accidental fires. An upper limit of 50% of sourveld and 33% of sweetveld areas for any burning is set; if this has already burnt in accidental fires, no further burning should be considered. If this is not the case, then areas can be burnt, up to this limit, provided that they have a grass biomass of greater than 4 000 kg/ha, and provided that grasses classified as "increaser II" species (see Van Oudtshoorn 1992) are not dominant in the sward. Fires that start accidentally in an area that meets the criteria for burning can be allowed to burn, or, in cases where the criteria are not met, such fires should be suppressed. Fires could be applied as point ignitions, rather than ringfires, and will require the maintenance of a network of firebreaks around management units (termed "blocks"). This system has been described, but has not yet been applied in practice.

Comparison of the three approaches

Each of the management approaches above will possibly result in a characteristic fire regime, which can be measured in terms of the frequency, season, intensity, size class distribution and spatial distribution of fires (Table 1). Each will presumably also have an associated set of ecological effects, many of which will be difficult to predict. This difficulty is both due to a limited understanding of the impacts of fire on all elements of the ecosystem, and the fact that fire cannot be considered in isolation from other factors such as herbivory and variation in rainfall. It should also be borne in mind that, in practice, none of these approaches will operate on its own; unplanned fires, both of human or natural (lightning) origin, will continue to form an important part of the fire regime, and any approach that is adopted will have to take this into account (although the patch mosaic system may limit the impact of unplanned fires by breaking up continuous grass fuels in early burns)

The main differences between the three proposed approaches will be found in their underlying philosophies. The lightning fires approach follows a "nature-knows-best" philosophy, and no goals are explicitly set with regard to the amount and distribution of fires that should take place. The patch mosaic approach is essentially driven by the assumption that fire patterns are effective surrogate measures of biodiversity (see below). It actively seeks to establish a heterogeneous mosaic of vegetation structure by applying a range of fires in different seasons, assuming that this is a good way to conserve biodiversity. It is explicit in its goals with regard to area and seasonal distribution of fire. The use of ecological criteria starts with a goal of driving the system towards a desired distribution of vegetation structure and composition through the use of fire. It is therefore explicit in terms of measures such as grass species composition and fuel loads; fire frequencies and season would be selected to achieve a desired result based on the best knowledge about the response of the biota to fire, and are not goals in themselves.

The outcomes of each of these approaches are not readily predicted, but can in some cases be based on experience (Table 1). An analysis of fire regimes in the Kruger

Table 1 (across two pages)

Salient features of the most likely outcomes (in terms of measurable features of the
Note that prescribed burning on a three-year cycle is no longer being considered as

	Prescribed burning on a three-year cycle	Lightning fires
Basic philosophy of approach	Regular fire is necessary to improve the quality of grass forage.	Lightning fires should produce the same patterns of frequency, season and intensity that characterised the regime under which the park's biota evolved.
Fire frequency	Mean fire return period of 6 years and median of about 3 years. Small areas survive without fire for up to 30 years. Supposed greater regularity of intervals between fires.	Mean fire return period of about 10 years and median of about 5 years.
Fire season	Can be chosen as desired. In the past 66% of area burnt in September, October and November.	Fires in the late dry or early wet season (85% between September and January).
Fire intensity	Relatively high due to ringburning.	A range of intensities will be achieved.
Fire size distribution	Most (70%) of fires smaller than 6000 ha. Largest fires equal to the size of the largest block (about 18 000 ha).	Some small fires, but fires tend to be larger. Very large fires (> 200 000 ha) possible after good rains.
Relative spatial distribution of fires	Coarse matrix of evenly distributed fires.	Coarse matrix of unevenly distributed fires.
Logistics and costs	Relatively expensive in terms of the maintenance of a network of firebreaks. Some wildfires have to be suppressed.	Low maintenance costs, but many wildfires of human origin may have to be suppressed. Risk of high fuel buildups around camps or other infrastructure.
Ecological effects	Frequent burning in dry periods leads to dominance by "increaser" grasses and a decrease in the diversity of perennial grasses. Homogenization of woody vegetation structure over large areas?	Longer periods between fires will favour woody species? Large fires, if followed by drought, could reduce available forage and increase herbivore mortality.

fire regime) of four approaches to fire management in the Kruger National Park an option, but is included here for comparative purposes

Patch mosaic burning	Assessment of ecological criteria
Patch mosaic burning should result in a heterogenous vegetation structure at a fine scale, and thereby maximise biodiversity	Given that the desired composition, structure and dynamics of the vegetation are known, a fire regime can be selected to produce that vegetation.
Mean fire return periods of about 4 years; median about 2–3 years.	Mean fire return period of about 8 years and median of about 4 years.
Fires begin early (May) and continue until the end of November. A greater proportion is burnt earlier following years of higher rainfall.	Can be chosen as desired.
A range of intensities will be achieved.	A range of intensities can be achieved if ringburning is not applied.
Mosaic of small and relatively large (up to 10 000 ha?) fires, but no very large fires.	Most (70%) of fires smaller than 6000 ha. Largest fires equal to the size of the largest block (about 18 000 ha).
Fine matrix of evenly distributed fires.	Coarse matrix of evenly distributed fires.
Low cost and lower risks of wildfires and fuel buildups. However, random ignition points may be difficult to reach in large undeveloped areas.	Relatively expensive in terms of the maintenance of a network of firebreaks. Some wildfires have to be suppressed.
Diversification in vegetation structure. Increase in biodiversity?	Dominance by "decreaser" grasses and improved quality of grazing. Opportunities for trees to develop to large sizes if fire excluded for longer periods?

Table 2 (across two pages)
Examples of causes of potential concern related to fire, their significance for the conservation of

Cause of potential concern	Method of measurement	Significance of element for conservation of biodiversity
Fires do not develop variable long-term patterns with respect to frequency.	Curve of probability of fire over past 30 years.	A range of fire return periods will maximize diversity. Frequent fires promote grasses, while infrequent fires promote trees and shrubs.
The risk that burning may be followed by drought	Proportion of area burnt in each month as the fire season progresses.	Burning removes forage and cover which, if not replaced by new growth, can lead to excessive mortality of herbivores.
The seasonal distribution of fires does not approach the desired distribution.	Proportion of area burnt in each month over the past 20 years	Most plant species can survive fires in the dry season when they are dormant. Late season or summer burns detrimental to "decreaser" grasses and/or to tree Continual concentration of successive fires in the same season could reduce diversity.
The range of fire intensities is too narrow.	Estimates of the dominant intensity over the past 10 years of each fire based on fuel consumption and tree scorch height.	Intense fires a major cause of tree mortality. Possibly important for germination of soil-stored seed.
The extent of fires in any year should be within reasonable limits.	Proportion of area burnt in the past 12 months	Lack of fire over large areas allows too much of the grass sward to become moribund. Extensive fires in the same year reduces refuge, forage during droughts, habitats for certain species.
Extremes in fire size distribution may lead to undesired effects	Size of individual fires over the past 10 years.	Smaller fires tend to concentrate herbivores. Very large fires may affect dispersal or colonization opportunities.
Cause of fires.	Recording of cause of fire.	No biological significance?

biodiversity and suggestions for thresholds of potential concern

Thresholds of potential concern (TPCs)	Rationale
Shifts in median fire return period; range of post-fire age for the 20% of the area with the greatest post-fire age; and the maximum post-fire age (see Fig. 1).	Correction of trends towards extremes in fire frequency.
Proportion of the area burnt in each month should not exceed limits in Fig. 2.	Risk of failure of rains can be more accurately predicted as season progresses.
Ratio of area burnt in winter/early spring to that burnt in late spring/summer should be between 2.25:1 and 1.75:1.	Biota adapted to dry season fires, but occasional early wet season/summer fires needed to enhance diversity.
The proportion of high, moderate and low intensity fires to be in the range of one quarter to half of all area burnt.	A range of intensities will promote diversity.
Calculate desired thresholds from grass biomass at the start of the fire season (see Fig. 3). TPC is reached if the area burned is above the upper limit or below the lower limit.	Fire occurrence should be kept within appropriate limits to provide a mix of habitats, and to prevent either excessive bush encroachment or deterioration of the grass sward.
Dominance of either large or small fires (Fig. 4).	A range of fire sizes promotes diversity.
Unplanned fires of human origin should not exceed 25% of all fires.	Exceeding this limit indicates lack of management ability to control or direct fire regime appropriately.

National Park over the past 56 years (Van Wilgen *et al. in press*) has given some indication of the outcomes that should result from prescribed burning on fixed rotations, or from lightning fire (although the latter has not been implemented for long enough to draw confident conclusions). The patch mosaic system has been implemented at the Pilanesberg National Park for 9 years, and the outcomes in Table 1 are based on experience there. The approach of using ecological criteria has not been implemented, making the estimates of outcomes speculative at this stage. However, it has been suggested (based on a retrospective assessment, Trollope *et al.* 1996b) that the frequency of burning in the Kruger National Park would have decreased by "over half" if burning had been conducted according to veld condition based on key grass species (Trollope 1990).

Thresholds of potential concern

Definition

The change in fire policy has accentuated the need for monitoring systems to identify any effects on biodiversity which may approach what have been termed "thresholds of potential concern" (TPCs). These have been defined as "those upper and lower levels along a continuum of change in a selected environmental indicator which, when reached, prompts an assessment of the causes which led to such an extent of change, and results in either (a) management action to moderate such causes, or (b) re-calibration of the threshold to a more realistic or meaningful level" (Anon 1997). Such thresholds are being defined for a wide range of biotic and abiotic ecosystem descriptors, and will underpin a comprehensive monitoring system in the park.

Because of the complexity involved in measuring biodiversity (e.g. Noss 1990), an approach of using surrogate measures is proposed here. Surrogate measures would track changes in measurable components of the ecosystem, and identify thresholds of potential concern in terms of impact on biodiversity. While biodiversity in all of its forms is complex to measure or monitor, the progress of a fire management plan towards stated goals will be easier to monitor. This approach has been proposed for fynbos ecosystems (Van Wilgen *et al.* 1994), and could be applied in savanna ecosystems as well.

Using the fire regime to define thresholds of potential concern

The term fire regime is used to describe the combination of frequency, season and intensity of fires that characterise a particular area. Fire frequency is the reciprocal of the time between fires. Season refers to the time of year that fires occur, particularly in relation to the growth state of plants. Fire intensity is a measure of energy release in fires, which varies (in similar fuel complexes) with the moisture, wind and slope conditions under which the fire burns. Fire type (sometimes regarded as an additional element of the fire regime) will also affect fire intensity. Fire type distinguishes between headfires (fires burning with the wind or upslope) and backfires (fires burning against the wind, or downslope), as well as between ground fire (fires burning in organic layers of the soil), surface fires (fires in the lower vegetation strata) and crown fires (fires in the canopies of trees). For practical purposes, savanna fires are all surface fires, burning in the grass layers below the trees, but they vary as head or backfires. The size and spatial arrangement of fires is another important aspect that should be considered, as it has ecological implications. Ignition sources are not seen as being significant elements of the fire regime in themselves, although some patterns of frequency and season may be associated with certain sources of ignition.

None of the above measures is a constant; they vary at the same place in or between successive fires. Such variation is important in maintaining biodiversity and the co-existence of species (Van Wilgen *et al.* 1994; Yeaton & Bond 1991). The mean, and the distribution around the mean, for the frequency, season, intensity and size of fires in an area would be needed to provide a complete picture of a fire regime. This distribution, rather than a fixed value for each measure, would constitute the surrogate measure of biodiversity that could serve as a goal for fire management programmes. Limits to this distribution, that would signal the potential elimination of any species from the community (or undesirable shifts in community structure) would constitute thresholds of potential concern. The various potential TPCs (Table 2) are discussed below.

Fire frequency

A long-term assessment of fire frequency can be obtained from a curve of fire probability, derived from successive fire records for an area (see Van Wilgen *et al.*, *in press*). Shifts in the shape of this curve (Fig. 1) will indicate either an increase or decrease in the mean, median and maximum fire return period. Thresholds for acceptable limits for both of these variables will differ for the different landscapes of the park, and will need to be set for such landscapes. In addition, these curves can indicate whether or not an acceptable degree of variation is being achieved with regard to fire frequency. Here, targets

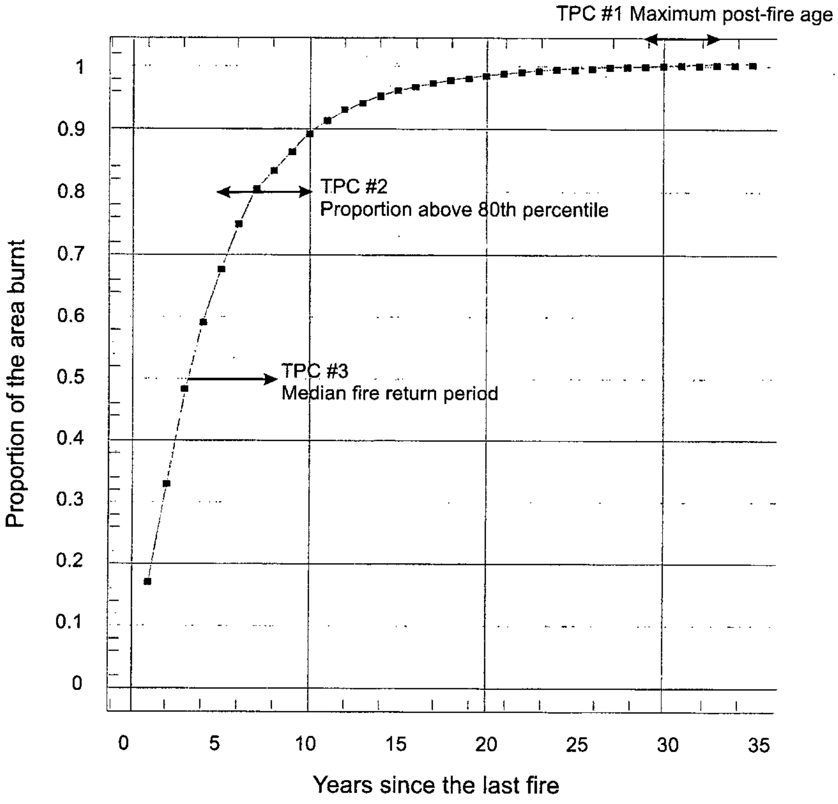

Fig. 1. The cumulative probability of fire, showing proposed thresholds of potential concern relating to the pattern over the 30 years prior to evaluation.

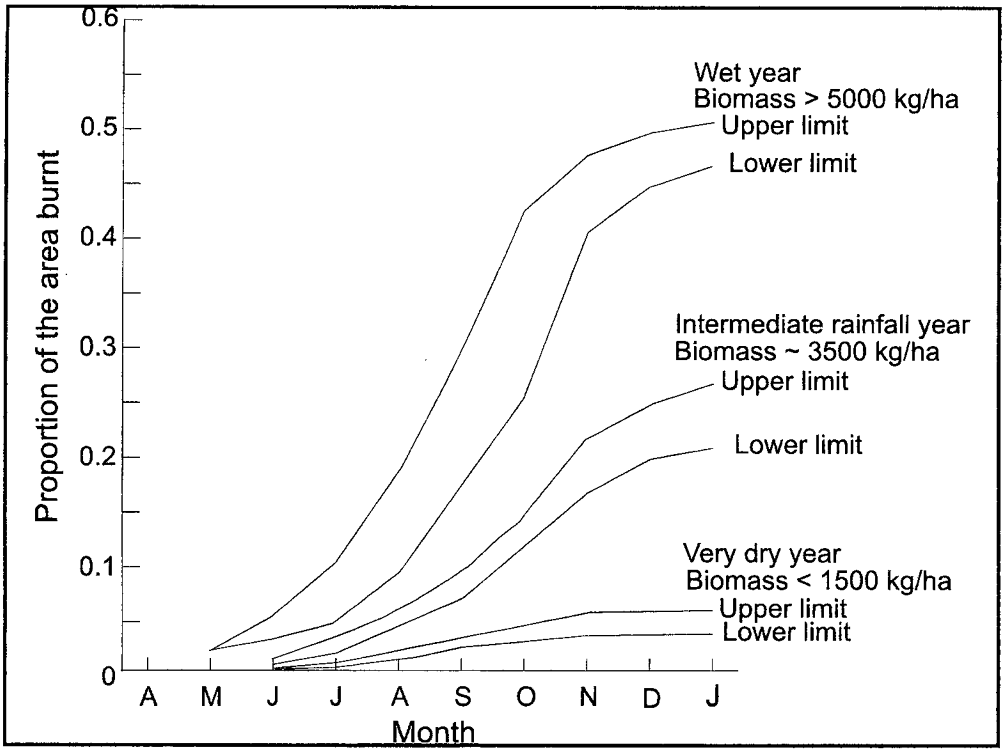

Fig. 2. Proposed thresholds of potential concern relating to the cumulative area burnt per month within a single fire season.

can be set for the proportion of the area that escapes fire for longer than a given time (which again should vary between landscapes). For example, small proportions of any area may need to escape fire for longer periods so that trees can establish, or switch from fire-suppressed "Gullivers" (Bond & Van Wilgen 1996) to trees of large stature.

Burning, drought, and forage availability

Fire followed by drought can lead to shortages of forage for grazing animals, where the consequences can be severe if burnt areas are extensive. For this reason, managers may be concerned if extensive areas are burnt early in the fire season, when the likelihood of drought is less predictable. Thresholds of potential concern can be defined in terms of time to the onset of the rain season, and can be made to vary according to grass biomass. Grass biomass, which results from rainfall in preceding years, is used in both the patch mosaic and the ecological criteria approaches to set targets for burning. Monthly thresholds with regard to progress towards these targets should be set (Fig. 2) to allow managers to continually assess the risk of drought, and to allow them to intervene (for example, by suppressing unplanned fires, or halting further ignition) if such risks are high.

Fire season

Targets can be set for the ratio of area burnt in late winter/early spring (August, September and October) to that burnt in late spring/summer (November, December and January). This ratio should be in the range of 2.25:1 to 1.75:1. This proportion is based on historic patterns of fire in the park (which were 2.25:1, Van Wilgen *et al. in press*), and allows for a shift towards later fires. The rationale behind this is that (i) the major proportion of the area burns in the dry season, when plants are dormant and adapted to survive fires, and (ii) that occasional early wet season or summer fires occur which, while detrimental to some species, will favour others through reduced competition after fire. The allowance for a proportion of fires to take place outside of the dry season is included to encourage a shift towards the late fires that would have made up part of a lightning-driven fire regime (Trollope 1993; Van Wilgen *et al. in press*).

Fire intensity

Most wildland fires would have burned under a range of intensities if they were ignited as point fires. They would have spread in all directions, thus burning as head, back and flank fires, and they would have burned both during the day (under hot, dry conditions) and at night (under cool, moist conditions), producing a range of intensities. Fire intensity plays a large role in the selective survival and recovery of species after a fire, and a range of intensities will therefore enhance co-existence of species and hence diversity. For each fire, the proportion that burns in low, moderate, and high intensity fires should be established. When the area burnt in any one of these classes is less than one quarter or more than half of the total area, then a TPC would have been reached. These thresholds are proposed to provide a range of intensities, which in turn should promote diversity. While it could be expected that headfires burning with the wind would always cover a larger proportion of any area burnt, the lowveld climate is not characterised by high windspeeds. This effect would therefore be limited, and 50% of the area could be seen as a reasonable threshold.

The extent of fires in any year

The extent of fires that can occur in any year is a function of grass biomass. Grass biomass is used to determine the extent of fire in two of the three proposed management approaches, and will in any case affect the area burnt if other approaches are followed. If the area burnt in any given year is small, concerns about deterioration of the grass sward in remaining unburnt areas (in terms of grazing value) may arise. On the other hand, if large areas burn in a single year, concerns around available habitat for certain species may arise. We suggest that thresholds be developed for different landscapes in the park, based on current grass biomass, to cater for the above concerns (Fig. 3). The management response will also be influenced if thresholds relating to long-term patterns of fire frequency are reached (Fig. 1). These may lead to alteration of annual targets in area burnt to adjust for long-term trends.

Fire size distribution

A distribution of fire sizes would be of interest to managers for a number of reasons. Too

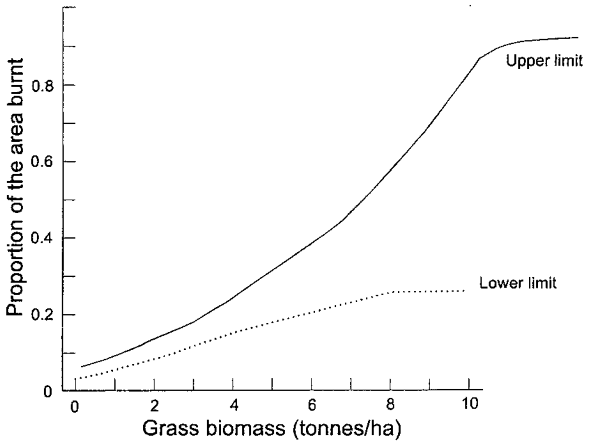

Fig. 3. Proposed thresholds of potential concern with regard to the area burnt within the current fire season, based on the amount of grass biomass at the beginning of the fire season (May).

many small fires could be of concern as herbivores would tend to concentrate on such areas, with possible detrimental effects. Very large fires, on the other hand, may impact on forage availability, even for highly mobile and wide-ranging animal species. Fire size distributions could be monitored against known patterns of distribution from past surveys, and any tendency towards extremes should trigger concern (Fig. 4).

The cause of fires

Although the cause of a fire has no ecological significance, it will be of concern if unplanned fires burn more than a certain percentage of the area burnt in all fires. It is suggested that this threshold be set at 25%. Exceeding this will indicate that managers are not achieving sufficient control over the fire regime to allow it to accomplish the desired effects (regardless of which approach is being followed).

Procedure to be followed

Under the different management approaches suggested for the Kruger National Park, many fires will not be confined to management blocks, but will be allowed to burn freely. Once any fire has burnt out, it's extent should be mapped at a scale of 1:50 000 and captured on a geographical information system (GIS), together with relevant information on the fire. The relevant information should include:

(i) the date(s) of the fire;

(ii) the cause, divided into lightning, prescribed burns (including firebreak burns), fires that enter the park from outside, escaped fires from burning operations, fires caused by unauthorised people (for example poachers or illegal immigrants), other known causes (to be specified), or fires of unknown cause;

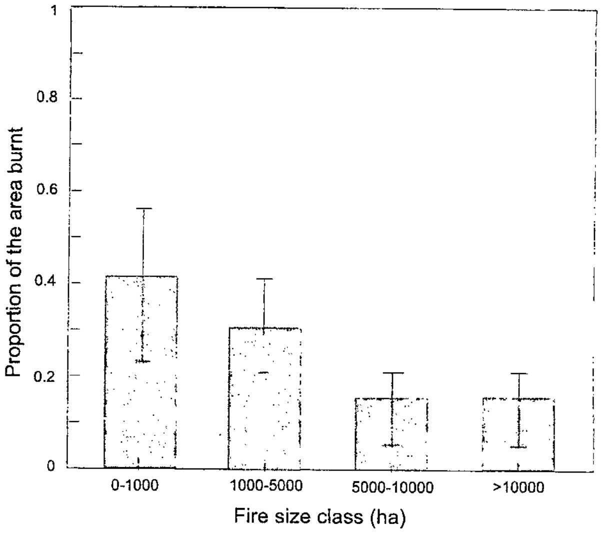

Fig 4. Thresholds of potential concern relating to the distribution of fires of different sizes over the 10 years prior to evaluation.

(iii) an estimate of the range of intensities of the fire (high, moderate or low), based on the efficiency of fuel consumption and tree scorch heights in the burnt areas (the estimates should state what proportion of the burnt area fell into each of these categories); and

(iv) an estimate of the percentage of the vegetation that remained unburnt within the area recorded. This estimate is needed to allow for the fact that many fires are very patchy, leaving "islands" of unburnt vegetation behind. If relatively large areas within a fire area did not burn, they should (as far as possible) be excluded from the area mapped as having burnt.

The GIS-based databases should be updated annually, by the end of February each year. At this stage, the long-term indices relating to fire frequency, seasonal distribution, the range of intensities, and the size distribution can be updated and examined to establish whether any thresholds of potential concern have been reached. If this is the case, then appropriate adjustments can be made to the annual burning targets to correct these trends. Once this has been done, all fires that occur as the year progresses should be mapped, and compared monthly to the thresholds relating to drought risk, extent of burn, and cause of fires. Again, if thresholds are reached, changes can be made to the annual targets for the year.

It is also important that data collected as part of other monitoring exercises be assessed against the background of a good database of fire occurrence. Monitoring data are notoriously unhelpful in showing the causes of recorded changes, and the fire records may help to address this problem by providing a causal backdrop. If thresholds are detected in any of these biological criteria (which includes information on veld condition, woody plant structure and composition, a range of animal populations, soils and erosion), then they should be related to the fire data in order to determine whether the threshold can be related to the occurrence and effects of fire.

Discussion

Appropriate goals for management

Management is goal-oriented, and in the past managers in the Kruger National Park have used fire to drive the system towards a desired stable state (Rogers 1997). With the more recent recognition that savanna systems are extremely dynamic and usually in a state of flux, goals need to change towards those that describe desired ranges of flux rather than fixed states. Fire, herbivory and cycles in rainfall are the major disturbances responsible for the dynamics of savannas; of these, fire and herbivory are the two that can be influenced by managers. Because of a history of stable-state thinking, ideas around "appropriate" fire regimes tended to descriptions of fixed return periods and seasons. The new goals of maintaining biodiversity "in all its facets and fluxes" will require fire management goals to be framed in terms of a range of return periods and seasons (where fire is being used as a surrogate measure for assessing the ultimate goal of biodiversity), or in a range of vegetation states (where fire is being used in an attempt to achieve such states). The former applies to the lightning and patch mosaic burning approaches, and the latter to the ecological criteria approach.

We have made some suggestions as to the descriptors of the fire regime that could serve as surrogate goals. Managers will have to agree on acceptable thresholds for these descriptors, and this process would have to be followed for each of the major landscapes of the park, as these differ significantly in their susceptibility and response to fire. The same applies if an approach based on ecological criteria is followed, except that the range of descriptors will have to be framed in terms of a distribution of vegetation structure and composition over space and time. We envisage that such distributions would provide for large proportions of certain types (for example grass swards dominated by decreaser grasses, and a representative distribution of size classes amongst tree species), but that there would be "tails" of smaller proportions of moribund, overgrazed, bush-encroached or treeless areas. Although these are undesirable in an agricultural sense, they could be acceptable in the interests of maintaining diversity in conservation areas.

While attempting to simulate natural processes, and allowing them to operate unchanged from historic conditions is obviously a primary goal of management in a National Park, there can, and should, be exceptions. Rare species (such as black rhino, roan antelope, or Pel's fishing owl, for example) could merit special intervention. Where these species' habitat requirements call for regular burning or protection from fire, and where their population levels call for special action to prevent local or even global extinction, then deviations from the general approach to fire management may be appropriate in some areas.

Dealing with uncertainty

The above attempt at predicting the outcomes of different fire management approaches (Table 1) has illustrated the difficulties in quantifying their outcomes in terms of the spatial and temporal patterns they will generate. Although each approach arises from a different philosophy (Table 1), they may, in reality, not differ in the physical fire patterns that they produce. The likelihood of this is increased by the fact that each approach will be affected to some degree by unplanned fires. Another source of uncertainty is that ecologists cannot accurately predict the biological consequences of these patterns on all elements of the biota. Despite the importance of fire in the dynamics of savanna ecosystems, demographic studies of savanna trees and grasses have been neglected (Bond & Van Wilgen 1996; Scholes 1997). In fact, for many years, ecologists working in savannas did not regard them as a separate biome—rather savannas were viewed as a special case of grassland or forest (Scholes & Walker 1993). Pasture scientists studied the grasses, and dealt with problems of "bush encroachment" (e.g. Trollope 1982); foresters dealt with tree species for timber production (e.g. Geldenhuys 1977). More recent studies have concentrated on determinants of savannas, such as water, herbivory and nutrients (see Scholes & Walker 1993, Solbrig *et al.* 1996 for reviews). Despite the huge advances that have been made in understanding the determinants of savannas, therefore, we are poorly equipped to predict the impacts of fires, in combination with other factors, even on key plant and animal species. The recent recognition that savanna ecosystems cannot be managed to remain in a desired state, but rather tend to be in constant flux, further reduces the scope for predictive ecology.

If ecologists are to have an influence on the direction of conservation management, appropriate responses to the lack of predictive ability must be developed. It should be recognised that conservation management is goal-orientated, and managers seek to manipulate (either passively or actively) the forces that alter the nature of the landscape mosaic (e.g. Rogers 1997). In the case of fire management in the Kruger National Park, the goal is to conserve biodiversity through the application of an appropriate fire regime. Because of the difficulties inherent in predicting the effects of fire on all facets of biodiversity, we can use fire patterns as surrogate measures of biodiversity. For argument's sake, if we postulate that each of the three candidate systems will be able to conserve biodiversity equally well, this must be tested by monitoring both the fire patterns that establish themselves (the surrogate measures), and the responses of various plant and animal populations. Each of the biotic elements that are being monitored have their own TPCs, and should any of these thresholds be reached, then an assessment of the causes that led to such change will be prompted. Provided that fire patterns are also monitored, the changes can be interpreted against the background of a known fire history. This may lead to either a change in fire management approach, or the initiation of a research project to develop further understanding of the response (a "response research framework", Rogers 1997), or both. In the meantime, the fire patterns themselves form goals against which managers can assess progress towards the goal of conservation of diversity.

The future of fire research in the Kruger National Park

The change in approach to fire management offers the opportunity to review the research programme that was designed to support it. The original fire experiment (van der Schijff 1958) has not provided answers to the problems facing managers today. With hindsight, the experiment was flawed principally because the plots were too small to exclude impacts of artificially high levels of herbivory, and no allowance was made for variable fire frequencies. In view of the large proportion of research resources that would be needed to maintain the experiment, and the limited prospects for efficient and useful returns, it would seem sensible to terminate this experiment after an analysis of the data collected to date.

It has been accepted that the lightning fire approach should be implemented over the majority of the park, with the exception of smaller areas where the other two approaches will be implemented on an experimental basis. This would provide the focus for future fire research activities. The fire patterns that emerge, and the effects of these on the biota, should be monitored and used to identify priorities for experimental research. In addition, they should also underpin an active process of assessment and review of the approaches themselves. The outcomes should continually be assessed against TPCs, which may result in the abandonment of any of the approaches. The conditions that could lead to any approach being discontinued include:

(i) If it becomes clear that the outcomes, in terms of the fire patterns that establish themselves, cannot be separated from those produced by any other approach;

(ii) If any approach results in thresholds of concern being reached for populations of plant or animal species (especially rare species), which can be shown to be a result of fire; and

(iii) If any approach cannot be practically implemented, for example due to the costs involved, or because unscheduled fires become the dominant source of ignition.

The monitoring and interpretation of fire patterns, and decisions on the continuation or not of any approach, is a clear function of management. In the past, the curation and maintenance of fire records has been a research function of the Scientific Services branch within the park. While this may have been appropriate at the time, advances in computer technology have resulted in powerful tools being available to managers (Richardson *et al.* 1994). This fact, combined with the advantages associated with a sense of ownership and empowerment that accompanies the transfer of such a function, are strong arguments for the park's managers to assume the responsibility for monitoring and interpreting fire data. The research role can be to design monitoring systems (as described here), assist in the interpretation when TPCs are reached, and to initiate investigations where further understanding is required.

Conclusion

The thresholds of potential concern outlined in this paper are descriptive and preliminary. They are intended to illustrate the principle of using elements of the fire regime as surrogate measures and management goals, and will require refinement. This will both be necessary to make them applicable to the wide range of land types within the Kruger National Park, and to ensure their continual improvement. Reassessment and improvement are embodied in the concept of TPCs, and they will provide a focus for debate around changes and improvements to the management approaches with regard to fire. Managers in the Kruger National Park are able to build on one of the most comprehensive fire records for any ecosystem anywhere in the world (Van Wilgen *et al. in press*), and this provides a unique challenge of building appropriate management systems based on this excellent set of information.

Acknowledgements

BvW thanks the CSIR Division of Water, Environment and Forestry Technology, and South African National Parks for supporting this work.

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Third paper: A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. *South African Journal of Science*.

A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996

B.W. van Wilgen[a], H.C. Biggs[b], S.P. O'Regan[c] and N. Marè[b]

This paper analyses the fire history of the Kruger National Park (1.9 million ha), South Africa, for different periods in the park's history, where fire protection was followed by prescribed burning and then a 'natural' (lightning) fire policy. Fires covering 16.79 million ha occurred between 1941 and 1996 (16% of the area burning each year on average). Of this area, 5.15 million ha was burnt between 1941 and 1957, when limited prescribed burning and protection from fire took place (16% burning each year on average). Between 1957 and 1991, 2213 prescribed burns covering 5.1 million ha (46.3% of the 10.98 million ha burnt during that period) were carried out. Lightning fires affected 2.5 million ha between 1957 and 1996, or 21.6% of the area. The mean fire return period was 4.5 years, with intervals between fires from 1 to 34 years. The distribution around the mean was not symmetrical and the median fire interval was 3.1 years. Some areas burnt more often than others, and mean fire return periods ranged from 2.7 to 7.1 years in the 11 major land systems of the park. Fires occurred in all months, but 59% of them took place from September to November. Prescribed burns were concentrated late in the dry season (September to November). Lightning fires were later, with 84.7% of the area burning between September and January. The implications of the analysis for the management of the park are discussed.

Savannas are tropical grasslands with scattered trees; they occupy about 20% of the land surface of the Earth, and 40% of Africa. These ecosystems are dynamic in their structure and composition, which changes in response to fluctuations in rainfall, levels of herbivory and occasional fires that burn through the grass swards. The role of fire in the maintenance of structure and function in African savannas is probably the oldest issue in savanna ecology[1] and remains contentious. In conservation areas, where early ideas were formed around equilibrium theory, fire was regarded first as something to be avoided, and was later applied at a fixed return period, when it was realized that fire was an integral part of the system. However, with the development of non-equilibrium theories of savanna dynamics, policy and practice in fire management have shifted towards burning under diverse rather than fixed conditions.[2,3]

Fire management in the Kruger National Park has followed a similar trend. After the proclamation of the park in 1926, occasional and limited burning was used until 1948 only to provide green grazing for wildlife. Between 1948 and 1956, prescribed burning was stopped and firebreaks were established to assist in the control of wildfires. This policy was changed in 1957 to a formal system of burning once every three years in spring on fixed management areas (termed 'blocks') ranging in size from 50 to 20 000 ha. In 1975, this policy was amended to allow for longer periods between fires in drier areas, with the season of burn varied between late winter, mid-summer and autumn.[4] In 1992, the policy was again changed to one of allowing natural (lighting-ignited) fires to burn freely, but where prescribed burning would not be carried out, and all other fires of human origin were suppressed. For the sake of analysis, we recognized three periods in this paper. The period prior to 1956 was one of protection from fire, from 1957 to 1991, prescribed burning was actively practised, and from 1992 only lightning fires were permitted to burn.

The shift away from rigid prescribed burning on a fixed cycle was in response to several recent concerns. For example, Trollope and co-workers[5] concluded that a dominance of grass species characteristic of poorly managed pastures and overgrazing was a result of 'excessively frequent burning'. In addition, there was concern over putative trends in woody vegetation structure.[6] It appears (for example, from examining early aerial photographs) that large areas have been homogenized, possibly due to the rigid application of a policy of burning at three-year intervals. Tree densities have declined, greatly for some species, and this decline may be due to an 'unnatural' fire regime (in combination with other factors, such as browsing by ever-increasing numbers of elephants). In a revision of the research objectives for the park, developing an understanding of the attributes of natural fire regimes has been identified as a priority.

The Kruger National Park has a comprehensive set of fire records spanning five decades. These data have only partially been analysed. For example, the records for fires between 1980 and 1993 showed that most (90%) fires were of human origin, while lightning fires affected only 10% of the park. Lightning fires, however, took place in spring and summer (September to February), whereas other fires were predominantly in late winter and spring (June to October).[7] While that analysis is useful, the available records span a much longer period and can also be evaluated spatially to provide information about the historical influences of fire on vegetation patterns and trends in the park.

This study reports on an analysis of fire patterns in the Kruger National Park based on fire records that date back to 1941, to quantify the nature of the fire regime that existed during the period of formal management. This record is probably the longest fire history for any savanna ecosystem in the world, and provides an important benchmark for interpreting the changes in vegetation structure that have taken place.

The study area

The Kruger National Park is situated in the low-lying savannas of the eastern parts of the Northern and Mpumalanga provinces of South Africa, adjacent to Mozambique in the east and Zimbabwe in the north (Fig. 1). The park was established in 1926, and covers 1 948 528 ha. Elevations range from 260 to 839 m

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above sea level. Mean annual rainfall varies from around 750 mm in the south to approximately 350 mm in the north (Fig. 2), but variations about the mean can be marked from year to year (Fig. 3).[8] The pattern of rainfall over the past century has been characterized by extended wet and dry periods, in which the rainfall tended to be either higher or lower than the long-term mean for between 6 and 12 consecutive years (Table 1).[9] These wet and dry periods have marked effects on the dynamics of the ecosystem, and on the occurrence of fires.

The park is crossed by seven perennial or seasonal rivers (the Crocodile, Sabie, Olifants, Letaba, Shingwidzi, Luvuvhu and Limpopo), which run from west to east. Geologically, the park can be divided into western and eastern halves. In the west, granites and their erosion products dominate, while the eastern sector is predominantly underlain by basalt, but includes the Lebombo Hills (primarily rhyolite formations) running from north to south. Two important areas of sandveld (on recent sands) also occur in the north, around Punda Maria and Pafuri.

Several studies have sought to classify the landscapes and vegetation formations of the park. One such study has divided the park into 35 'landscapes' based on geomorphology and vegetation.[10] Another subdivided the park into 56 'land types' on the basis of soil and vegetation patterns and landform characteristics.[11] These land types were combined into 11 'land systems' on the basis of geological, geomorphological and climatic characteristics. The boundaries of these divisions have been captured on a geographic information system (GIS) and provided a framework for the examination of fire regimes in this study.

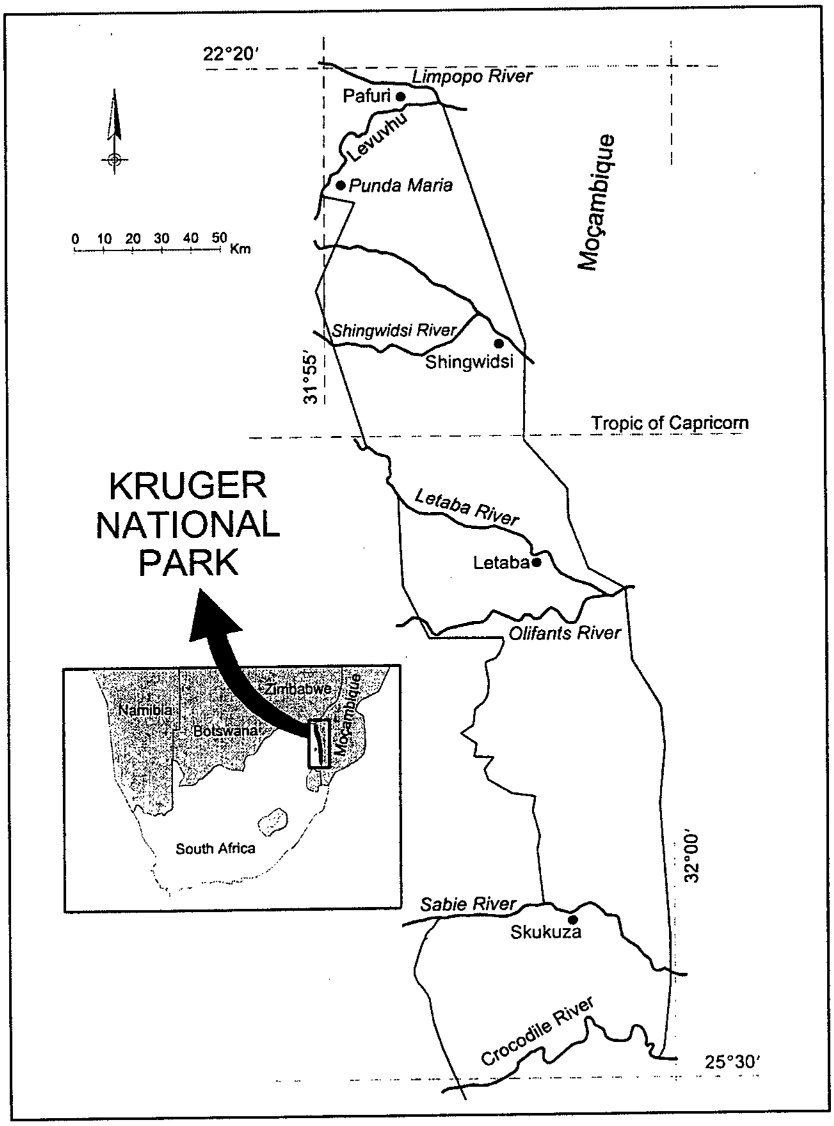

Fig. 1. Map of South Africa showing the location and topographical features of the Kruger National Park.

The flora of the park comprises 1983 species (N. Zambatis, pers. comm.), including over 400 tree and shrub species,[12] and over 220 grasses. Broadly speaking, there are four dominant vegetation types in the park. In the southwest, the low nutrient status of the soils results in a relatively low grazing pressure, and grass fuels accumulate during the growing season; rainfall is also higher, and as a result of these factors fires tend to be relatively frequent in these areas. The area is well wooded, and important tree species include the red bushwillow *(Combretum apiculatum)*, knobthorn *(Acacia nigrescens)*, tamboti *(Spirostachys africana)* and marula *(Sclerocarya birrea)*. In the southeast, on basalt substrates, grasses are more palatable and tend to be heavily grazed. Important tree species include the knobthorn, leadwood *(Combretum imberbe)* and marula. North of the Olifants River, the granite areas in the west are poorly grassed; mopane *(Colophospermum mopane)* and red bushwillow are dominant trees. The northeastern areas on basalt are dominated by multi-stemmed mopane shrubs about 1 to 2 m in height.

The fauna of the park is also diverse, including 147 species of mammals[13] and 492 species of birds.[14] Important herbivores include elephant *(Loxodonta africana)*, buffalo *(Syncerus caffer)*, impala *(Aepyceros melampus)*, zebra *(Equus burchelli)*, wildebeest *(Connochaetes taurinus)*, waterbuck *(Kobus ellipsiprymnus)*, kudu *(Tragelaphus strepsiceros)*, giraffe *(Giraffa camelopardalis)*, white and black rhinoceros *(Ceratotherium simum* and *Diceros bicornis)* and hippopotamus *(Hippopotamus amphibius)*. Herbivory, particularly by grazers, has an important influence on fires through the consumption of grass fuels. In addition, browsing (particularly by elephants) has a strong impact on subsequent tree mortality after fires.

The fire record

Fires in the Kruger National Park were traditionally recorded in ranger's diaries prior to the introduction of a programme of prescribed burning in 1957. When prescribed burning was introduced, the park was subdivided into over 400 management areas, or 'blocks', ranging in size from 50 to 23 800 ha (mean = 4198 ha, Fig. 4). The boundaries of the 453 blocks that existed at

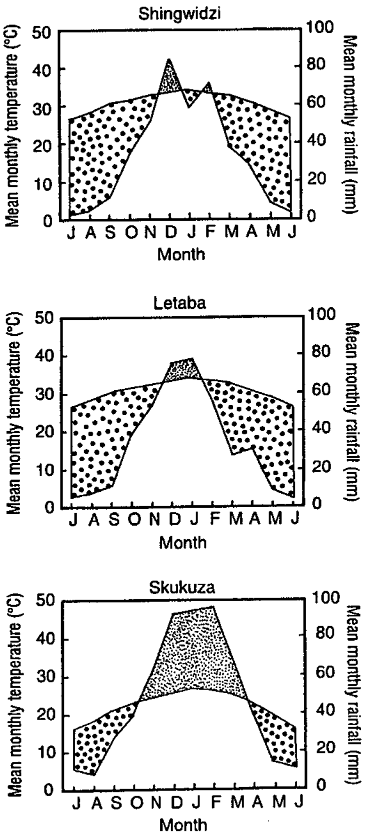

Fig. 2. Climate diagrams for three locations in the Kruger National Park (see Fig. 1 for the localities of stations).

the time of this study were captured on a GIS, and formed the basis of our analysis. The fire records for different periods were in three formats, as follows:

(i) Sketch maps of the distribution of fires for each year from 1941 to 1956, available from a previous analysis of ranger's diaries.[15] These were digitized, and overlaid on the boundaries of existing fire blocks to establish the percentage of the block that was burnt in each year. These fires were recorded at a coarse scale (1:500 000), resulting in partially burnt blocks only providing a crude estimate of percentage burnt.

(ii) The board controlling the park took a decision to institute prescribed burning in fixed blocks on a three-year cycle in 1957.[15] Fire records for each of these blocks, giving the dates and causes of fires, and in some cases an estimate of the percentage of the block that burned, were available from 1957 to 1991. These records were extracted from the management files for each block.

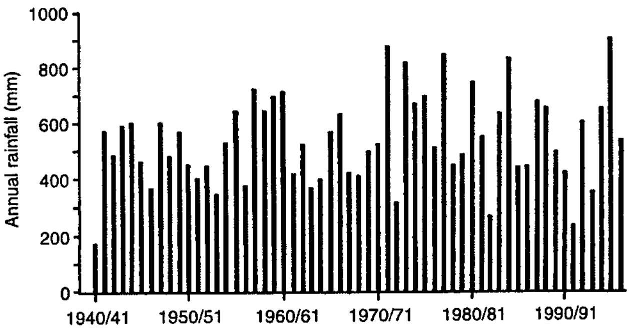

Fig. 3. Total annual rainfall at Skukuza, Kruger National Park, between 1940/41 and 1996/97. Data are for climatic years (1 July to 30 June).

(iii) As from 1992, all prescribed burns were stopped. Natural (lightning) fires were allowed to burn in line with a management policy, although other fires did occur. These fires were mapped (using fire reports and satellite images to establish boundaries on 1:50 000 topographical maps) and added to the database by allocating a date, percentage burnt, and cause of each fire to the existing fire management blocks.

Between 1957 and 1988, numerous adjustments were made to the boundaries of blocks. We established the extent and dates of these changes by comparing older maps to the existing set of blocks. Where necessary, fire records were re-allocated to the existing blocks by assigning the date of the fire and its cause, together with an estimate of the percentage of the existing block that would have burnt in that fire.

The cause of fires was recorded in seven categories: prescribed fires (where the whole block was intentionally burnt); firebreak fires (where the boundaries of the block were ignited under conditions where the fire would not progress very far, with the intention of creating a buffer strip — we refer to these strips as 'firebreaks' throughout); fires caused by lighting; escape fires (where prescribed or firebreak fires unintentionally spread to the block concerned, or where any fires originating outside the park burnt a block inside the park); other fires of human origin (poachers or trans-border migrants being the most common causes); other fires of known cause; and fires of unknown origin.

The fire record consisted of 5512 individual burns between 1957 and 1992, that burnt an area of 10.97 million ha. The total number of fires between 1941 and 1956 is not known (only the annual extent of fires was available), but during this period burnt 5.15 million ha. The period between 1992 and 1996 was initially characterized by a severe drought, and not many fires occurred. However, extensive lightning fires occurred in 1996, following good rains in 1995, burning 359 424 (50.4%) of the 712 055 ha burnt between 1992 and 1996.

Table 1. Cyclical patterns of rainfall from available recording stations in the Kruger National Park, showing the extent and duration of wet and dry periods between 1919/20 and 1992/93.[9] The mean annual rainfall for all stations was 534.2 mm.

Dates	Number of recording stations	Length of period (years)	Type of period	Mean rainfall for period (mm)
1919/20–1924/25	1–2	6	Wet	650.2
1925/26–1935/36	3–7	10	Dry	462.3
1936/37–1942/43	8–11	6	Wet	590.1
1943/44–1952/53	9	9	Dry	510.6
1953/54–1960/61	9–14	7	Wet	586.4
1961/62–1970/71	14–17	9	Dry	457.5
1971/72–1981/82	17–19	10	Wet	638.7
1982/83–1994/94	19–27	12	Dry	450.0
1994/95–1996/97	29–34	2	Wet?	560.7

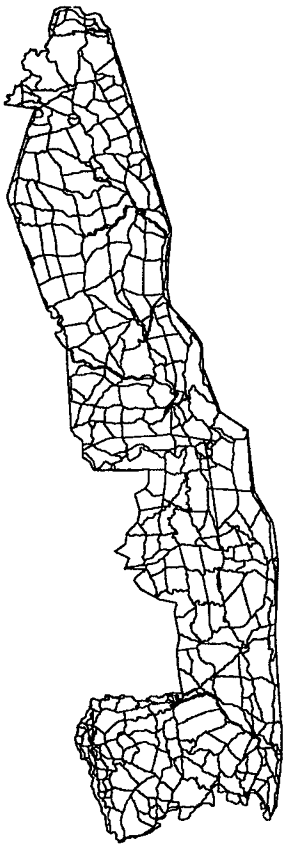

Fig. 4. Distribution of management units ('blocks') which formed the basis for a spatial analysis of fire regimes in the Kruger National Park. See Fig. 1 for scale.

Data analysis

Estimation of percentage of block burnt

The 1137 records for individual fires between 1980 to 1993 were complete in terms of estimates of the percentage area of the blocks that burnt.[7] Many (60%) of the fire records from 1957 to 1979 did not have these estimates; however, the cause of fires was consistently recorded. To fill in missing values of percentage burn, we assumed that firebreak burns (743 of the 4375 records between 1957 and 1979) burnt 20% of the block concerned, based on the estimates for fires from this source (firebreak burns were usually ignited to create a fuel-break around the periphery of the block, under conditions that would normally cause the fire to die out at night). Where more than one firebreak burn occurred in a block in the same year, we assumed that the total area of all firebreak burns that year was 20%, and reduced the estimates for individual burns proportionally.

For those records where the percentage area of the block burnt was recorded (73% of the 5512 fires between 1957 and 1992), a clear annual trend was evident. This trend was significantly correlated with annual rainfall five years earlier (Fig. 5). We used this relationship to estimate percentage burn for the fires where this was not recorded, excluding the firebreak burns (where we assumed that 20% of the area of the block was burned). In order to obtain an estimate, we first subtracted the extent of firebreak burns that occurred before the burn in question in the same year from the area of the block. We then used the relationship to estimate the proportion of the remainder of the block that would have burnt. Where more than one non-firebreak burn occurred in a block in the same year, we assumed that the total area of all non-firebreak burns that year was equal to the estimate, and reduced the estimates for individual burns proportionally.

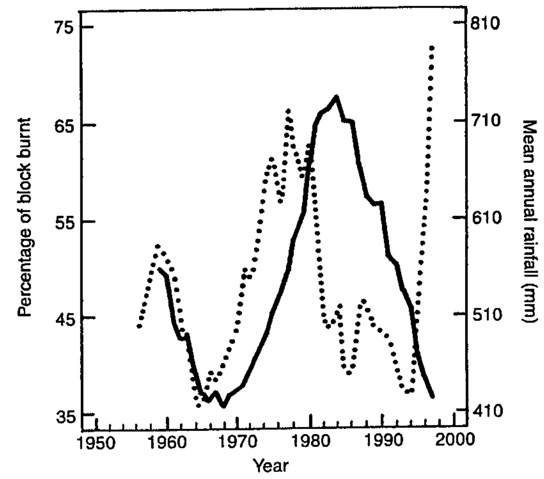

Fig. 5. Trends in percentage burn recorded in fires between 1957 and 1992 (5-year running mean, solid line), and annual rainfall (3-year running mean, dotted line). There is a significant relationship between percentage burn and annual rainfall five years before the fires ($y = 29.95$, $x = 0.034$, where y is the percentage of the block burnt and x is the annual rainfall five years prior to the burn; $r^2 = 0.17$, $P < 0.012$).

Frequency of fires

Fire frequency was examined in three ways. First, where we wished to test for significant differences in fire return periods between areas of interest, the mean return period was calculated as

$$RP = \frac{\left(\sum i_j a_j\right)}{\left(\sum n_j a_j\right)},$$

where RP is the return period in years, j is the number of blocks in the area of interest, i is the inter-fire period in years, a is the area of block j, and n is the number of inter-fire periods (the number of fires minus 1). Using this method, we were able to test for differences between areas using one-way analysis of variance.

Secondly, where return periods were determined for short intervals, cases arose where only one fire had occurred in some blocks in the period concerned (that is, there was no inter-fire period on record). This precluded the use of the above formula, and we used $RP = y/(b/a)$, where RP is the return period in years, y is the number of years over which fires were recorded, b is the extent of all fires recorded over y years, and a is the area over which fires were recorded. In this case, only one number is produced, and it is not possible to test for the significance of any differences.

Thirdly, we estimated the frequency distribution around the mean by determining the period between successive fires in each block. To do this, we divided each block into 10 equal sub-blocks, and randomly assigned sub-blocks as burnt or not in each year based on the percentage burnt (i.e., if 20% of a block had burnt, two randomly selected sub-blocks were designated as having burnt). A key assumption in doing this was that each subdivision of a block had an equal chance of burning; this assumption was the only way to deal with the data, as the exact location of each fire within blocks with incomplete burns was not known. These data were used to determine the distribution of periods between successive fires in each block. To determine the distribution for the whole area being examined, we totalled the periods for all blocks, weighted by area.

We used maps of the land systems[11] and of rainfall to examine patterns of fire frequency. The rainfall distribution was derived from a national database that models rainfall from existing recording stations and topographical factors at a resolution of one minute by one minute.[16] We also divided the data into different periods in order to determine the effects of climatic periods, and periods of differing management policies, on fire frequency.

Seasonality of fires

Seasonality of fires was examined monthly. The area burnt in each month was totalled for the area, time period, and cause. We used these data to establish whether seasonal differences in the proportion of area burnt varied between the land systems in the park, and between wet or dry periods. We also examined whether fires of different origin (particularly those started by lightning) differed in their seasonal occurrence.

Size of fires and extent of area burnt

The extent of fires was calculated from the area of the management blocks, and the estimates of the percentage of the block that burnt. These were then totalled for different landscapes, rainfall zones or time periods of interest (such as wet and dry climatic cycles, and periods of differing management policy). The estimation of the size of fires was constrained by the fact that fire records were kept for individual management blocks and not for individual fires. Thus, if a fire burnt over more than one block, this was not recorded. However, occurrences of the same fire burning in more than one block prior to 1992 were rare, as fires were almost always confined to a single block by effective backburning from the boundaries. For the fires that occurred after 1992, accurate maps of individual fires were available. We were able, in these cases, to estimate the areas of individual fires from these maps, using the areas of management blocks as a basis.

Fire climate

Climate and weather are important in determining the opportunities for fires to occur and spread, and together with fuel properties will affect their size and intensity. We obtained daily weather data from two representative weather stations in the park (Skukuza and Letaba, see Fig. 1) for the period 1981 to 1997, and used the U.S. National Fire Danger Rating System[17] to calculate daily indices of fire danger. The data used included daily maximum and minimum temperature and relative humidity, cloud cover, rainfall duration and wind speed, and an estimate of the fuel composition and structure (we used fuel model L). Results are expressed in terms of a 'burning index', which can be related to the spread and intensity of a fire under prevailing conditions.

Effect of fuel load on the occurrence of fire

Grass biomass (fuel) estimates were defined from one to four points per management block for approximately two-thirds of the blocks in the park from 1989 onwards. These points were distributed across the whole park and all land systems, and were taken to be representative of fuel loads throughout the block. The single point (or in the case of blocks with multiple sampling points, the mean) biomass per block was determined for each year from 1989 to 1996. The annual occurrence of fire (other than in firebreak burns) in blocks was recorded as a binary variable — burnt or not burnt. The probability of a fire of any size occurring in a block in a given year was then estimated as a function of biomass using logistic regression.[18]

Results

Fire frequency

The mean fire return period for the entire dataset was 4.5 years. However, the distribution around the mean was not symmetrical (Fig. 6), and the median fire interval was 3.1 years. This indicates a skewed distribution in the data, with many short-interval fires, but a few areas experiencing relatively long intervals between fires, thus increasing the mean interval between them. Fires that burnt within one year of a previous fire accounted for 16% of the area burnt over the past 56 years; a further 17% of the area burnt within 2 years of a previous fire, and another 16% within 3 years (Fig. 6). Thus, for more than half a century, about half the area burnt within 3 years of the previous fire. About 80% of the area burnt within 7 years of the previous fire, and a small proportion (about 10%) burnt 10 years or more after the previous fire. As can be expected in a large and diverse area, the spatial distribution of mean fire return periods varied spatially (Fig. 7).

Mean and median fire return periods ranged from 2.7 to 7.1, and 1.8 and 4.6 years, respectively, in the 11 major land systems of the park (Table 2) between 1941 and 1996. The range of intervals between fires for the different land systems was from 1 to between 30 and 40 years. Most land systems had mean fire return periods of between 4 and 5.8 years, and two (the Klipkoppies and Phalaborwa systems) had mean fire return periods of 6 years or more. The median fire return period was generally shorter than the mean, and was much less for the Malelane system (1.8 as opposed to 5.3 years). Few areas (less than 1% of the Malelane land system to 10% of the Klipkoppies land system) managed to escape fire for more than 15 years (Fig. 8).

Rainfall has a marked effect on the production of grass fuels, and therefore on fire return periods. This was evident for areas that receive a mean annual rainfall of over 700 mm (Table 3). Here, the mean return period was 3.5 years, compared with around 5.2 years for areas with annual rainfall between 400 and 700 mm. Fire returns were longer in dry periods (where grass productivity, and hence fuel loads, would have been low) than in wet (Table 4). For the 10 years between 1971 and 1980 (a wet cycle, see Table 1), the mean return period was 4.3 years over the whole of the park. Over a similar period between 1983 and 1992 (a dry cycle), the corresponding period was 9.1 years. Mean fire return periods were similar between 1941 and 1956, prior to prescribed burning, and between 1957 and 1992, when prescribed burning was actively practised (5.9 and 6.2 years, respectively, Table 4). It would appear, therefore, that attempts at protection from fire did little to reduce fire frequencies. With the adoption of a policy of lightning fire, indications are that the

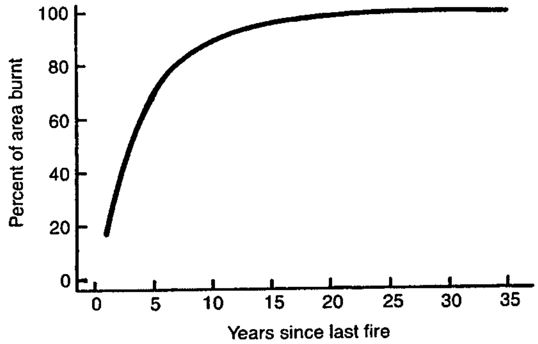

Fig. 6. The cumulative probability of fire in the Kruger National Park, calculated from fire records between 1941 and 1996.

mean fire return periods have become longer. Because this policy has only operated for 5 years, we compared the mean fire return periods between 1992 and 1996 (where prescribed burning was not carried out, and lightning fires were allowed to burn) with a period of equal length and similar rainfall (1981–85). The mean return period under the lightning fire policy was 13.3 years, more than double that in the prescribed burning era (6 years, Table 4). This indicates that, for dry periods at least, the new policy could lead to longer intervals between fires.

Fire season

Fires occurred in all months of the year for the period of analysis (1957 to 1996), but most of the area (80%) burnt in the months from June to November (Fig. 9). September, October and November had the largest proportions of area burnt (23, 21 and 15%, respectively). Firebreak burns were conducted earlier in the year, with most (70% of the area) being carried out between May and July. Prescribed burns, which accounted for 43.7% of the total area burnt (see below), were concentrated late in the dry season, with 66.5% of the prescription-burnt area being burnt in the months of September, October and November. Lightning fires tended to be later in the year, with 84.7% of the area attributed to this cause burning between September and January. Other fires (most of which were of human origin) followed the same seasonal pattern as prescribed burns (80% of the area burning from July to November).

The seasonal distribution of fires was examined for the period when the lightning fire policy was in operation (1992–96). Here, a total of 712 031 ha was burnt in 5 years (Table 4). These fires were

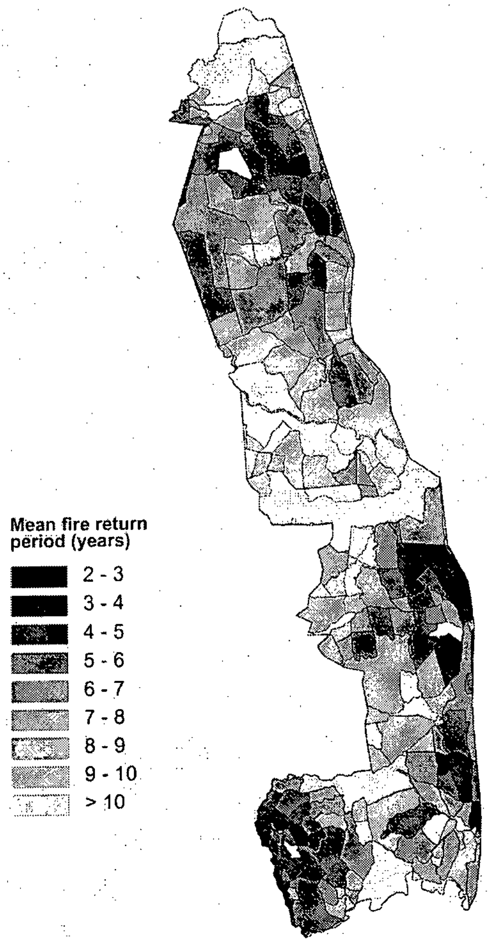

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Fig. 7. Map of the Kruger National Park showing mean fire return periods calculated from fire records between 1957 and 1996. See Fig. 1 for scale.

Table 2. Fire return periods in 11 land systems (after Venter[11]) in the Kruger National Park, South Africa, between 1941 and 1996. Means with the same superscript letter do not differ significantly at $P < 0.0005$.

Land system	Salient features	Area (km^2)	Extent of fires between 1941 and 1996 (km^2)	Fire return periods (years)		
				Mean	Median	Range
Malelane	*Combretum apiculatum* bush savanna on granite. Rainfall 600–700 mm/yr	400.3	5415	5.3^{ac}	1.8	1–34
Skukuza	*Combretum apiculatum/Terminalia sericea* bush savanna on granite. Rainfall 500–750 mm/yr	3742.6	35 496	4.2^{bd}	3.3	1–40
Satara	*Acacia nigrescens/Sclerocarya birrea* tree savanna on basalt and gabbro. Rainfall 500–650 mm/yr	2599.7	27 766	5.0^{c}	2.9	1–35
Vutome	*Acacia welwitschii/Euclea divinorum* tree savanna on Karoo sedimentary rocks. Rainfall 500–650 mm/yr	746.6	5767	5.8^{c}	3.8	1–39
Sabiepoort	*Combretum apiculatum/Pterocarpus rotundifolius* bush savanna on rhyolite. Rainfall 500–650 mm/yr	855.0	9362	4.1^{bd}	2.6	1–34
Phalaborwa	*Colophospermum mopane/Combretum apiculatum* bush savanna on granite. Rainfall 450–600 mm/yr	4981.9	40 521	7.1^{e}	3.4	1–32
Letaba	*Colophospermum mopane* bush savanna on basalt and gabbro. Rainfall 450–500 mm/yr	3418.2	29 884	4.4^{ad}	2.9	1–33
Bulweni	*Terminalia sericea/Combretum zeyheri* bush savanna on deep recent sands. Rainfall 450–500 mm/yr	395.3	2459	3.7^{bdf}	3.3	1–30
Klipkoppies	*Colophospermum mopane/Combretum apiculatum* tree and bush savanna on rhyolite. Rainfall 450–500 mm/yr	482.4	3457	6.1^{ce}	4.6	1–32
Nwambiya	*Baphia massaiensis* bush savanna on recent sands. Rainfall < 400 mm/yr	508.1	3884	3.6^{bf}	3.4	1–35
Pafuri	*Colophospermum mopane/Burkea africana* tree and bush savanna on volcanic rocks and floodplains. Rainfall 400–650 mm/yr	861.7	3935	2.7^{f}	4.5	1–35
Total		18 991.8	167 947	4.5	3.1	1–40

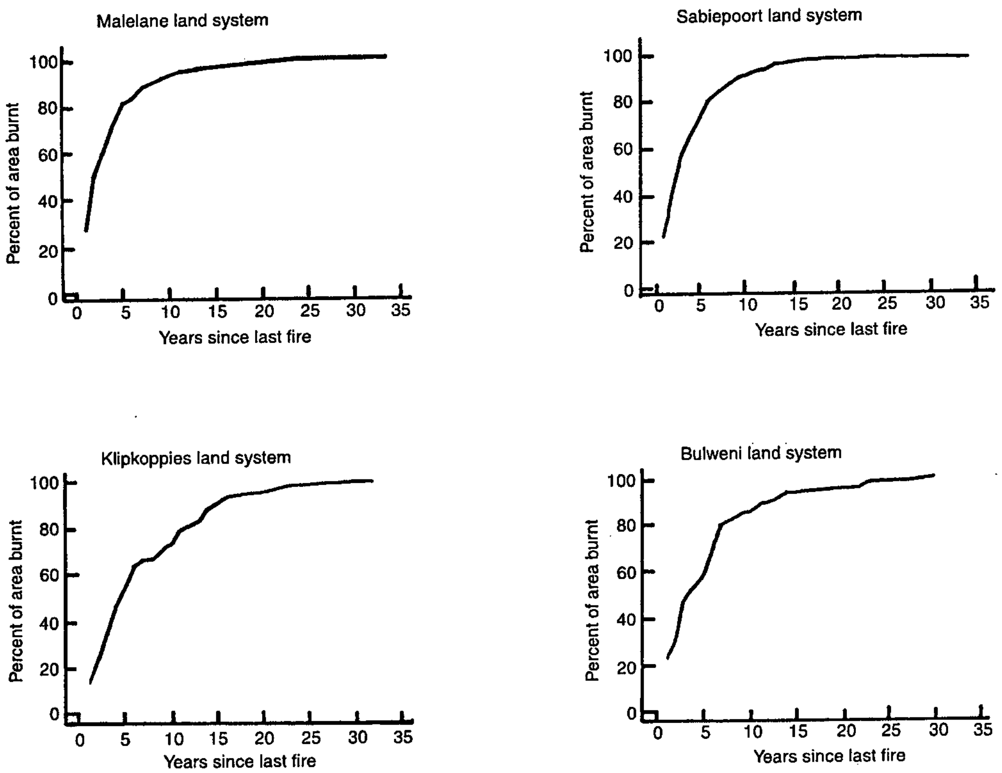

Fig. 8. The cumulative probability of fire in four land systems (see Table 2) in the Kruger National Park, calculated from fire records between 1941 and 1996.

concentrated in the three months from September to November, when 83% of the area was burnt (Fig. 10). We also examined a period of equal duration and similar rainfall (1981–85), when the policy of prescribed burning was in operation. Here, a much greater area was burnt (1.57 million ha), with 82% of the burns occurring over either an earlier or longer period (six months from June to November). The adoption of a lightning fire policy has therefore led to a discernible shift in fire season.

Size of fires and extent of area burnt

Fires covering 16.79 million ha occurred during the 56 years between 1941 and 1996 in the park. Of this area, 5.15 million ha burnt from 1941 to 1956, for which the records are not detailed enough to provide more than an annual total for each year. During the era of prescribed burning, 2213 prescribed burns were carried out, and these affected about 5.1 million ha (46.3% of the 10.92 million ha burnt during that period). There were also

Table 3. Fire return periods for zones of mean annual rainfall in the Kruger National Park. Means with the same superscript letter do not differ significantly at $P < 0.0005$.

Mean annual rainfall zone (mm)	Area (km^2)	Area burnt between 1957 and 1996 (km^2)	Mean fire return period (years)
400–500	6251	37 852	5.0^{a}
500–600	8663	54 919	5.3^{b}
600–700	2745	16 976	5.2^{ab}
700–800	314.6	1665	3.5^{c}
800–900	69.5	1238	3.5^{c}

Table 4. Mean fire return periods for wet and dry climatic periods, and for periods of varying management policies in the Kruger National Park (18 991.8 km^2).

Period of analysis	Extent of fires (km^2)	Mean fire return period (years)
Wet climatic cycle (1971–1980)	44 149	4.3
Dry climatic cycle (1983–1992)	20 834	9.1
Limited prescribed burning and active fire protection (1941–1956)	51 541	5.9
Active prescribed burning (1957–1992)	109 750	6.2
Active prescribed burning (1981–1985)*	15 733	6.0
Lightning fire policy (1992–1996)	7120	13.3

*This period was chosen for a similar rainfall pattern to the period under which the lightning fire policy had been operative, for comparative purposes.

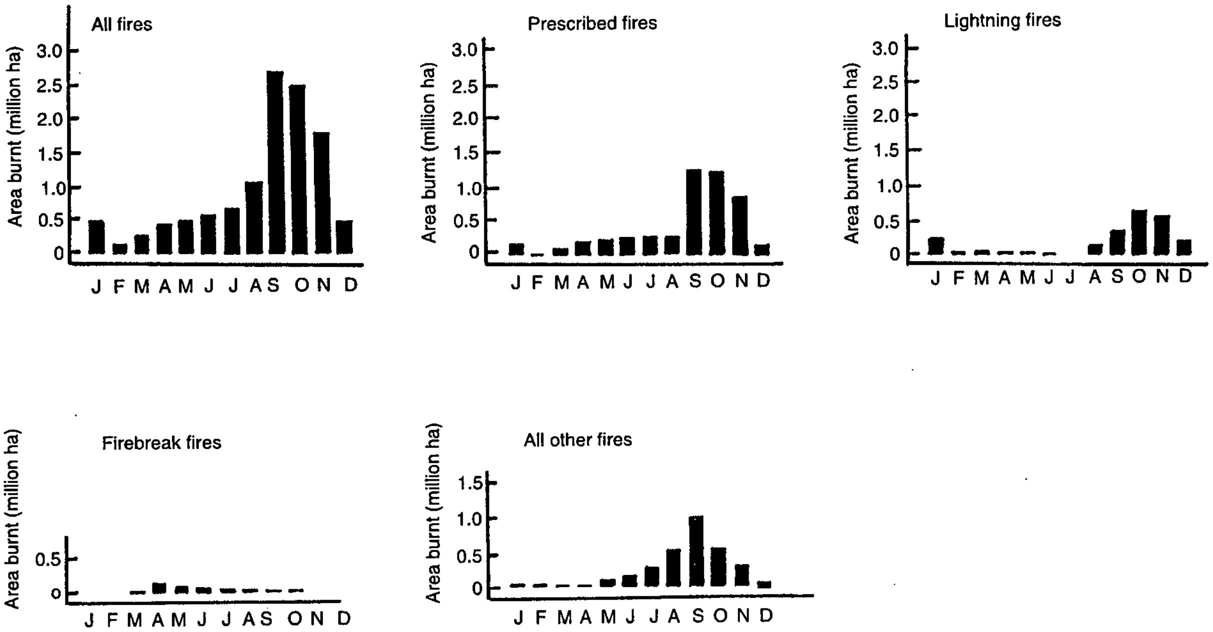

Fig. 9. Monthly distribution of total area burnt by different sources of ignition in the Kruger National Park between 1957 and 1996.

742 firebreak burns during this period, which affected an estimated total of 577 140 ha (see methods). Thus, formal management accounted for only 52% of the area burnt during this period. Lightning fires accounted for 2.5 million ha, or 21.6% of the area burnt between 1957 and 1991. Because these fires tended to occur later in the season, it can be assumed that their extent would have been greater if prescribed burning, which removed fuels that could have burnt in lightning fires, had not taken place. The balance of fires was caused mainly by poachers and refugees or were escape fires from burning operations.

Between 1957 and 1991, most fires were between 2000 and 4000 ha in size (Fig. 11A). Those more extensive than 10 000 ha burnt only 6% of the total area; the largest fire on record for this period was 18 110 ha. The period between 1992 and 1996 was characterized by 102 small fires of <10 000ha, and twelve really large ones (Fig. 11B). The large fires (>10 000 ha) accounted for 73% of the area burnt; four of these fires were greater than 30 000 ha in size (52 811, 75 396, 75 831 and 204 172 ha, respectively). These four fires all occurred in 1996, and were the largest fires recorded in the park's history.

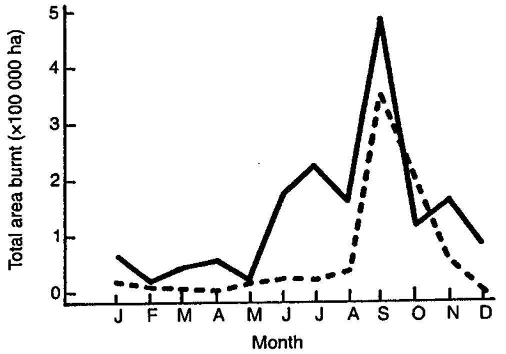

Fig. 10. Monthly distribution of area burnt in all fires under two fire management policies (lightning fires, dashed line, and prescribed burns, solid line) for two periods with similar rainfall (1981–85 for prescribed burning, and 1992–96 for lightning fires).

Fire climate

The mean burning index for each month at both of the stations analysed (Fig. 12) shows that conditions conducive to fires were highest during July, August and September, and lowest from December to March. Skukuza has higher mean burning indices as it experiences higher mean windspeeds than Letaba. Because the burning indices are mean (monthly) conditions, it is more useful to determine when extreme conditions occur, as are the times when large fires can be expected. Daily burning indices of greater than 50 (at Skukuza) and 39 (at Letaba) are in the top 5% of all values recorded at these stations. The occurrence of these conditions shows a far greater seasonal trend (Fig. 12). Such conditions occur frequently from June to October, and hardly ever between December and April (Letaba had higher occurrences in these months, as it is much drier than Skukuza, see Fig. 2).

The conditions that prevailed during the large fires of 1996 are of particular interest. These fires, in the south of the park, burnt between September 25 and October 5 of 1996. On these days, the burning index was always above 27, and exceeded 50 on three of the days. The park's managers contended that these conditions were unusual, and not likely to occur frequently. We determined that these conditions occurred at least once in 7 of the 16 years between 1981 and 1996 (Fig. 13). However, in at least 3 of these years (1989, 1992 and 1994), mean fuel loads (as determined in routine pre-fire surveys) were low (<2500 kg ha^{-1}, ranging from 1132 to 2128 kg ha^{-1}). Higher fuel loads were present in 1990 and 1991 (2740 and 2686 kg h^{-1}, respectively), while in 1996 the mean fuel load was 3653 kg ha^{-1}. Estimates of fuel load were not available for the only other year in the period analysed that had extended periods of severe fire weather (1986, Fig. 13). While this analysis covers only a short period, it appears that conditions of severe fire weather that coincide with fuel loads in excess of 3500 kg ha^{-1} are necessary for extensive (>30 000 ha) fires. The frequency of occurrence of such conditions over the long term is not known, but may be rare.

Effect of fuel load on the occurrence of fire

There was a significant relationship between grass biomass

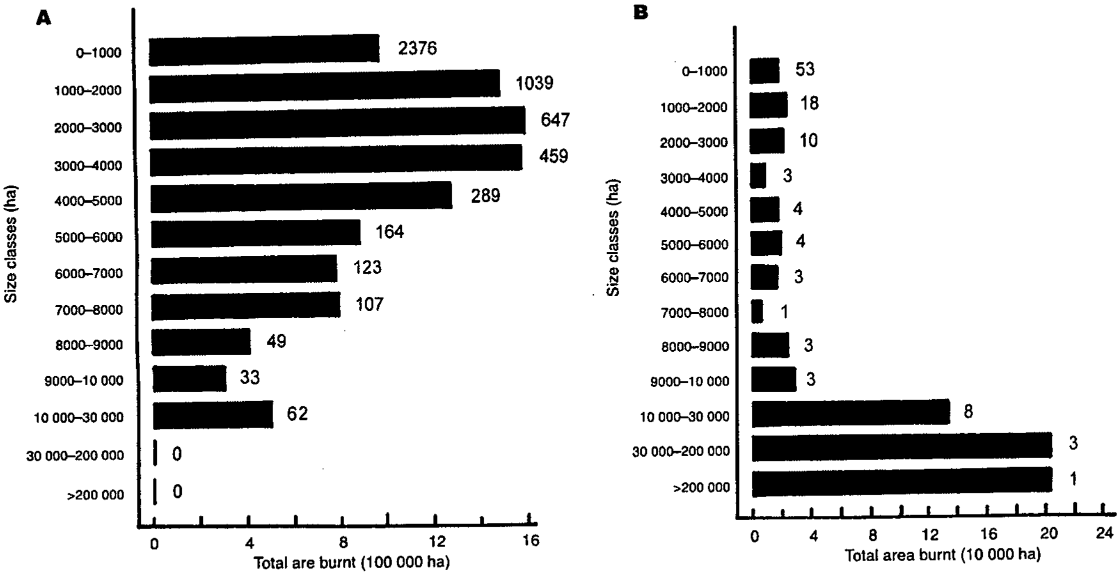

Fig. 11. Distribution of area burnt in fires of different size classes in the Kruger National Park. **A**, fires burnt between 1957 and 1991, when prescribed burning on fixed blocks was conducted; and **B**, fires burnt between 1992 and 1996, under a policy of lightning fires. The number of fires is shown next to the bars. Note the changes of scale for fires >10 000ha.

(fuel), and the probability of a fire occurring in any given block, and this relationship varied between years (Fig. 14, Table 5). The probability of a fire of any size occurring depends on grass biomass. The reason for the relationship differing between years may be due to the severity of fire weather, with the probability of fire increasing in those years where severe fire weather coincides with higher fuel loads. This is indicated in Fig. 14, where the probability of fire was higher in 1996 (a year with severe fire weather) than in 1995 (a year without such weather).

Discussion

The fire history in the Kruger National Park

There are many difficulties associated with constructing a fire history in ecosystems where long-lived trees that bear fire scars and annual rings are absent. As a result, detailed analyses of fire frequencies in such ecosystems tend to be rare. The lack of detailed analyses can lead to erroneous interpretations of fire frequency. This was the case in the Kruger National Park, where perceptions among managers were influenced by the mean fire return periods of around 7 years, based on analysis of data for 1980–1992.[7] Because mean return intervals are normally calculated without considering the shape of the frequency distribution about the

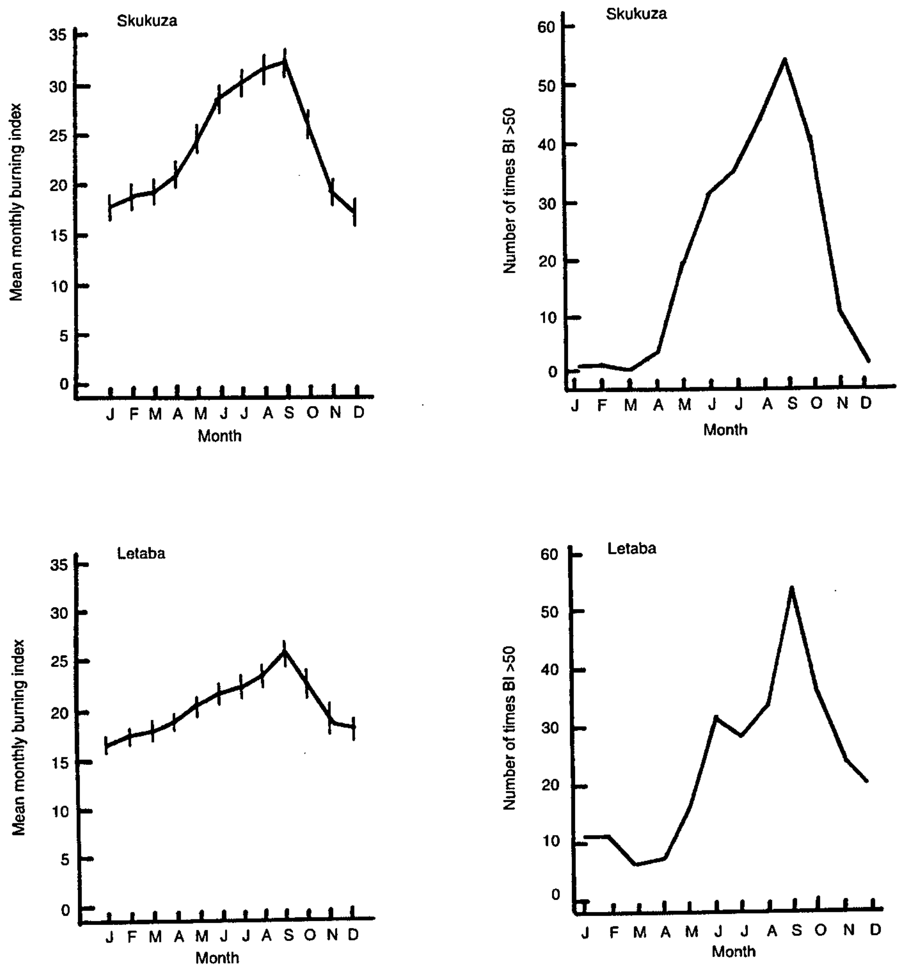

Fig. 12. Annual cycle of mean monthly burning index, and the number of days in each month that the burning index (BI) was in the top 5% of all values recorded, at two stations in the Kruger National Park. Data are for the period 1981–97; bars represent 95% confidence intervals of the mean.

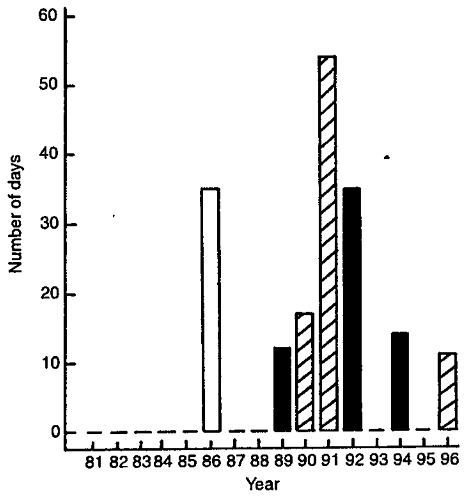

Fig. 13. The occurrence of extended periods (>10 days) of high fire danger (burning index >27 on each day, with at least three days >50) at Skukuza between 1981 and 1996. Shaded bars show years where conditions occurred together with high (> 2500 kg ha^{-1}) fuel loads. Solid bars indicate years when fuel loads were below 2500 kg ha^{-1} (fuel estimates were not available for 1986).

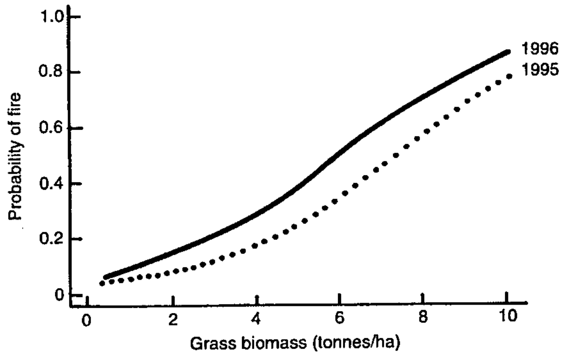

Fig. 14. The relationship between grass biomass (fuel) and the probability of fire in two individual years in the Kruger National Park. Severe fire weather conditions occurred in 1996, but not in 1995. The regression equations were $P(f) = e^Z/(1 + e^Z)$, where $P(f)$ = the probability of fire, e = the base of natural logarithms, and $Z = -3.47 + 0.00047b$ for 1995, and $-2.47 + 0.00051b$ for 1996 (b = grass biomass in kg ha^{-1}).

mean,[19] it was assumed that periods between fires were acceptably long. This study has shown that the return period between fires is much shorter than originally believed, as the median value for fire return period was well below the mean for most land systems. Concerns have recently been raised that the park has been burnt too frequently,[5] resulting in deterioration of the grass sward and in relatively high mortality of trees. Our data support the notion that the park has been burnt frequently. Large areas of the park have been subjected to annual and biennial burns, and this could have important implications for the conservation of vegetation structure and biodiversity.

Fire season is another element of the fire regime that can have important biological effects. This analysis has shown that most fires take place in relatively rain-free winter months, when grasses are dormant and dry. However, there appears to be an important difference in seasonality between fires caused by lightning and other fires. Lightning fires tend to occur later in the year, and even in the period after the start of summer rains. Proponents of a policy of lightning fires (where lightning-ignited fires dominate) argue that the shift in fire season brought about by prescribed burning differs significantly from the regime under which the ecosystem evolved, and that this shift could have undesirable consequences. The effects of changes in fire season on grass species is relatively well understood,[20,21] but the impacts on the balance between grass and woody species is less well understood and may be significant. This is one area where savanna ecologists could profit from an improved understanding of the physiology, reproductive biology and life history characteristics of the most important woody species. The lack of such knowledge has been identified as a conspicuous deficiency in the understanding of savanna dynamics,[22] and will be needed to interpret the response of woody species to shifts in fire season.

Variation between and within land systems

The range of fire return periods varied almost threefold, from 2.7 to 7.1 years. The reasons for this variation are complex and related to the dynamics of the fuel layer and to sources of ignition. Fuel loads in savanna ecosystems are largely dominated by the grass layer; the grass biomass is a function of rainfall, soil fertility and herbivory.[23] Some examples of these interactions are discussed below.

The Malelane land system had the shortest median return period (1.8 years, Table 2). Here, relatively high rainfall and low fertility combine to produce a high biomass of grass. These grasses are seasonally unpalatable, and such areas are known locally as sourveld. Herbivory levels in sourveld are lower, and fire frequencies are consequently higher.[20] The true sourveld areas make up a smaller proportion of the Malelane and Skukuza land systems; these are described by Gertenbach[10] as two landscapes that make up 846 km^2. Median fire return periods for both areas were 1.9 years. In addition to higher fuel loads, the areas are also on the boundary of the park, where additional sources of ignition and firebreak burning affect fire frequency.

The Satara land system has lower rainfall than the Malelane, but is characterized by relatively nutrient-rich, basalt-derived soils. Grasses in this area tend to be palatable throughout the year (a condition known locally as sweetveld), and herbivory levels are high. Despite lower rainfall and higher levels of herbivory, the mean fire return period does not differ significantly from that of the Malelane system. We attribute this to the ability of the fertile soils to produce good crops of grass in years of relatively high rainfall, which in turn support a similar number of fires to the Malelane system.

Table 5. Diagnostics of two logistic regressions giving the relationship between grass biomass and the probability of fire in the Kruger National Park in 1995 and 1996 (see Fig. 14).

Year	Estimates	Standard error of estimates	% deviance explained	Significance (P)
1995	Constant (–3.7)	0.4504	7.006	0.0004
	Biomass coefficient (0.00047)	0.000134		
1996	Constant (–2.47)	0.3539	13.358	<0.0005
	Biomass coefficient (0.00051)	0.000080		

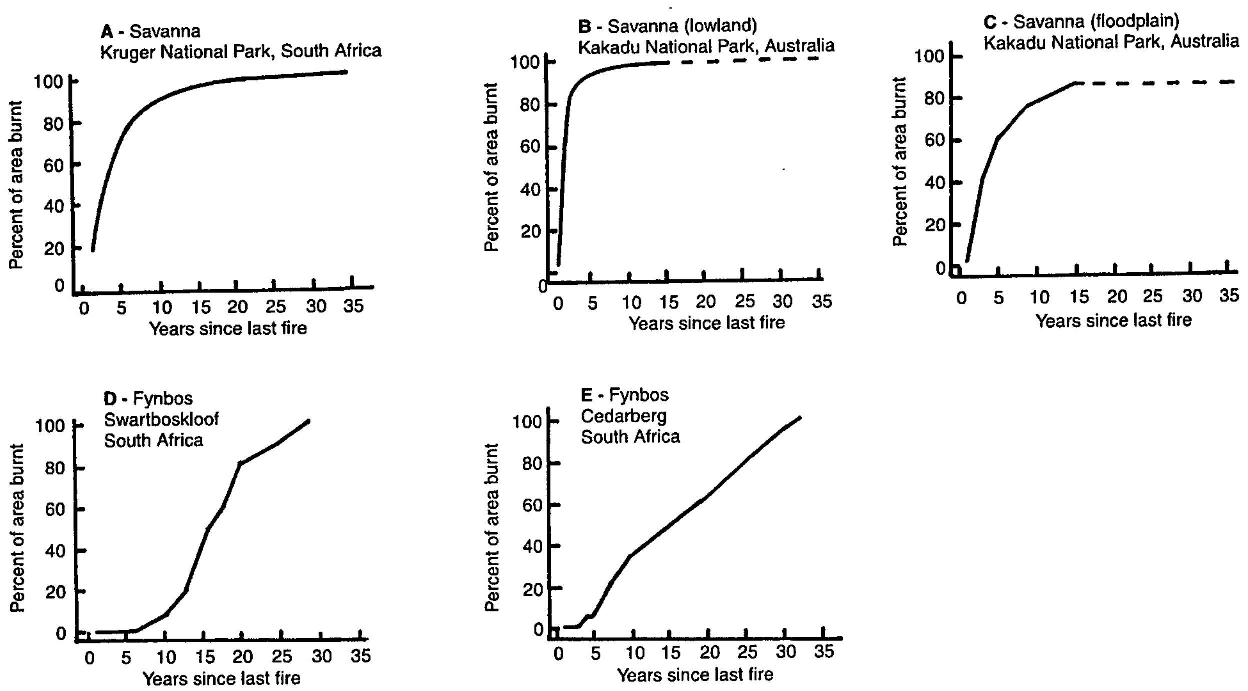

Fig. 15. The cumulative probability of fire in various ecosystems for which detailed fire histories are available. **A**, savannas in the Kruger National Park (this study); **B** and **C**, savannas in the Kakadu National Park, Australia;[25] **D**, fynbos shrublands at Swartboskloof;[27] and **E**, fynbos shrublands in the Cedarberg mountains.[26] Dashed lines indicate extrapolations beyond the available data.

The Phalaborwa (on granite) and Letaba (on basalt) land systems, north of the Olifants River, are dominated by mopane trees and shrubs. This species dominates on both granite and basalt, because of shallow soils underlain by impervious bedrock.[24] On basalts, grass biomass (and thus fuel) is presumably higher after good rains on the relatively fertile soils, which could explain the difference in mean fire return periods (4.4 and 7.1 years) despite similar rainfall.

Variation in mean fire return periods can be as great within land systems as between them. This can be seen in the mosaic of different return periods in adjacent areas (Fig. 7). The fact that these periods vary substantially between blocks with the same underlying geology and vegetation type, and the same climate and weather is probably due to differences in the dynamics of the fuel layer. This is probably a function of differential rates of herbivory. For example, Russell-Smith and co-workers[25] attributed a marked increase in fire frequency to increased herbaceous fuel loads associated with the removal of feral water buffalo in Kakadu National Park in Australia. Herbivory in turn is possibly related to the distribution of artificial water points. There are 611 boreholes and 129 dams in the park, and these have a strong influence on the spatial distribution of grazing pressure. The relationships between the artificial provision of water, herbivory, fire and feedback effects on vegetation dynamics are topics that need to be researched to be able to assess the consequences of ecosystem management in the area.

Comparison with other ecosystems

Detailed accounts of the fire history of savanna ecosystems are rare, but Russell-Smith and his co-workers[25] assembled a 15-year fire history for savanna vegetation types in the Kakadu National Park, northern Australia, from LANDSAT MSS imagery (Fig. 15). Here, fire frequencies were very high in lowland vegetation, with a median return period of less than 2 years. The floodplains at Kakadu, on the other hand, were characterized by less frequent fires, and a median return period of around 4 years. It would appear, therefore, that fire frequencies in the Australian park were similar to those in the Kruger National Park. The Kakadu data were also analysed with respect to fire size; while the median fire size was <300 ha, some very large, late dry season fires (>400 000 ha) did occur. These are typical of uncontrolled, late dry season fires in the vast unpopulated expanses of northern Australia.[25] Such fires have not, until recently, been a feature of the Kruger National Park, as fires were confined to management blocks.

Fire histories are also available for several fynbos (shrubland) ecosystems from the mediterranean-climate areas of the Western Cape, South Africa.[26,27] Here, fire return periods are longer (in the order of 15 years). A further feature of these ecosystems is that the distribution of fire return periods tends to be symmetrical around the mean (Fig. 15), so that median and mean values for fire return periods are similar. This indicates a normal distribution of return periods around the mean, as opposed the savanna systems which have skewed distribution. Fire return periods are also longer than for savanna, probably as a result of the coarser nature of fynbos fuels, coupled with slower build-up rates and less frequent occurrences of weather conditions conducive to large fires. The approach for depicting the distribution of fire return periods provides a useful descriptor of the fire regime in grasslands, savannas, and shrublands such as chaparral, fynbos, or heathlands. This is because fires in these ecosystems tend always to be surface fires burning in grass layers (for savannas and grasslands) or shrub canopies (in shrublands). In coniferous and boreal forests, on the other hand, the approach is less informative. In these ecosystems, fires can burn as low-intensity surface fires, or high-intensity crown fires, and these fires will have fundamentally different effects with the same frequency and return periods.

The management of fire regimes

The current fire management policy in the Kruger National Park allows 'natural' fires to burn freely. Prescribed burning is not carried out, and fires of human origin are extinguished. However, anthropogenic fires have been a feature of the last 35 000 years or more. Because lightning alone may not ignite sufficient fires to simulate the park in historical times, some consideration must also be given to allowing additional fires to burn. These would make up for fires that would have been started by man in the past, or those that would have entered the park from outside but are not now able to do so. Managers are required to contain fires that are not started by lightning, and it is assumed that the area burnt by non-lightning fires will be sufficient to make up for the additional fires that would have occurred in the past. Because of the uncertainty about the nature of the historical fire regime, managers will have to monitor the occurrence of fires, and base the need to intervene on the patterns of fire that establish themselves. The application of these principles is discussed in another paper.[28] The present analysis provides a benchmark around which rules can be developed to test whether an acceptable fire regime does eventuate. The indications to date are that some significant shifts have already taken place. The overall area that has burnt under the lightning fire policy is smaller, and the fires have been in the form of a few very large conflagrations, and relatively fewer small ones. Mean return periods between fires has increased, and there has been a shift in the occurrence of fire to later in the season. The degree to which these shifts can be accommodated will depend on their actual or predicted impacts. We suggest that managers draw up hypothetical thresholds to the distribution curves for fire frequency and season that can be taken as indicators of potential concern.[28] Fire records can be updated annually, using computer technology,[29,30] and tested against these thresholds. In addition, managers can monitor trends in the plant and animal communities in the park. Any changes in the structure or composition of these populations or communities can be interpreted in terms of the fire regime and its history.

B.v.W. thanks the CSIR Division of Water, Environment and Forestry Technology, and South African National Parks for supporting this work. N. Zambatis and A. Potgieter were responsible for the curation of the fire database on which this paper is based. R. Burgan of the Intermountain Fire Sciences Laboratory, Missoula, Montana, kindly ran the fire danger calculations against a tight deadline. B. Brebnor, A. Potgieter, J. van Wilgen, J. Wrench and N. Zambatis provided valuable assistance at various stages of the project.

Received 13 December 1999. Accepted 20 January 2000.

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Fourth paper: Response of savanna fire regimes to changing fire management policies in a large African national park. *Conservation Biology*.

Response of Savanna Fire Regimes to Changing Fire-Management Policies in a Large African National Park

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Abstract: *Approaches to fire management in the savanna ecosystems of the 2-million ha Kruger National Park, South Africa, have changed several times over the past six decades. These approaches have included regular and flexible prescribed burning on fixed areas and a policy that sought to establish a lightning-dominated fire regime. We sought to establish whether changes in management induced the desired variability in fire regimes over a large area. We used a spatial database of information on all fires in the park between 1957 and 2002 to determine elements of the fire regime associated with each management policy. The area that burned in any given year was independent of the management approach and was strongly related to rainfall (and therefore grass fuels) in the preceding 2 years. On the other hand, management did affect the spatial heterogeneity of fires and their seasonal distribution. Heterogeneity was higher at all scales during the era of prescribed burning, compared with the lightning-fire interval. The lightning-fire interval also resulted in a greater proportion (72% vs. 38%) of the area burning in the dry season. Mean fire-return intervals varied between 5.6 and 7.3 years, and variability in fire-return intervals was strongly influenced by the sequencing of annual rainfall rather than by management. The attempt at creating a lightning-dominated fire regime failed because most fires were ignited by humans, and the policy has been replaced by a more pragmatic approach that combines flexible prescribed burning with lightning-ignited fires.*

Key Words: grass fuels, Kruger National Park, natural fires, prescribed burning, rainfall, South Africa

Respuesta de los Regimenes de Fuegos de Sabana a Cambios en las Políticas de Gestión de Fuego en un Parque Nacional Africano

Resumen: *Durante las seis últimas décadas, los métodos de gestión de fuego en los ecosistemas de sabana han cambiado varias veces en el Parque Nacional Kruger (2 millones de ha), Sudáfrica. Estos métodos incluyeron quemas prescritas regulares y flexibles en áreas determinadas y una política que buscaba establecer un régimen de fuego dominado por relámpagos. Buscamos establecer si los cambios de gestión indujeron la variabilidad deseada en los regimenes de fuego en un área extensa. Utilizamos una base de datos espacial de la información de todos los incendios en el parque entre 1957 y 2002 para determinar elementos del régimen de fuego asociados con cada política de gestión. El área quemada en cualquier año fue independiente del método de gestión y se relacionaba cercanamente con la precipitación pluvial (y por lo tanto con pastos combustibles) en los dos años precedentes. Por otro lado, la gestión afectó a la heterogeneidad espacial de los incendios y su distribución estacional. En comparación con el intervalo de fuego por relámpagos, la heterogeneidad fue mayor en todas las escalas durante el período de quemas prescritas. El período de fuego por relámpagos también presentó una mayor proporción (72% vs. 38%) de área quemada durante la época de secas. Los intervalos promedio de retorno de fuego variaron entre 5.6 y 7.3 años, y la secuencia de la precipitación anual, no la gestión, influyó notablemente en la variabilidad de los intervalos de retorno de fuego. El intento de crear un*

Paper submitted August 11, 2003; revised manuscript accepted March 7, 2004.

régimen de fuego dominado por relámpagos fracasó porque la mayoría de los incendios fueron iniciados por humanos, y la política ha sido reemplazada por un método más pragmático que combina quemas prescritas flexibles con incendios iniciados por relámpagos.

Palabras Clave: fuegos naturales, pastos combustibles, Parque Nacional Kruger, precipitación pluvial, quemas prescritas, Sudáfrica

Introduction

Despite decades of experience and research, the issue of how to manage fires and fire regimes in conservation areas remains contentious. Currently, many conservation areas have goals that explicitly require the promotion of "natural" processes (including fire), but examples of the deliberate maintenance or restoration of a natural fire regime over large areas are hard to find. In the United States, for example, only 88 of 596 designated wilderness areas (where natural fires should be allowed to burn) had approved fire-management plans that allowed even some natural ignitions to burn (Parsons 2000). As a result of the failure to implement natural fire regimes, their suitability as a management approach is in question.

In African savanna ecosystems, active fire management has also been practiced for many decades (van Wilgen et al. 1990), and policies and practices have changed as new evidence on the role of fire has emerged (Mentis & Bailey 1990; Bond & Archibald 2003). In the absence of comprehensive predictive models, managers have argued variously for fire exclusion, regular prescribed burning, adaptive management, or the re-creation of "natural" fire regimes. Bond and Archibald (2003) concluded that none of the existing fire-management policies in South Africa are universally applicable and that policies that promote variable fire-return intervals and fire sizes are preferred in arid savannas to maintain a greater diversity of grassland swards and grazing mammal species.

In practice, the implementation of a chosen fire regime is difficult, even when agreement on its nature is reached. Unplanned fires (often resulting from factors beyond the control of managers) burn large areas, upsetting agreed-upon fire targets or policy decisions. The question of how well managers of large conservation areas, with different management approaches, have been able to influence the fire patterns that establish themselves is also difficult to answer because it requires comprehensive fire records from large areas, and such records are rare. The Kruger National Park in South Africa provides an exception, and good fire records are available (van Wilgen et al. 2000). Fire has also been implicated in changes in the park's ecosystems, and managers are concerned about the potential negative consequences for conservation (Eckhardt et al. 2000; van Wilgen et al. 2003). As a result of these concerns, fire-management policies have been changed a number of times over the past six decades.

The recent changes in fire-management policy in the Kruger National Park, from prescribed burning to "natural" fires, resulted from the adoption of new management objectives in the early 1990s and changes in ecological thinking. Earlier management was based on stable-state thinking, in which managers aimed to conserve optimal numbers of animals and a cover of vegetation deemed optimal for mammal populations, reflecting "game reserve" and "balance of nature" ethics. The new management objectives are based on biodiversity and "flux of nature" ethics—the park's formal objectives call for the conservation of biodiversity "in all its facets and fluxes"—as opposed to the conservation of stable populations of species, reflecting thinking that encompasses variability in space and time (Pickett et al. 1992; Weins 1997). There is little scientific evidence to support arguments for changing fire-management approaches in the Kruger National Park, other than the observation that the composition of the grass sward during the era of flexible prescribed burning had become typical of areas that were too frequently burned (Trollope et al. 1995) and that there had been a decline in the numbers of large trees over the same period (Eckhardt et al. 2000). Rather, changes to fire management have amounted to experimenting with different conceptual frameworks that reflect changing ideas about the stability or dynamics of the ecosystem.

If management should aim to promote more variable fire-return intervals and sizes to conserve diversity in arid savannas (Bond & Archibald 2003), the question arises as to whether or not recent changes in fire management have resulted in more variability, both spatially and temporally. Managers also need to understand which elements of a fire regime can be influenced by different interventions. We explored the influence of three fire-management policies, applied for 9, 11, and 24 years respectively, on the park's fire regimes.

The Kruger National Park and Its Fire Policies

The Kruger National Park was established in northeastern South Africa in 1926, and covers 1,948,528 ha. Elevations range from 260 to 839 m above sea level, and mean annual rainfall varies from around 350 mm in the north to around 750 mm in the south. The rainfall regime is characterized by extended wet and dry periods, in which the rainfall is either higher than the long-term mean or lower than the mean for between 6 and 12 consecutive years. These extended wet and dry periods have marked effects on the occurrence of fires, mainly through their influence on grass fuel loads.

The vegetation of the park is a well-wooded savanna, dominated by trees in the genera *Acacia, Combretum, Sclerocarya*, and *Colophospermum*. The flora of the park comprises 1983 species, including over 400 tree and shrub species and over 220 grasses. The fauna of the park includes 147 mammal and 492 bird species. Megaherbivores (Owen-Smith 1988) are an important component of the fauna and include the elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), and hippopotamus (*Hippopotamus amphibious*). Grazing influences the occurrence of fires through the consumption of grass fuels, and browsing (particularly by elephants) significantly increases tree mortality in combination with fires (van Wilgen et al. 2003).

Fire management of the park has passed through six phases over the past six decades. From 1926 to 1947, occasional and limited deliberate burning was conducted. Fires were ignited to consume old grass that escaped other fires in the area, mainly to provide new growth for grazing. From 1948 to 1956, attempts were made to reduce the impacts of fire by ensuring, wherever possible, that no area burned more often than once every 5 years. From 1957 to 1980, regular prescribed burning was conducted every 3 years in spring after the first rains on fixed areas of around 4000 ha ("burning blocks"). A network of firebreaks was established to delimit burning blocks.

From 1981 to 1991, flexible prescribed burning was conducted, in which fires in burning blocks were timed to account for fuel loads, post-fire age, and mean annual rainfall. Managers aimed to burn up to 50% of the park following high-rainfall years but only 20% following low-rainfall years. Seasonal fire distribution was also varied to allow for some burns before the first spring rains and in midsummer during periods of high rainfall. The approach was intended to result in a more variable fire-return interval, a wider seasonal distribution of fires, and longer fire-return intervals in drier areas.

From 1992 to 2001, a "natural" fire policy was in place, in which all lightning-ignited fires were allowed to burn freely, and attempts were made to prevent, suppress, or contain all other fires. The network of firebreaks was reduced by half to facilitate the spread of fires.

At present, point ignitions are used to start fires in areas where fire is deemed necessary. At the start of each fire season, grass-sward composition and grass fuel loads are used to identify areas to be burned (van Wilgen et al. 1998). Point-ignited fires are allowed to burn until a monthly target area is reached. The annual target area increases (to a limit of 50%) with increasing grass biomass at the start of the fire season (Brockett et al. 2001). If wildfires occur in areas where fire is deemed necessary, they are allowed to burn unless the monthly target area has been exceeded, in which case they are suppressed. Fires are also suppressed in areas where fire is not considered necessary, and all lightning fires are tolerated.

The history of the first five phases of fire management is well documented (Brynard 1971; van Wilgen et al. 1990; Biggs & Potgieter 1999; van Wilgen et al. 2003). The change from prescribed burning to lightning fires at the start of the 1990s came about in response to concerns about the putative negative effects of fire on vegetation, including a decrease in large trees and a low diversity of grass species. The arguments against prescribed burning were that fires were too regular, too frequent, and too intense. High intensity was associated with the practice (between 1957 and 1991) of "ringburning," in which fires are ignited around the periphery of burning blocks. These burns commence with downwind backfires to create a fuelbreak and are then allowed to burn with the wind toward the center. As a result, the largest proportion of the block is burned in a headfire of relatively high intensity. Natural fires—for example, those associated with lightning strikes—spread out in all directions from a point, allowing the fire to develop a range of intensities as it spread. High fire intensities associated with ringburning are also magnified because they are carried out primarily during the day. By changing to a "natural" (lightning-driven) policy, managers hoped to develop a more variable, less intense fire regime.

Managers in the Kruger National Park also introduced the concept of management by "thresholds of potential concern" in the early 1990s, in line with changes in thinking that embraced variability. Under this framework, upper and lower thresholds have been defined for a range of ecosystem indicators and are set according to current understanding of ecosystem dynamics after extensive consultation with scientists, park research staff, and managers (e.g., Whyte et al. 1999). If a threshold is reached, then management actions to prevent the deleterious consequences of exceeding the threshold are considered. Alternately, the threshold could be recalibrated to a more appropriate level if it becomes clear that management intervention will not prevent it being exceeded. Because of the difficulties inherent in predicting the effects of fire on all facets of biodiversity, van Wilgen et al. (1998) proposed a range of thresholds relating to fire patterns that, if exceeded, should prompt a reevaluation of the fire policy. The framework included thresholds relating to fire-return intervals, the seasonal distribution of fires, the range of desired fire intensities, and the size-class distribution of fires. For example, the distribution of fire-return intervals is assessed annually, based on fires over the past 30 years. The thresholds require mean fire-return intervals of 4, 6, and 10 years to occur over at least 25%, 50%, and 75% of the park, respectively, based on this analysis. Deviations from these thresholds alert managers to the possibility that fires were either too frequent or too infrequent in the area concerned.

None of the thresholds related to fire regime has yet been invoked to consider changes to management. Management change was triggered, however, by a threshold that sought to limit human-caused fires to <25% of the area burned in a given year (this threshold was included because the "natural-fire" policy rested on promoting lightning ignitions). When the threshold was exceeded in 1996, managers first changed the target area from 25% to 50%, and then from an annual total to an average over 10 years. Before the 10-year period had been reached, however, it became clear that the threshold would be exceeded. Most of the area that burned in the 10 years that the lightning policy was in force burned in fires not started by lightning (lightning fires burned only 757,660 out of 3,210,543 ha, or 23.6%, and most fires were ignited by immigrants seeking to gain illegal entry into South Africa from Mozambique). This, coupled with growing pressure from managers, who were required to contain most fires, led to the policy being changed in April 2002 to a combination of deliberately ignited patch burns in areas where fire is deemed necessary and tolerance of all lightning fires.

Methods

The Kruger National Park's Fire Record

Following the introduction of prescribed burning in 1957, the Kruger National Park was subdivided into over 400 burning blocks, and records were kept of all fires in each block. These records were kept until 1991 and have been captured on a spatial database (van Wilgen et al. 2000). Following the introduction of the lightning-fire approach in 1992, fires were no longer intended to be confined to burning blocks. All fires that occurred after 1991 were recoded on 1:250,000 maps and were captured on the spatial database. The results reported here are based on data gathered between 1957 and 2002. Sketch maps showing the extent of fires between 1941 and 1956 are available, but we considered these too inaccurate to include.

Influence of Fire Policy on the Extent and Seasonal Distribution of Fires

In an earlier study, van Wilgen et al. (2000) found a significant relationship between grass biomass and the probability of fires in the park. Because grass biomass is dependent on variable rainfall in preceding years, we examined the influence of mean rainfall in the past 2 years on the extent of area burned in any given year (the effect of rainfall on the biomass of perennial grasses persists for more than 1 year, and using mean rainfall for the past 2 years instead of a single year provided a better fit to the data). Total annual rainfall was estimated as the mean of totals recorded at 10–34 rain gauges within the park (the number increased over the period examined). We examined this relationship for the three periods between 1957 and 2001 with different management approaches to test whether the management approach influenced the relationship. We also determined the total area burned each year in dry (May–September) and wet (October–April) months for the periods under different management. Where the rainfall in September was double the long-term mean for that month, fires occurring in September were included in the wet season.

Influence of Fire Policy on the Spatial Heterogeneity of Fires

The achievement of a high degree of spatial heterogeneity has recently been included as an important goal of conservation management in African savannas (Brockett et al. 2001; Bond & Archibald 2003). We examined the effects of management on the spatial heterogeneity of fire patterns for periods associated with prescribed burning and with lightning fires. The lightning-fire policy was in place for 10 years (1992–2001), during which 5 years of below-average rainfall were followed by 5 years of above-average rainfall. Because of the strong influence of rainfall on the extent of fires, we sought a 10-year period during the prescribed burning era when rainfall patterns were similar. The mean rainfall for 1992–2001 was 575 mm (SD 282.2, range 227.7–1175.4 mm). The period with the most similar rainfall (both the mean and the sequencing of annual totals) was 1977–1986, when a mean of 565.6 mm fell (SD 176.4, range 271.0–963.3 mm), so this period was chosen for comparison.

We estimated heterogeneity by overlaying grids on the fire maps for each of the 10 years chosen to represent the two management approaches. Grids of 3 × 3, 5 × 5, and 7 × 7 cells were assembled. Cell sizes of 1, 25, and 100 ha were used. We scored each grid as homogenous if all cells were either burned or unburned. Partially burned grids (where some cells were burned and others not) were scored as heterogeneous. We calculated a percent heterogeneity score as the number of heterogeneous grids as a percentage of all grids in the park. Scores were calculated for all fires in a calendar year, and means were calculated for the 10 years under consideration.

Influence of Fire Policy on Fire-Return Intervals

We determined the mean, range, and coefficient of variation associated with fire-return intervals. Mean fire-return intervals were estimated as $RP = y/(b/a)$, where RP is the return interval in years, b is the extent of all fires recorded over y years, and a is the area over which fires were recorded. This method delivers a single estimate of the fire-return interval but does not provide insight into the variability associated with fire-return intervals. The range and variability of fire-return intervals were estimated by overlaying a 1-km grid on digital fire maps. In this way, the number of years between each successive

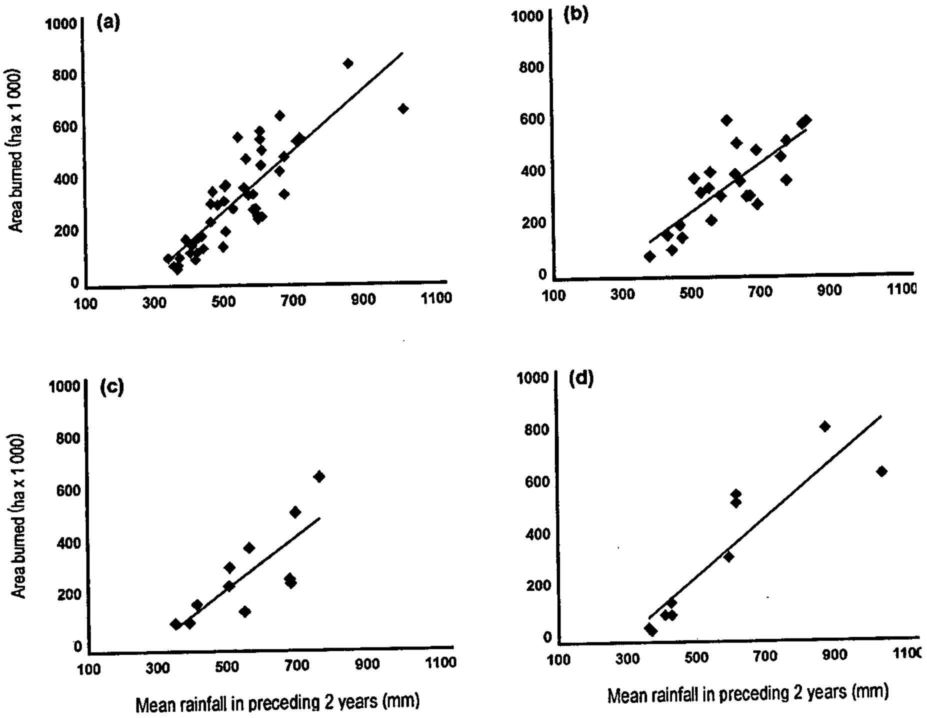

Figure 1. Relationship between mean annual rainfall over the preceding 2 years and the extent of fires in the Kruger National Park. Data are for (a) all years between 1957 and 2001 ($y = 1296.6\,x - 393,031$; $r^2 = 0.7037$); *(b) 1957-1980, when regular prescribed burning took place* ($y = 1269.1\,x - 358,302$; $r^2 = 0.6107$); *(c) 1981-1991, when flexible prescribed burning took place* ($y = 1408.6\,x - 447,446$; $r^2 = 0.6221$); *and (d) 1992-2001, when a policy of lightning-driven fires was in place* ($y = 1298.7\,x - 395,818$; $r^2 = 0.8126$). *Lines for different management eras did not differ significantly* ($F = 0.76$; $p > 0.05$).

fire at each of the 19,605 squares (each 1 km^2) in the park was established (partially burned squares were considered burned). This analysis excluded 343 km^2 that was added to the park in 1964. We limited our analysis to the interfire intervals delimited by fires at each end. We also recorded the number of squares that had no fires, or only one fire (and thus no interfire interval), in the interval of interest and excluded these from our analysis. For each of the intervals of interest, we confined our analysis to interfire intervals contained fully by the period of interest, so that if a fire during the period of interest was delimited by a previous or future fire outside the period of interest, that interfire interval was excluded from the analysis.

We used these data to calculate the range of fire-return intervals associated with different management approaches as $a_i = (n_i/y)$, where a_i is the mean area (in square kilometers) subjected to a fire-return interval of i years; n_i is the number of interfire intervals of i years, and y is the number of years the management approach was in place.

We developed a simple model to examine whether variability in annual rainfall influenced variability in fire-return intervals, as reflected by the mean coefficient of variation for each grid square. We used the relationship between mean annual rainfall and area burned (Fig. 1a) to estimate the percentage of area burned for each year from 1957 to 2001, based on actual rainfall. We distributed this percentage at random over a grid of 1000 squares and analyzed the simulated fire-return intervals as above. The distribution of burned squares at random means that intervals between the simulated fires would be independent of other influences, such as postfire age, weather patterns, or sources of ignition.

Results

Influence of Fire Policy on Extent and Seasonal Distribution of Fires

Mean annual rainfall had a strong influence on the extent of fires between 1957 and 2002 (Fig. 1). When mean annual rainfall over 2 years was below 500 mm, fires did not cover more than 10% of the park. When mean annual rainfall was above 700 mm, the area burned was between 25% and 45% of the park. The relationship remained the same (Fig. 1), regardless of the prevailing fire policy, indicating that rainfall (and consequently grass biomass) had an overriding influence on area burned in any given year.

In the allocation of burned areas to wet and dry periods, the burned areas in September were included in the wet season in 6 years, 4 between 1957 and 1980 and 2 between 1981 and 1991. Most (89%) of the rain fell in the wet season as defined in this analysis. There was a progressive shift from wet-season to dry-season fires between 1957 and 2001. Most (62%) of the area burned in the wet season when regular prescribed burning was practiced. After flexible prescribed burning was introduced, the majority of fires (56%) occurred in the dry season. The proportion of dry-season fires rose to 72% after the

Table 1. Mean heterogeneity scores at different scales associated with two fire-management approaches over 10 years in the Kruger National Park.*

Grid size (ha)	*Cell size (ha)*	*Arrangement of cells*	*Mean heterogeneity score (%)* *prescribed burning on fixed areas (1977-1986)*	*Mean heterogeneity score (%)* *fires not confined to fixed areas (1992-2001)*
9	1	3 × 3	2.6	1.4
25	1	5 × 5	5.1	2.8
49	1	7 × 7	7.5	4.1
225	25	3 × 3	11.9	6.5
625	25	5 × 5	22.1	12.6
900	100	3 × 3	21.7	11.8
1225	25	7 × 7	31.0	16.8
2500	100	5 × 5	38.2	20.9
4900	100	7 × 7	50.2	28.5

**Scores were calculated as heterogeneous grids (a mixture of burned and unburned cells) expressed as percent of all grids. All scores (except for the 25-ha grids) were different between fire-management approaches (Wilcoxon paired sample test, $p > 0.02$).*

policy of encouraging a lightning-driven fire regime was introduced.

Influence of Fire Policy on Spatial Heterogeneity of Fires

The spatial heterogeneity scores of fire patterns increased with an increase in the scale at which they were measured (Table 1). Scores increased from around 2% when measured on 3 × 3 (9-ha) grids to over 50% when measured on 7 × 7 (4900-ha) grids. The spatial heterogeneity of fire patterns was higher at all scales when the prescribed burning policy was in place, with scores at all scales being consistently almost double for prescribed burning on fixed blocks compared with the period of lightning fires, when fires were not confined to burning blocks.

Influence of Fire Policy on Fire-Return Intervals

Mean fire-return intervals were highest when flexible prescribed burning was practiced and lowest when a policy of natural fires was followed (Table 2). In our analysis of variability associated with fire-return intervals, we excluded 2.8%, 16%, and 22.7% of the squares from our analysis for regular prescribed burning, flexible prescribed burning, and lightning fire, respectively, because these had only one or no fires in the interval of interest. Fire-return intervals of 1, 2, and 3 years dominated the fire regime in all phases of management (Fig. 2). For example, 13.7% of the park burned either annually or biennially between 1957 and 1980 (accounting for 65% of all fires), despite the prevailing policy of triennial burns. The natural fire policy also led to the least variability in fire-return intervals, whereas regular prescribed burning produced the most variability in fire-return intervals (Table 2). This result was surprising, but our simulation with random placing of fires based on rainfall produced similar results (Table 2). The sequence of actual annual rainfall showed a high degree of variability between 1957 and 1980 compared with the other two periods under consideration. It appears, therefore, that the sequencing of annual rainfall had an overriding influence on fire-return intervals, regardless of the management approach adopted at the time.

Discussion

Effects of Changing Management on Fire Regimes

Our findings suggest that management had little if any effect on the extent of area burned or on the variability in interfire intervals. These elements of the fire regime appear to be strongly influenced by rainfall patterns (amount and sequencing of annual totals), regardless of management approaches. Management, on the other hand, was able to influence the seasonal distribution of fires and the spatial heterogeneity of fire patterns. Because there is no information on fire intensities, we were unable to assess whether this element of the fire regime was influenced by management approach. However, managers can probably influence fire intensity by choosing the weather for burning, by preempting late dry-season (more intense) fires by igniting them early in the dry season, and by selecting the ignition pattern, such as initiating fires from point ignitions rather than perimeter ignitions.

Table 2. Mean fire-return intervals and their variability resulting from three fire-management approaches in the Kruger National Park.

Fire-management approach	*Mean fire-return interval (years)*	*Mean coefficient of variation (mean of coefficients calculated for each grid square)*	*Mean coefficient of variation of simulated interfire intervals (see text)*
Regular prescribed burning (1957-1980)	6.09	73.4	78.1
Flexible prescribed burning (1981-1991)	7.28	53.3	57.9
Lightning fires (1992-2001)	5.62	44.5	54.6

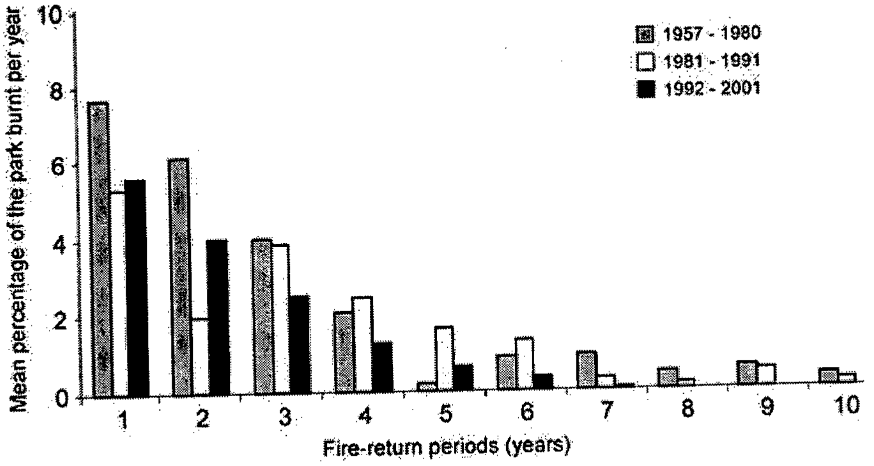

Figure 2. Mean percentage of the Kruger National Park burned at different fire-return intervals during three phases of fire management. The phases are regular prescribed burning (1957-1980), flexible prescribed burning (1981-1991), and lightning fires (1992-2001). Fire-return intervals of between 11 and 23 years (not shown) burned an annual mean of 0.66% of the area of the park burned during the phase of regular prescribed burning.

Unanswered Questions and the Way Forward

Plant species in arid savannas have attributes that allow them to survive repeated fires, mainly through sprouting. Consequently, the conservation of fire-sensitive species in fire-prone landscapes is not an issue, as in some other tropical savannas (e.g., Gill & McCarthy 1998; Russel-Smith et al. 1998). Fires do not normally kill African savanna trees, but they do affect the size of trees. The aerial parts of small trees subjected to fire are killed ("topkill"), and they sprout from the base. Most larger trees can survive fires without topkill. The proportion of trees that are topkilled is a function of tree size and fire intensity (Trollope 1984). Trees need to be tall enough to avoid a topkill, and this critical height increases with fire intensity. It has been demonstrated (Higgins et al. 2000) that variability in fire intensity is important for the maintenance of tree-grass assemblages in savannas because variability allows enough trees to reach a size at which they can avoid topkill. We suggest that occasional longer interfire intervals may be as important as variability in intensity for maintaining tree-grass assemblages because longer intervals would allow enough time between fires for trees to reach sufficient size to avoid topkill.

Fires also cannot be considered in isolation in African savannas. In combination with fire, elephants significantly increase tree mortality. Browsing by elephants frequently removes the protective bark from trees, allowing successive fires to burn into and weaken the exposed wood so that trees eventually collapse (van Wilgen et al. 2003). Neither the variability in interfire interval nor the impacts of elephants has been explicitly modeled to date. The role, if any, of differences in the season and spatial heterogeneity of fires in influencing tree survival is not understood, but our results suggest that these elements of the fire regime can be influenced by management. The amount of burning and variability in interfire intervals, which would presumably play a role in tree survival, appears not to be easily influenced by management. This suggests that managers should focus on achieving variability in fire intensity to ensure the long-term survival of tree populations.

The latest change in fire management is expected to deliver a number of advantages. It will allow managers to initiate at least some fires in areas of their choice, and by pre-empting later wildfires it will reduce the requirement to suppress many fires (a significant source of dissatisfaction with the lightning-fire approach). It could also feasibly lead to a greater area burning in less intense backfires, thus changing the fire-intensity regime (by replacing many high-intensity, daytime fires associated with prescribed burning on fixed blocks) that could have led to the decline in numbers of large trees.

Changing ecological paradigms, and changing management ethics and goals, have raised a suite of new questions about the effects of fire in African savannas. These questions will be used to guide research effort in the park over the next few decades. The most important of these include the effects of fire on the structure of tree populations, but research will also expand to include a wider range of organisms, in line with goals of conserving all elements of biodiversity. The extent to which the spatial heterogeneity of fire patterns and changes in fire intensity associated with different ignition patterns affect elements of the biota also need to be better understood.

Acknowledgments

We thank D. Woods for assistance with data analysis. B.vW. thanks the CSIR Division of Water, Environment and Forestry Technology and South African National Parks for supporting this work.

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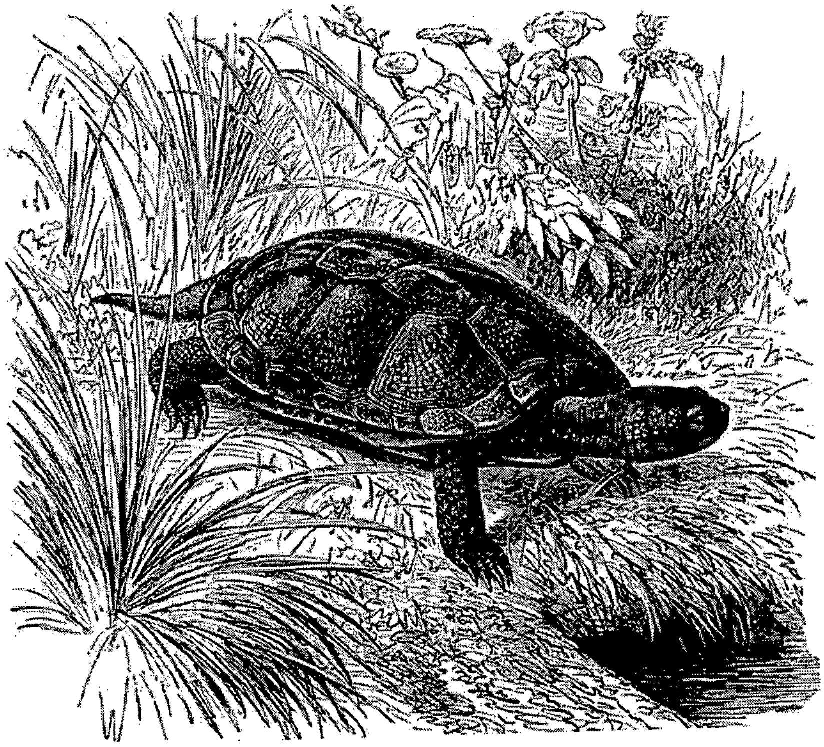

Fifth paper: The contribution of fire research to fire management: A critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire*.

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International Journal of Wildland Fire, 2007, **16**, 519–530

The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa

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Abstract. The present paper reviews a long-term fire experiment in the Kruger National Park, South Africa, established in 1954 to support fire management. The paper's goals are: (1) to assess learning, with a focus on relevance for fire management; (2) to examine how findings influenced changes in fire management; and (3) to reflect on the experiment's future. Results show that fire treatments affected vegetation structure and biomass more than species composition. Effects on vegetation were most marked in extreme treatments (annual burning, burning in the summer wet season, or long periods of fire exclusion), and were greater in areas of higher rainfall. Faunal communities and soil physiology were largely unaffected by fire. Since the inception of the experiment, paradigms in savanna ecology have changed to encompass heterogeneity and variability. The design of the experiment, reflecting the understanding of the 1950s, does not cater for variability, and as a result, the experiment had little direct influence on changes in management policy. Notwithstanding this, managers accept that basic research influences the understanding of fundamental ecosystem function, and they recognise that it promotes appropriate adaptive management by contributing to predictive understanding. This has been a major reason for maintaining the experiment for over 50 years.

Additional keywords: elephants, fire frequency, fire regimes, fire season, savanna.

Introduction

Fire is an important process in savanna ecosystems, where it acts both as a generalist herbivore (see Bond and Keeley 2005), and as a facilitator of the coexistence of trees and grasses (Higgins *et al.* 2000). Fire has long been used in the management of savannas, and this management has been informed and adapted by the findings of ongoing research. In southern African conservation (and rangeland) areas, fire was initially viewed as an evil to be avoided, and later as an agent that would maintain these areas in a pristine 'state', through its application in fixed seasons and at fixed return intervals. As savanna ecology adopted a new paradigm of non-equilibrium theory, management sought to implement more flexible approaches to the use of fire in southern African conservation areas (Mentis and Bailey 1990; van Wilgen *et al.* 1998; Bond and Archibald 2003). These developments reflected those in other parts of the world, where there has been a growing realisation that the homogeneous and regular application of fire reduces the overall productivity of rangelands, and that this has critical impacts on biodiversity and wildlife habitats (Fuhlendorf and Engle 2001, 2004). These changes in thinking have taken place over more than half a century, during which time they have gradually become accepted, and implemented in many areas.

The development of an understanding of the effects of fire is often supported by research based on the experimental application of selected fire regimes on fixed areas (see, for example, Knapp *et al.* 1998; Andersen *et al.* 2003). Such experiments reflect the thinking of the time of their initiation, but they are usually long-term in nature, with treatments often repeatedly applied for many decades. Interest in long-term ecological research has grown internationally over the last quarter century, as evidenced by the International Long-term Ecological Research initiative (www.ilternet.edu/, accessed 25 September 2007). Although the case for such research is well articulated and solid, carrying out such long-term research is beset with challenges. For example, experimental objectives often change over time, and almost all experiments are periodically threatened with closure. In many cases such experiments, once initiated, gradually become forgotten because they do not produce an ongoing stream of products, or because priorities change. The value of and continued support for such experiments is therefore the subject of ongoing debate and contention.

In the present paper, we provide a critical review of one such experiment – a long-term, plot-based, replicated fire experiment in the Kruger National Park in South Africa. The experiment was established in 1954 to provide a basis for scientific fire management of the park. Our review has three goals: (1) to assess what we have learnt from this experiment, with a special focus on the relevance of findings for fire management; (2) to examine whether and how these findings influenced changes in fire management policies in the park, against a backdrop of changing ecological paradigms; and (3) to reflect on the value and

10.1071/WF06115 1049-8001/07/050519

future of the experiment. As our focus is on the relevance of the experiment to the ongoing improvement of fire management in the park, we also briefly review the history of fire management in the park.

The Kruger National Park

The Kruger National Park was proclaimed in 1926, and covers 1 948 528 ha. It has a mean annual rainfall that varies from ~350 mm in the north to ~750 mm in the south. The rainfall regime is characterised by extended wet and dry periods, in which the rainfall is either higher than the long-term mean, or lower than the mean, for between 6 and 12 consecutive years. These extended wet and dry periods have marked effects on the occurrence of fires, mainly through their influence on grass fuel loads (van Wilgen *et al.* 2004). The vegetation of the park is a well-wooded savanna, dominated by trees in the genera *Acacia*, *Combretum*, *Sclerocarya*, and *Colophospermum*. The fire regime in the park is characterised by fires concentrated in the late dry season. Mean fire-return intervals between 1941 and 1996 ranged between 2.7 and 7.1 years in different landscapes of the park, with an overall mean of 4.5 years (van Wilgen *et al.* 2000).

Experimental fire research in the Kruger National Park

Fire research began formally in the Kruger National Park with the establishment in 1954 of an experiment to test the effects of fire on the vegetation (Van der Schijff 1958). The aim of the experiment was to study the effects of fire on the vegetation of the Kruger National Park under the grazing pressure of indigenous herbivores. This was in contrast to the fire research that had been undertaken by the government's Department of Agriculture at the time, which considered primarily domestic livestock (Van der Schijff 1958). The experiment consisted of the application of fires at varying return intervals and seasons, and protection from fire, on a series of 7 ha plots in four of the major vegetation types (Sourveld, Combretum, Knobthorn-Marula and Mopane vegetation types) of the Kruger National Park (Fig. 1, Table 1). The experiment was open to grazing and browsing by a diverse suite of herbivores, and this may have mediated or masked the effects of fire. The treatments originally included annual winter fires in August and biennial and triennial fires in August, October, December, February and April. In 1976, further treatments to examine the effects of fires every 4 and 6 years in October were added to the experiment (Table 2). Although considerable effort was made to adhere to the fire frequency and season treatments over the ~50+ year duration of the experiment, not every plot was burnt according to schedule – mainly owing to weather, lack of standing biomass, or unintentional burning. Adherence to the planned treatments tended to deviate more in the relatively arid landscapes (Fig. 2). Full details of the experimental design and application of treatments are available elsewhere (Biggs *et al.* 2003).

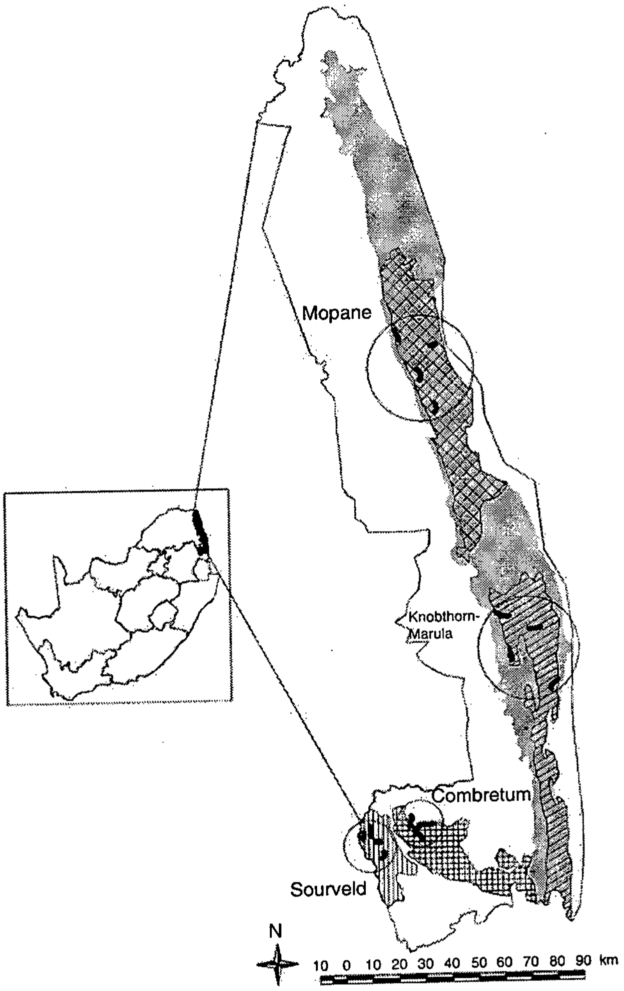

Fig. 1. Location of replicates of a fire experiment in four major vegetation types (hatched and striped areas, see Table 1) of the Kruger National Park, South Africa. The experiment was spread across a north–south precipitation gradient and among two dominant geological types (unshaded = granite, grey shading = basalt).

Table 1. Salient features of four vegetation types in which the Kruger National Park's fire experiment was replicated

Vegetation type	Dominant tree species	Geology	Mean annual rainfall (mm)
Sourveld	*Terminalia sericea*, *Dichrostachys cinerea*	Granite	705
Combretum	*Combretum collinum*, *C. zeyheri*	Granite	572
Knobthorn-Marula	*Acacia nigrescens*, *Sclerocarya birrea*	Basalt	507
Mopane	*Colophospermum mopane*	Basalt	451

In contrast to the considerable effort to adhere to the scheduled experimental treatments, there were relatively few attempts at the analysis and interpretation of data arising from the experiment during the first four decades of the experiment's existence. In order to assess scientific output, we compiled a list of all research products (published papers, reports, theses and datasets) emanating from the fire experiment. We used an earlier report (Trollope *et al.* 1998) as a starting point for the list, but eliminated many products that clearly had little or no connection with the fire experiment, and added new products produced after 1998. In total, 67 products have been produced since the

Table 2. Burning treatments applied in the fire experiment in four major vegetation types in the Kruger National Park

The symbol 'X' indicates treatments initiated between 1956 and 1958, and 'Y' in 1976 (fires at 4- and 6-year intervals were only applied in the Knobthorn-Marula and Mopane vegetation types). A dash (–) indicates that the combination of treatment and frequency did not exist

Fire treatment	Planned fire frequency (years)					
	1	2	3	4	6	>50 (no fire)
February (late summer)	–	X	X	–	–	–
April (autumn)	–	X	X	–	–	–
August (late winter)	X	X	X	–	–	–
October (after first spring rains)	–	X	X	Y	Y	–
December (mid-summer)	–	X	X	–	–	–
Protection from fire (control)	–	–	–	–	–	X

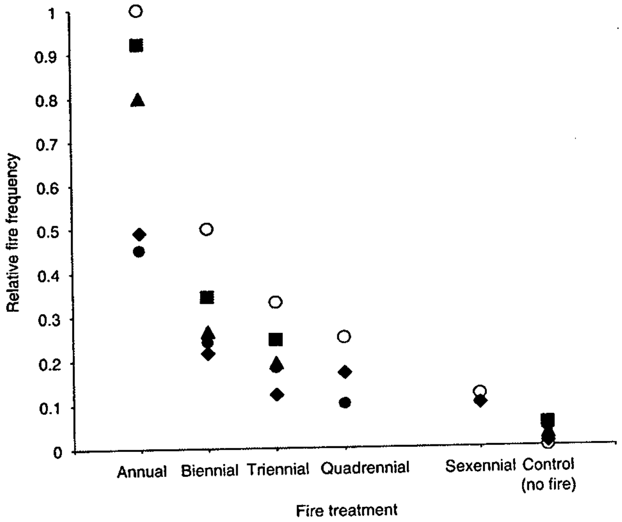

Fig. 2. The relative fire frequency (calculated as x/y, where x = the number of fires applied and y = the years of existence of the treatment) achieved for different fire treatments (various frequencies or protection from fire) on experimental burning plots in the Kruger National Park in Sourveld (■), Combretum (▲), Knobthorn-Marula (◆) and Mopane (●) vegetation types. Open circles (○) indicate the intended level of treatment.

inception of the experiment; most of these have been produced in the past decade (Fig. 3).

Focus of research during the fire experiment

The experiment commenced in 1954 with baseline surveys of the condition of the vegetation, following which routine weather observations were instituted in 1958, along with the application of planned treatments (Fig. 4). Occasional efforts were subsequently made to improve on field survey techniques (Davidson *et al.* 1961; Trollope *et al.* 1989); later, the experimental sites were used to ground-truth remotely sensed satellite data (Hetherington 1997; Landmann 2003). At the end of the 1960s, a technician (Mr A. L. F. Potgieter) was appointed with the primary responsibility of overseeing the ongoing implementation of the fire experiment. In 1971, he completed a comprehensive resurvey of the woody (but not herbaceous) vegetation on all of the experimental plots. Between 1960 and 1979, partial analyses of the response of the vegetation to burning treatments were published (Anon. 1960; van Wyk 1971; Gertenbach and Potgieter 1979; W. P. D. Gertenbach and A. L. F. Potgieter, National Parks Board of South Africa, unpubl. data).

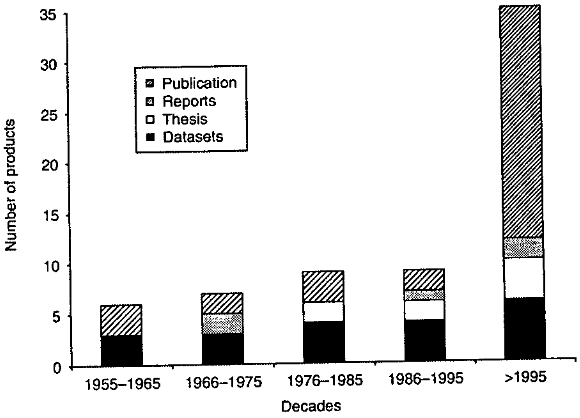

Fig. 3. The number of research products arising from the Kruger National Park's fire experiment per decade. Shading shows the type of product.

By the mid-1970s, concern was being expressed that attempts at rigid adherence to fixed-interval burning may have undesirable effects (based on a growing realisation that a degree of variability would be required in 'natural' ecosystems), and the management policy in the park was changed to allow for more flexible, and longer, intervals between fires (Biggs and Potgieter 1999; van Wilgen *et al.* 2003). In 1976, the fire experiment was modified to allow for fire treatments at longer intervals (4 and 6 years) in spring, with the additional objectives of establishing the effects of these longer intervals between fires (Biggs *et al.* 2003). The experiment's objectives and design have remained unaltered since then. Between 1977 and 1992, the plots were used, opportunistically it seems, to study the impacts of fire treatments on small mammals (Kern 1977, 1981) and on soil physiological features of the ecosystems (Webber 1979; Jones *et al.* 1990; Otter 1992).

Serious interest in the experiment was revived in 1980 when Prof. W. S. W. Trollope, a fire ecologist from the University of Fort Hare, spent a period of sabbatical leave in the park. During this year, Prof. Trollope developed and instituted a system for the routine recording of fire behaviour at all experimental burns, a step that introduced new thinking into the experiment, particularly with regard to the impacts of fire intensity on tree mortality (Trollope and Potgieter 1985; Trollope *et al.* 1995, 1996). Between 1992 and 1996, the fire experiment (again opportunistically) became a vital component of a large, international field experiment, aimed at establishing the role of savanna fires in the dynamics of atmospheric chemistry (Lindesay *et al.* 1996). This experiment, dubbed 'SAFARI-92' (an acronym for Southern African Fire–Atmosphere Research Initiative), made extensive use of the Kruger National Park's fire experiment to gather data on gaseous emissions (Andreae *et al.* 1996; Lacaux *et al.* 1996; Levine *et al.* 1996; Parsons *et al.* 1996; Shea *et al.* 1996; Ward *et al.* 1996). This highlighted the value of the experiment as a template for testing new ideas over and above those

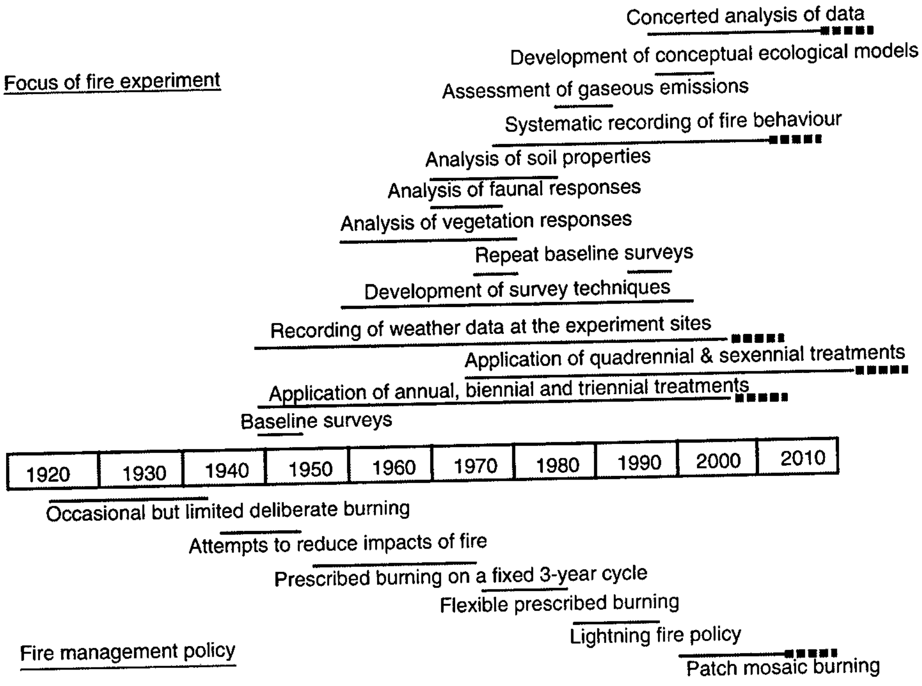

Fig. 4. Activities that formed the focus of the fire experiment in the Kruger National Park over the past century, and corresponding policies adopted for guiding fire management.

envisaged at the experiment's inception. With advances in computer technology at the start of the 21st century, data from the experimental plots were used in the development of more ecosystem simulation models, to explore the effects of fire on ecosystem dynamics (Higgins *et al.* 2000; Van Langevelde *et al.* 2003).

During the 1990s, criticism was levelled at the park's management for the lack of analysis and evaluation of its research efforts, and this (coupled with fresh capacity and enthusiasm for analysis) led to a decision to conduct a program of analysis of historic datasets (Freitag 1998). Students and visiting scientists were encouraged to assist in this process, and the wealth of data and opportunity led to several assessments of the impacts of fire on the experimental plots.

Ecological understanding gained and its relevance to management

It is not possible to do justice, in a paper such as this, to the volume of information that has emanated from the fire experiment over the past decade. Our purpose is rather to distil the essence of the findings in such a way that the broad implications for fire management can be identified (Table 3). These findings and implications are discussed below with reference to individual ecosystem components.

Effects on woody plants

Higgins *et al.* (2007) concluded that fire frequency, fire season, and total fire exclusion did not influence the size of tree populations. Counter to what was expected, there was no decrease in tree density with increasing fire frequency, and this resilience was attributed to the ability of all woody species to resprout from the base after fire. Repeated fires kept individuals small, but they rarely were killed by fire. However, fire had a marked effect on the size, structure and biomass of tree populations. The fire exclusion plots are dominated by larger trees, whereas plots treated by fire had many stunted individuals (Fig. 5). The experiment also showed that different fire regimes had little effect on the species richness of woody plants (Enslin *et al.* 2000; Shackleton and Scholes 2000; Jacobs and Biggs 2001; O'Regan 2005). In some cases, tree height was reduced slightly in dry-season burns, compared with early wet-season burns (Kennedy and Potgieter 2003). The effects of fire exclusion on woody plants were also more marked in areas of higher rainfall. For example, the increase in biomass following protection from fire over the duration of the experiment (6 tonnes ha^{-1}) at the Sourveld's experimental plots (mean annual rainfall 737 mm) was two to six times greater than that at plots in other landscapes experiencing between 496 and 550 mm of rainfall annually (Higgins *et al.* 2007).

The quantification of fire intensity at experimental fires allowed for the assessment of this aspect of the fire regime on woody plants. The degree to which the aerial parts of woody plants are scorched, forcing them to resprout from the base (topkill), was found to increase with increasing fire intensity, and to decrease with increasing plant height (Trollope *et al.* 1995). Fire season had a significant effect on fire intensity (Govender *et al.* 2006). Mean fire intensities were lowest in summer fires (1225 kW m^{-1}), increased in autumn fires (1724 kW m^{-1}), and were highest in winter fires (2314 kW m^{-1}); this was associated with a three-fold difference between the mean moisture content of grass fuels in winter (28%) and summer (88%). Mean fire

Table 3. The effects of fire on a range of ecosystem features, as determined on experimental burning plots in the Kruger National Park, and the associated implications for fire management in the park

Ecosystem feature examined	Effect of fire	Implications for management
Woody plant composition and structure	Tree and shrub density are unresponsive to fire regimes or fire exclusion; tree size is reduced as fire frequency increases. Species richness and composition are little affected by different fire treatments and fire exclusion. Exclusion of fire promotes dominance by large trees.	Fire is not critical for the maintenance of woody plant biodiversity, but does affect structure. Managers wish to reverse declines in the numbers of large trees, which is driven by interactions between fire and elephant browsing. However, given the complexity of ecosystems, manipulating fire frequency or reducing elephant numbers alone to address this issue may lead to unexpected results.
Woody plant mortality in fires	Lethal scorching of the aerial parts of woody plants, forcing them to resprout from the base, increases with increasing fire intensity, and decreases with plant height.	Managers can retard or increase the rate at which trees are recruited into the larger, fire-resistant classes by selecting appropriate fire intensity levels (see below).
Herbaceous plant composition	Community composition changes little with fires in the dormant season, but more so with fire in the wet growing season, and with fire exclusion. Impacts are most marked in wetter areas.	The manipulation of fire regimes is not critical for the maintenance of herbaceous plant species diversity. Extensive fire exclusion, or wet season fires, which would affect composition, will not be possible in reality.
Small mammals	There are noticeable effects of fire on small mammal mammal communities, with unburnt sites supporting the most species and the highest densities.	Protection from fire seems the best option for small diversity, but is not practically achievable. Some species may have to rely on fire refugia for survival.
Birds	Species richness and composition do not vary in response to fire intensity.	Bird communities are likely to be maintained within a wide range of fire regimes.
Ants	There is no significant effect of burning on ant species richness and abundance between fire treatments, but significant differences in ant assemblage composition exist between burnt and unburnt plots.	Fire is unlikely to affect the maintenance of ant diversity. The conservation of ant species associated with unburnt areas should be achieved in fire refugia.
Mycorrhizae	Mycorrhizal colonisation increases, and root branching and fine root development decreases with decreasing fire frequency, allowing for optimal acquisition of resources under different fire frequencies.	Grasses are able to cope with a range of fire frequencies, and their conservation will not depend on the maintenance of a narrow range of fire regimes.
Soil structure and nutrients	Nitrogen losses during fires are replenished regardless of the fire treatment, although the mechanisms for this are not understood. Frequent (annual) burning increases soil crusting.	There is no evidence, yet, that infrequent burning (every 2–6 years) may lead to severe nutrient losses and soil crusting. Frequent fires that cause crusting are unlikely on a large scale.
Emissions	Carbon and nitrogen emissions increase with biomass and post-fire age. Post-fire biogenic emissions of nitric oxide increase after fire.	This work alerted managers to problems, of which they were previously aware, relating to atmospheric pollution and nutrient cycling.
Fire behaviour	Mean fire intensities vary with fuel moisture but not post-fire age; seasonal fuel moisture effects thus override those of fuel load. Fire intensity can be predicted from relationships between rainfall, fuel load, and fire season.	Managers can manipulate fire intensity (and thus tree mortality) by choosing the season of fire. Estimated fire intensities from rainfall, fuel load, and fire season can enhance fire records, and the later interpretation of biotic responses to fire.

intensities showed no significant differences between annual burns and burns at 2-, 3- and 4-year intervals, despite lower fuel loads in annual burns, suggesting that seasonal fuel moisture effects overrode those of fuel load. The understanding gained as a result of this work will allow managers to potentially manipulate fire intensity (and thus tree stem mortality) by choosing the season of fire.

In general, these findings suggest that trees and shrubs will persist under a wide range of fire regimes, and that manipulation of fire is not critical for the maintenance of woody plant biodiversity. However, managers are concerned that there has been a decline in the number of large trees in the park (Eckhardt *et al.* 2000), and that this decline is driven by the interactions between fire and browsing by elephants (van Wilgen *et al.* 2003). Although total fire exclusion will promote the retention of large trees, it is not a practically achievable or otherwise desirable option. Currently, there is a vigorous debate around the management of elephant populations (Owen-Smith *et al.* 2006), as managing the size of elephant populations may offer the only practical solution to the problem of declines in the numbers of large trees. Whereas managers can possibly increase the rate at which trees are recruited into the larger, fire-resistant classes by selecting for conditions of lower fire intensity and topkill, it is not known whether manipulating fire alone would solve the

Fig. 5. Experimental burning plots in the central area of the Kruger National Park in 2006. Fire was excluded from the plot on the right for 50 years, whereas the plot on the left was subjected to fire every 2 years (Photo N. Govender).

problem. In a recent review of the implications of current ecological thinking for biodiversity conservation, Wallington *et al.* (2005) point to the fact that ecosystems are complex and are made up of many different species and processes that interact in different ways. Management actions that target a single species (such as elephants) or process (such as fire) alone are likely to lead to unexpected results that could cascade through the whole system, and a broader, systems approach may be required (e.g. Zavaleta *et al.* 2001).

Effects on herbaceous plant composition

Detailed analyses currently in progress indicate that fires in the dormant season had relatively little effect on the community composition of herbaceous plant species (M. D. Smith, unpubl. data). In contrast, fires in the wet season, and fire exclusion, resulted in changes to the herbaceous plant community composition over the duration of the experiment. For example, plots earmarked for different treatments were found to have been similar in terms of grass species richness at the start of the experiment, whereas after 50 years of treatment, plant species richness was consistently lowest on plots where fire had been excluded, or where they had been burnt in the wet growing season (February). As was the case with woody species, mean annual rainfall also influenced the results, with the effects of fire exclusion and of wet season fires being most marked on plots in areas of higher rainfall. In more arid areas, where fire treatments could not be applied as often as intended (Fig. 2), the responses of the herbaceous plants to different fire treatments were less clear, and possibly masked by the competing effects of herbivory and climatic variability.

These findings also suggest that the manipulation of fire regimes is not critical for the maintenance of herbaceous plant species diversity. Fire exclusion or extensive wet season fires, which would affect composition, are not practical options as it would not be possible to apply them consistently over large areas. The manipulation of grazing pressure (for example through the establishment or removal of artificial water sources, which have been employed extensively in the park) may be more effective ways of influencing herbaceous plant community composition (Gaylard *et al.* 2003).

Effects on small mammals

A study of small mammal dynamics on the experimental burning plots identified 11 species (nine rodents, one shrew and one elephant shrew). Protection from fire led to relatively high, stable small mammal density, biomass and diversity (Kern 1981). Annual fires, on the other hand, led to domination of the small mammal community by a single rodent species (*Tatera leucogaster*), whereas triennial burning treatments were characterised by a cycle of species determined by post-fire age. On plots burnt every 3 years, *T. leucogaster* dominated in the first year after fire, followed by domination by other rodent species, and finally by the shrew species *Crocidura hirta* in the third year after fire. Thus, whereas protection from fire seemed the best option for the conservation of small mammals, it was recognised that this would neither be possible nor desirable. Kern (1981) concluded that many small mammal species would be conserved, albeit in smaller numbers, in fire refugia across the park. This work indicated, therefore, that managers would not have to focus on the establishment of a narrow range of fire regimes to conserve small mammals.

Effects on ants

A study of the responses of ant communities to fire treatments at the Sourveld, Knobthorn-Marula and Mopane sites found no significant effect of burning on mean ant species richness and abundance between treatments, although there were significant differences in ant assemblage composition between the burnt and unburnt (control) plots (Parr *et al.* 2004). The study concluded that epigaeic ant assemblages appeared to be highly resistant and resilient to burning. The response of ants to fire was linked to changes in habitat cover and structure: the effect of fire on vegetation and ants was less pronounced in lower rainfall areas, where differences in vegetation structure between burnt and unburnt plots were less pronounced than in higher rainfall areas. Because of the very small effects of fire on ant communities, the study specifically recommended that conservation managers need not be concerned about the effects of fire on ant species diversity, but that they should rather 'focus concerns regarding the subtleties of fire regimes on other taxa or areas of particular concern'.

Effects on birds

Although an attempt was made to assess the effects of long-term burning treatments on bird species, the experimental burning plots proved to be too small for this purpose. The impact of fire on bird communities was therefore assessed by comparing larger areas burnt in low- and high-intensity fires with unburnt sites (Mills 2004). The study found that species richness did not differ between these treatments. Some species were less common in some treatments (for example ground-feeding and granivorous species were less common at sites that had high-intensity burns), but in none of the treatments was any species entirely absent. The study concluded that bird communities are likely to be robust to all but the most extreme fire policies, such as, for example, total fire exclusion. It was specifically noted that a 'hands-off fire policy is unlikely to affect bird communities negatively'.

Effects on mycorrhizal symbiosis

Mycorrhizal symbiosis is recognised as a key factor that could influence the response of grasses to fire and herbivory. The relationships between fire treatments, grass root architecture and mycorrhizal symbiosis were investigated on the experimental burning plots (Hartnett *et al.* 2004). Eighteen grass species were sampled on plots burnt every 1 and 3 years, as well as in unburnt plots. All 18 species were found to be highly colonised by arbuscular mycorrhizal fungi (AMF). Both mycorrhizal symbiosis and root system architecture were strongly affected by fire, with an increase in AMF colonisation and a decrease in root branching and fine root development with decreasing fire frequency. The fact that mycorrhizal colonisation and root system fibrousness showed opposite trends across the range of fire frequency treatments indicated that maintaining an extensive system of fine roots or an extensive network of mycorrhizal hyphae represent alternative strategies for maximising acquisition of soil resources under different fire regimes. Although Hartnett's study did not specifically address the management implications of these findings, it implies that managers need not be concerned that adherence to narrow fire regimes would have any disadvantages in terms of grass species' abilities to retain adequate levels of access to nutrients.

Effects on soil

Nitrogen is lost through volatilisation during fires, but studies on the experimental burning plots revealed that soil % nitrogen did not decrease with increasing fire frequency, suggesting that nitrogen losses are replenished in both regularly (annually) and less regularly burnt areas (Aranibar *et al.* 2003). In apparent contrast to the findings regarding effects on woody shrubs in other studies, the relative abundance and nitrogen fixation of woody legumes decreased with increasing fire frequency, suggesting that woody legume nitrogen fixation is not the mechanism that balances nitrogen losses. The relatively constant % nitrogen in all fire treatments suggests the presence of other mechanisms to balance nitrogen losses by fires. A study of soil microbial communities on all burn treatments (Feig 2005) assessed overall bacterial community structure, and inferred metabolic activity through the measurement of soil respiration. It was found that there was no significant difference in soil respiration rates between fire treatments, soil types or seasons. Annual burning was also found to increase soil crusting (Mills and Fey 2004). Mills and Fey's study suggested that this may be self-perpetuating, because increased runoff is likely to increase the loss of soluble salts. However, there is no evidence, yet, that infrequent burning (every 2–6 years) may lead to severe nutrient losses and soil crusting. Frequent (annual) fires that cause crusting are unlikely on a large scale.

Effects on gaseous emissions

The SAFARI-92 initiative (Lindesay *et al.* 1996) made extensive use of the Kruger National Park's fire experiment to gather data on gaseous emissions, both during flaming and smouldering combustion, as well as from biogenic emissions following fires. The SAFARI work was not intended to address the aims of the experiment, but rather it made use of the infrastructure and fire management expertise available to address questions relating to the role of fire in affecting the chemistry of the atmosphere (Andreae *et al.* 1996; Lacaux *et al.* 1996; Levine *et al.* 1996; Parsons *et al.* 1996; Shea *et al.* 1996; Ward *et al.* 1996). The findings included that the magnitude of carbon and nitrogen emissions during fires is influenced by biomass, which is in turn influenced by post-fire age. Post-fire biogenic emissions of nitric oxide increased after fire, and were highest following fire on plots that had been unburnt for 35 years (this finding required that one of the control plots in the Sourveld area be burnt). The main focus of the SAFARI work was to provide information of relevance at a subcontinental to global scale, in terms of understanding the role that vegetation fires play in the dynamics of atmospheric chemistry. Although this work had macroscale aims from which the park's managers originally expected a low level of direct benefits, it brought home the realities of potential deposition of industrial and motor vehicle emissions and possible nitrogen leaks from upstream areas. These are important areas in which conservation authorities could easily have remained conceptually disconnected (Biggs 2003). Through having these links pointed out, managers and researchers in the park gained valuable integrative insights. These have enabled them to engage in debates on activities outside the park's boundaries that would impact on ecosystem function and conservation within the park.

Overall effects of fire

The picture that emerges from this is that fire has less effect than may have been expected. The effects of fire on the vegetation were more marked in areas that received higher rainfall, but the most notable effects are from treatments that deviate most from the existing (and for all practical purposes the achievable) fire regime. These include extremes of fire frequency (either annual burning, or total exclusion of fire), or burning in the summer wet season. None of these are practical or desirable options for fire management. Whereas fire had little effect, the total exclusion of fire had striking effects, especially in terms of increases in aboveground plant biomass, and especially in areas of higher rainfall. It is important to consider, though, that because the experiment was open to grazing and browsing, the effects of fire may have been mediated or masked; herbivory and fire are known to strongly interact in other grassland ecosystems (Collins *et al.* 1998).

Changing paradigms in savanna fire ecology

In addition to findings based on the fire experiment, many new insights into the role of fire in African savannas have arisen from other research. The adoption of a heterogeneity paradigm, with variability as a central concept (Mentis and Bailey 1990; Rogers 2003) has required thinking about the use of fire in ways quite different to the fixed-area, fixed-return interval approach that characterised the 1950s to 1980s. The fact that grasses and trees coexist in savannas has been explained by disequilibrium models that invoke the irregular occurrence of fires in preventing the development of a stable state in savanna ecosystems (Scholes and Archer 1997). Higgins *et al.* (2000) were able to demonstrate a plausible mechanism that underlay this process – the need for variability in the intensity of successive fires. A study of the fire records for the entire Kruger National Park over more than 40 years also revealed that the area that burnt in any given year was strongly related to rainfall (and therefore grass fuels) in the preceding 2 years (van Wilgen *et al.* 2004); it was variability in rainfall that governed the extent of fires, and not management. Variability in fire-return periods was also strongly influenced by the sequencing of annual rainfall rather than by management. It is many of these new insights, rather than information arising from the fire experiment, that have provided the impetus for changes in management approaches in the park (see below).

How well did the treatments approximate the park's fire regimes?

The fire treatments chosen for inclusion in the fire experiment were assumed to be representative of a potential suite of regimes that could underpin management at the time that the experiment was initiated. The mean fire frequencies in the landscapes in which the experiment was established have subsequently been found to be longer (up to 7.2 years) than the 1–3-year range initially chosen for the experiment (van Wilgen *et al.* 2000). This was realised in 1976, when fires on 4- and 6-year cycles were added to the experiment. In reality, fire-return periods in the park are variable and skewed. For example, fires at 1- or 2-year return intervals were found to account for 65% of all area burnt per year in the Kruger National Park, but occasional longer fire-return periods (up to 30 years or more) ensured a higher mean (van Wilgen *et al.* 2000). Thus, although annual, biennial and triennial burn treatments are probably representative of most individual fires, they do not account for occasional longer periods between fires, which may have important ecological effects, especially in terms of the recruitment of trees into fire-resistant size classes (Higgins *et al.* 2000; Van Langevelde *et al.* 2003). The fire intensities achieved in the experimental burns were probably also not representative of the full range of actual intensities found over large areas. This is because experimental fires were mainly carried out under milder conditions for reasons of safety, resulting in fire intensities between 700 and $2800\,\mathrm{kW\,m^{-1}}$. Many landscape-scale fires would be of higher intensity (a small number of experimental plot fires exceeded $15\,000\,\mathrm{kW\,m^{-1}}$; Govender *et al.* 2006), again with significant ecological consequences for trees (Trollope *et al.* 1995).

Fire management in the Kruger National Park

Since the proclamation of the park, fire management has passed through several phases (van Wilgen *et al.* 2003). Between 1926 and 1947, occasional but limited burning was carried out to promote grazing. Between 1948 and 1956, deliberate attempts were made to reduce the impacts of fire, by ensuring, wherever possible, that no area burnt more often than once every 5 years. From 1957 to 1980, prescribed burning was introduced with the intention of establishing a regular, 3-year fire-return interval. The park was divided into around 400 fixed areas (called 'burning blocks'), and a program of prescribed burning intended to ensure that these blocks burnt every 3 years was initiated. This was to have continued until such time as evidence could be produced to support an alternative management approach. Between 1981 and 1991, this was changed to become more flexible. Fires were timed to take fuel loads, post-fire age and mean annual rainfall into account, with the intention of establishing more variable return intervals. Between 1992 and 2001, a 'natural' fire policy was introduced, in which lightning-ignited fires were allowed to burn freely, while at the same time attempts were made to prevent, suppress or contain all other fires. Since 2002, the park has adopted a hybrid system of patch mosaic burning (Brockett *et al.* 2001) and lightning fires, with tolerance of wildfires under certain conditions. Fire patterns are monitored, and tested against 'thresholds of potential concern' (van Wilgen *et al.* 1998; see below) within a framework of adaptive management (Biggs and Rogers 2003).

The concept of management by 'thresholds of potential concern' was introduced in the Kruger National Park in the mid-1990s (Biggs and Rogers 2003). Under this framework, upper and lower thresholds were defined for a range of ecosystem indicators. If a threshold is reached, then management interventions are considered; alternatively, the threshold could be recalibrated. In line with this policy, a range of thresholds relating to fire patterns was proposed (van Wilgen *et al.* 1998). The framework included thresholds relating to fire-return periods, the seasonal distribution of fires, the range of desired fire intensities, the size-class distribution of fires and the cause of fires (whether they were 'natural' lightning fires, or fires initiated by humans). Deviations from these thresholds were intended to alert managers to the possibility that fires were either too frequent, too infrequent, or otherwise deviating from acceptable limits in the area concerned. The way in which this influenced fire management policy is discussed further in the next section.

Recent studies (van Wilgen *et al.* 2004; Govender *et al.* 2006) investigated the impact of changing management approaches on the park's fire regimes between 1956 and 2001. They found that, at the scale of the entire park, the area that burnt in any given year was independent of the prevailing management policy; rather, it was strongly related to rainfall (and therefore grass fuels) in the preceding 2 years. Mean fire-return periods varied between 5.6 and 7.3 years under the different management policies, and variability in fire-return intervals was strongly influenced by the sequencing of annual rainfall rather than by management. These findings were surprising as they indicated that management had less influence on fire occurrence than many would have believed. On the other hand, management did affect the spatial heterogeneity of fires, their seasonal distribution, and the intensity of fires.

The relative influence of fire research on fire management policies

Scientific data and understanding do not constitute the only basis for management or policy decisions, but they can and should provide important inputs (Polikansky 1998). At the initiation of the Kruger National Park's fire experiment, it was the intention that information gathered, and periodically synthesised, would be used to improve fire management from time to time. The question can now be asked whether that was in fact the case, and also whether or not the research constitutes a valuable ongoing investment for managers. This question is best addressed by examining the rationale behind the changes in fire management approaches in the park, following the initiation of the fire experiment.

There is only one published account of the earlier management recommendations arising from the burning experiment (Anon. 1960). The report reviews preliminary experimental findings, and goes on to make several surprisingly detailed recommendations without linking them to the results of the experiment. These include the proposed exclusion of the catchment areas of rivers and wetlands from the burning program, the need for inspections of areas due to be burnt before a final decision was made to burn, the abandonment of burning in August and September and the requirement that at least 2 inches (50 mm) of rain should fall before any burning was initiated, and the total exclusion of areas in the north from the burning program because of their 'exceptional' plant growth. This approach essentially sought to inform management decisions by utilising expert opinion. Such expertise resided in individuals whose task it was to gain understanding from field observation and experimentation. Although the recommendations made could not have been based on the results of the fire experiment, they provide an early example of the close links that developed between researchers and managers in the park over the next few decades.

The first policy change after the initiation of the fire experiment came about in 1981. At this time, the intention to replace the more rigid attempt to apply fires on a 3-year cycle with flexible prescribed burning was made. The concerns expressed at the time are listed by van Wilgen *et al.* (2003), and were based on widespread observations of deteriorating grassland condition, and declining numbers of large trees. In addition, there were growing opinions that perimeter ignitions (rather than point ignitions, such as those associated with lightning-ignited fires), and a lack of variation in fire regimes, were detrimental. The degree to which the fire experiment influenced these changes is not clear, or documented, although experience gained by researchers in the application of (or inability to apply) scheduled treatments must have informed the debate to some degree.

The second major policy change in 1992 led to the introduction of a lightning-driven fire policy. The rationale for implementing this policy is summarised by Biggs and Potgieter (1999) as follows:

> In 1992, forces within park management supporting notions of wilderness ecosystem management, and to an extent those striving to promote landscape patchiness, were able to obtain an overwhelming majority decision to alter the nearly 40-year run of rotational burning to an intended system of lightning-induced fires. The decision to change was taken in the face of an available alternative ... developed for the Kruger National Park in 1991.

(The alternative was based on the assessment of grass sward composition as a basis for deciding to burn or not.) As with the earlier change in 1980, information from the fire experiment apparently did not play any significant role in the decision, which hinged on ideals of wilderness management, and was influenced by developing ecological paradigms of heterogeneity.

The rationale behind the next policy change in 2001 is summarised by van Wilgen *et al.* (2004) as follows:

> (The change) was triggered by a threshold that sought to limit human-caused fires to less than 25% of the area burnt in a given year (this threshold was included because the 'natural-fire' policy rested on promoting lightning ignitions). When the threshold was exceeded in 1996, managers first changed the target area from 25 to 50%, then from an annual total to an average over 10 years. However, before the 10-year period had been reached, it became clear that it would in any case be exceeded. Most of the area that burnt in the 10 years that the lightning policy was in force burnt in fires not started by lightning (lightning fires burnt only 757 660 out of 3 210 543 ha, or 23.6%, and most fires were ignited by transborder migrants). This, coupled with growing pressure from managers who were required to contain most fires, led to the policy being changed in April 2002.

It is clear, therefore, that this final change was also uninfluenced by results from the fire experiment.

The above assessment indicates that the fire experiment was not as important in influencing changes in policy as its originators may have intended it to be. There appear to be three important reasons for this. First, changing paradigms in ecology rendered the suite of chosen fire treatments unsuitable for addressing new questions, as they were not designed to cater for variable fire intervals and seasons on the same spot. Second, major policy changes were made in the absence any comprehensive analyses of the effects of the fire treatments; although the experiment had been maintained, it was not subjected to detailed analysis until the late 1990s (Fig. 3). Finally, changes in policy were not based on scientific evidence alone; philosophical issues were often the dominant reason for change. Other than for the addition of new treatments to the experiment (in 1976) and the subsequent policy change from fixed to flexible prescribed burning in 1981, there does not appear to be obvious correspondence between the experiment and fire management (Fig. 4).

Despite this, it should not be concluded that the experiment did not have value. It has provided experience in the application of various fire treatments over a long period and the opportunity for observation of responses, and allowed the development of understanding in a cohort of people who are now, as a result, able to debate and decide on issues relating to fire and its effects with a degree of confidence. In addition, as discussed below, the experiment will also provide a template for testing new ideas.

Conclusions

The Kruger National Park's long-term fire experiment has faced problems typical of many such experiments elsewhere. The objectives of fire management have changed over the past half a century in response to changing paradigms in savanna ecology (from 'balance of nature' to 'flux of nature' concepts) and a new focus on the broader conservation of biodiversity (as opposed to the conservation of large game animals; Bond and Archibald 2003). The experiment was therefore not ideally equipped to deal with new questions, or to address the full suite of 'thresholds of potential concern' relating to fire patterns that were developed in the 1990s to guide the park's fire management (van Wilgen *et al.* 1998). For these and other reasons, the experiment has been criticised, and has been under threat of closure. For a long period, the experiment produced very few tangible products (Fig. 3), and as a result was not highly visible – this would have caused an unintended increase in its vulnerability.

The fact that the Kruger National Park's fire experiment has been, and still is, maintained is remarkable, given that it has not played an obviously dominant role in informing major management decisions – the principal reason for its establishment. Its continued existence today is probably the result of a combination of factors. These include its dedicated maintenance by a small number of people, as well as a widely held belief among managers that basic research will influence the understanding of fundamental ecosystem function, and hence ultimately promote appropriate management (Biggs 2004). There is recognition, embedded in the park's culture and based on a history of science-based management, that basic research is necessary to make good decisions about how to manage ecosystems. This has led to an ongoing support of research, including support for the fire experiment, even if the results did not have obvious immediate application. Today, given the growing importance of adaptive management (Biggs and Rogers 2003), the fire experiment forms an important component of the integrated approach that incorporates inventory and monitoring, research, and adaptive management (Wallington *et al.* 2005).

The experiment has also delivered some benefits that were unforeseen at the time of establishment. The baseline surveys conducted at the start of the experiment provide a sample of the vegetation condition in the park in the 1950s, and are the only existing, detailed information on the state of the vegetation at the time. As such, they are a valuable resource in their own right, and have recently provided the only data against which the impact of growing numbers of elephants can be assessed. The management of the park's burgeoning elephant population, and the effects of such management on vegetation, have developed into a major issue (Whyte *et al.* 2003; Owen-Smith *et al.* 2006). Having a benchmark against which these impacts can be assessed is extremely valuable, and would not have existed if it were not for the fire experiment's baseline surveys. The use of the experiment to address new and unforeseen questions (such as the role of vegetation fires in the dynamics of the atmosphere; Lindesay *et al.* 1996) provides further confirmation of its value, as does its use in the interpretation of satellite images (Heatherington 1997; Landmann 2003) and for the development of conceptual ecological models (Higgins *et al.* 2000; Van Langevelde *et al.* 2003). Currently, and in the light of these considerations, the experiment is viewed as a comprehensive scientific outdoor laboratory to be utilised to promote the understanding of fire–herbivory interactions and the effects of different combinations of fire frequency and season on the ecosystem. The experiment will in all likelihood also become part of the South African Earth Observation Network (SAEON; Van Jaarsveld and Biggs 2000). The SAEON network aims to provide long-term reliable data for scientific research and for informing decision-making for a knowledge society and an improved quality of life.

Seen from an ecological perspective, the experiment remains extremely valuable, and provides useful opportunities for the testing of ideas, by virtue of having been subjected to rigorous, repeated, and documented fire treatments over many decades. Such sites are very difficult to find, and the experiment has already been fruitfully used to test emerging ideas in ecology and global change. Indications are that this role is set to grow in importance. The fire experiment has recently provided the basis for examining new research questions, with a view to developing an improved conceptual and predictive understanding of savanna ecology. This will be attempted through the additional experimental manipulation of the vegetation under different fire treatments. The additional treatments include, for example, the complete fencing of some plots, and the erection of smaller exclosures, and irrigation and shelter from rainfall on others. These experiments have already been initiated utilising research funding from donor foundations, and are aimed at examining the combined effects of fire, herbivory, and rainfall on the dynamics of the vegetation. The effects of fire may not manifest themselves over the short time periods covered by most experiments, and this experiment provides an ideal template for examining the long-term consequences of ecosystem manipulation. In addition, the existence of this established, long-term experiment located in an area that still supports the full complement and diversity of large mammalian herbivores under whose influence the vegetation evolved make it a unique asset.

Finally, the experiment also provides the opportunity to physically demonstrate the consequences of the application or exclusion of fire over many decades to a range of stakeholders, from policymakers to ecosystem managers and students. With regard to the last group, the experiment is regularly used as part of the field curricula of local and international students of ecology, and as a basis for research by masters and doctoral students. We conclude, therefore, that the experiment is and will remain extremely valuable.

Acknowledgements

We thank South African National Parks for access to data and information, and Mendy Smith for valuable comments on the manuscript. The team that maintained the experiment for many decades, especially Andre Potgieter, deserve special mention. We also acknowledge the significant contribution of Winston Trollope in rekindling and developing the science behind the experiment in the 1980s.

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Manuscript received 12 August 2006, accepted 23 July 2007

First paper: The effect of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *Journal of Applied Ecology*.

Selected papers on the ecology and management of invasive alien plants.

Journal of Applied Ecology (1985) **22,** 955–966

THE EFFECTS OF ALIEN SHRUB INVASIONS ON VEGETATION STRUCTURE AND FIRE BEHAVIOUR IN SOUTH AFRICAN FYNBOS SHRUBLANDS: A SIMULATION STUDY

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SUMMARY

(1) South African fynbos vegetation is fire-prone and susceptible to invasion by alien shrubs. Alien shrubs change the nature of the fuel bed and thus affect fire behaviour.

(2) Changes in biomass, size and distribution of plant parts as fuel and plant moisture and energy contents were determined at two sites invaded by the important alien shrubs *Hakea sericea* Schrad. and *Acacia saligna* (Labill.) Wendl.

(3) The data were used to define fuel models and to simulate fire behaviour using Rothermel's fire model. This simulation was used to test the hypothesis that invasion increases fire hazard through increasing fuel loads.

(4) Invasion by *H. sericea* resulted in a 60% increase in fuel load and lowered the moisture content of live foliage from 155 to 110%. Simulated rates of fire spread and intensity were nonetheless lower than in fynbos due to a densely-packed fuel bed.

(5) Invasion by *A. saligna* resulted in a 50% increase in fuel load. The high moisture content of foliage of this shrub (about 270%) effectively reduces the fuel load and fuel bed depth, resulting in low rates of fire spread and intensity in the simulation.

(6) Shortcomings in Rothermel's model prevented the accurate simulation of high intensity fires which have occurred in invaded areas under extreme weather conditions. Such fires vigorously consume the increased biomass of shrub crowns, are difficult to content of foliage of this shrub (about 270%) effectively reduces the fuel load and fuel bed Under such conditions, the fire hazard will be increased by invasion.

INTRODUCTION

The sclerophyllous shrubland vegetation of the south-western Cape Province of South Africa is known locally as fynbos. The name is derived from the Afrikaans terms for 'fine' and 'bush', reflecting the finely-divided and bushy nature of the vegetation. Most remaining fynbos vegetation occurs in mountain areas which are managed as water catchments and for nature conservation. Fires occur in fynbos vegetation at intervals of between 6 and 40 years (Kruger & Bigalke 1984). Fynbos vegetation is fire-adapted (Bond 1980; van Wilgen 1982) and fire is necessary for species survival, but fires also cause control problems in semi-developed areas.

Alien woody weed species invade fynbos with remarkable success in many areas. They often form dense and impenetrable stands which dominate the vegetation and replace native shrubs entirely. Kruger (1979) lists the major disadvantages of such invasions as: (i) drastic changes in natural community structure, including reduction in species diversity; (ii) increase in fire hazard through increased fuel loads and decreased accessibility; (iii) reductions in surface water resources; and (iv) reduction in aesthetic, recreational and scientific values of fynbos communities. Macdonald & Jarman (1984) list thirty-three species of invasive plants which pose a threat to fynbos ecosystems. These were ranked according to the extent of current infestation and their potential as invasive species. The small Australian tree *Acacia saligna* (Labill.) Wendl. (Fabaceae) is listed as posing the greatest threat to fynbos ecosystems, while the Australian shrub *Hakea sericea* Schrad. (Proteaceae) has invaded the largest area. The management of fynbos consists largely of controlling and applying fire, and of controlling invasions of woody weed species.

The changes in vegetation structure brought about by invasion need to be quantified in order to assess their effect on fire hazard. The term 'fire hazard' is concerned with the condition of fuel and takes into consideration such factors as quantity, arrangement, current or potential flammability and the difficulty of suppression if fuel should be ignited (Luke & McArthur 1977). Potential fire behaviour is central to the fire hazard rating problem and it will be changed by changes in vegetation structure. Some data on fire behaviour in fynbos are given by Van Wilgen, Le Maitre & Kruger (1985), who obtained reasonable estimates of fynbos fire behaviour using Rothermel's (1972) fire model. A review of the development of this model, its uses and limitations is given by Albini (1984). The model requires estimates of the physical and chemical makeup of the fuel, and the environmental conditions under which it burns. Fuel characteristics are summarized in fuel models, which are sets of values that quantify vegetation stands as fuel beds. The following data are required to define a fuel model (Deeming & Brown 1975): (i) Fuel loads (biomass) divided into dead and live components. Dead fuel is further divided into size classes and live fuel into herbaceous or woody (leaves and twigs < 6 mm diameter only) components. Dead fuel size classes are based on the time their moisture content takes to adjust to changes in atmospheric conditions, and are 1 h timelag fuels (0–6 mm), 10 h timelag fuels (6–25 mm), 100 h timelag fuels (25–75 mm) and 1000 h timelag fuels (>75 mm); (ii) Surface area to volume ratios of the above fuel components; (iii) The fuel bed depth; (iv) A mean fuel energy content for the combined fuel mass. Structural changes due to invasion can be incorporated into fuel models and comparisons can be made by estimating fire behaviour for different structural categories of vegetation under identical weather conditions.

This study was aimed at quantifying changes in above-ground biomass, stratification, height, the size of plant parts as fuel and plant moisture and energy contents brought about by converting pristine fynbos vegetation to vegetation dominated by *H. sericea* or *A. saligna*. The data are used to define fuel models for the invaded sites. Estimates of fire behaviour in invaded areas are compared to estimates using a fynbos fuel model (van Wilgen 1984), to test Kruger's (1979) hypothesis that fire hazard is increased through increased fuel loads brought about by invasion.

THE STUDY AREAS

Biomass and structure of invaded areas were determined at two 50 × 50 m sites. The first is situated on the Vergelegen Estate, where there was a heavy infestation of *H. sericea* (*c.* 8900 stems ha^{-1}). The presence of scattered individuals of the native shrubs *Protea repens* (L.) L. and *P. neriifolia* R. Br. and comparison with adjacent uninvaded areas indicated that the original vegetation was a tall shrubland dominated by these two species. The second site was situated on a rocky slope above the town of Muizenberg. The original fynbos vegetation in the area had been replaced through invasion by *A. saligna* (*c.* 9800 stems ha^{-1}). The data from invaded sites were compared to data from two pristine fynbos sites in the Kogelberg and Cederberg Forest Reserves. Previous studies on these sites include the development of a fynbos fuel model (van Wilgen 1984) and the measurement of fire behaviour (van Wilgen, Le Maitre & Kruger 1985). Salient features of these four sites are given in Table 1.

TABLE 1. Principal features of four sites used to determine fuel models in pristine and invaded fynbos vegetation

Site	Vegetation	Position	Geology	Mean annual rainfall (mm)	Altitude (m)	Slope (%)	Aspect	Vegetation post-fire age (years)
Vergelegen Estate	*Hakea*-invaded fynbos	34°02′S 18°56′E	Sandstone-granite mixtures	1200	375	0	—	9
Muizenberg	*Acacia*-invaded fynbos	34°04′S 18°27′E	Sandstone	1000	120	23	N.E.	20
Kogelberg	Fynbos	34°16′S 19°00′E	Sandstone	1020	110	0	—	18
Cederberg	Fynbos	32°20′S 19°03′E	Sandstone	660	470	17	E.	18

METHODS

Biomass and fuel loads of invaded areas

Biomass was determined by collecting all plant material, except for dominant alien shrubs, from a random sample of ten plots (2 × 2 m). Clipped material was divided into the following categories: (i) woody shrubs other than dominant shrubs; (ii) herbaceous (non-woody) plants; and (iii) litter (all dead material including standing dead). These categories were separated into pieces with diameters of less than and greater than 6 mm. This division followed the convention used in estimating available fuel in fuel models (Countryman & Philpot 1970; Deeming & Brown 1975; van Wilgen 1982). Estimation of the biomass of dominant alien shrubs was done by regression analysis. Twenty shrubs, selected to cover a representative range of diameters, were harvested outside the sites after measuring their diameters 10 cm above the ground. Each shrub was divided into potential fuel (pieces with diameters <6 mm) and larger pieces, weighed and then subsampled for moisture content to estimate the dry weight of the original material. Linear, power and exponential regressions of stem diameter on dry weight were fitted. In all cases power curves gave the highest r^2 values. The resultant equations for *H. sericea*, where x is the diameter (cm) and y the mass (g) were

(i) diameter and total dry weight:

$$y = 100{\cdot}76\, x^{2{\cdot}30},\ r^2 = 0{\cdot}95 \qquad (1)$$

(ii) diameter and dry weight of fuel:

$$y = 80{\cdot}48\, x^{1{\cdot}83},\ r^2 = 0{\cdot}94 \qquad (2)$$

A similar allometric model for *A. saligna* gave

(i) diameter and total dry weight:

$$y = 58{\cdot}67\, x^{2{\cdot}49},\ r^2 = 0{\cdot}99 \qquad (3)$$

(ii) diameter and dry weight of fuel:

$$y = 19{\cdot}30\, x^{2{\cdot}00},\ r^2 = 0{\cdot}93 \qquad (4)$$

The stem diameter of each *H. sericea* shrub occurring on two random transects of 50 × 2 m was measured and the dry mass of the shrubs calculated from eqns (1) and (2). The same procedure was followed on the second site for *A. saligna* using eqns (3) and (4).

Size of plant parts as fuel

Surface area to volume ratios were determined for the fuel component of the two invasive species. The diameter of twenty leaves of *H. sericea* were measured in two places using callipers, and a mean diameter was calculated. The leaves were regarded as cylinders for the purposes of calculating surface areas and volumes. The area of each of a sample of twenty leaves of *A. saligna* was calculated using a surface area meter. Leaf thickness was measured using callipers. Surface areas and volumes were calculated using these estimates.

Vegetation height and stratification

Data on vegetation height and stratification were obtained from a transect (1 × 10 m) at each of the invaded sites and from the Kogelberg site. The transects were positioned in an area with vegetation judged to be representative of the site. The following data were recorded on each transect: (i) mean depth of the litter layer at 0·5 m intervals across the transect; and (ii) the height, crown diameter and height of the lowest leaves of each plant on the transect. Plants were recorded as either dominant shrubs (*A. saligna*, *H. sericea* or other microphyllous shrubs similar to the indigenous genus *Protea*), other microphyllous shrubs, picophyllous shrubs similar to the indigenous genus *Erica*, evergreen herbaceous plants similar to the indigenous genus *Restio* and standing dead plants. The data were used to draw profile diagrams and to define fuel bed depths.

Fuel moisture contents

The moisture content of foliage of *H. sericea* and *A. saligna* shrubs was compared to that of the indigenous shrub *Protea repens*. *Protea repens* is widespread and often dominant in fynbos vegetation, and it was used in defining the fynbos fuel model (van Wilgen 1984). A site where all three species grew within 20 m of each other was located in the Jonkershoek valley (33°57′ S, 18°55′ E). Five samples of the foliage of each species were taken on five different days in December 1984. Samples were sealed in air-tight bottles to prevent moisture loss, weighed and oven dried. The percentage moisture content was calculated on a dry weight basis.

Fuel energy contents

The energy contents of three samples of the foliage of both *H. sericea* and *A. saligna* were determined using standard bomb calorimetry.

Simulation of fire behaviour

Biomass and other structural data were used to define fuel models for each site. Fire behaviour predictions were made using a Texas Instruments TI-59 programmable calculator, equipped with a special module preprogrammed with Rothermel's fire spread model. Fuel models were entered on magnetic strips. Weather parameters and fuel moisture contents were then entered manually to produce fire behaviour estimates. The method is described by Burgan (1979).

RESULTS

Biomass and fuel mass of invaded areas

Biomass estimates for the two invaded sites and a mean biomass estimate for pristine fynbos from the Kogelberg and Cederberg sites are presented in Table 2. There was a marked increase in the biomass of the dominant shrub component following invasion. The *H. sericea* site had 4·4 times the dominant shrub biomass of the mean for fynbos sites, while that of the *A. saligna* site was 6·2 times that of fynbos. Estimates of the fuel component (<6 mm) of dominant shrubs were 5·2 and 2·4 times greater than fynbos for *H. sericea* and *A. saligna* respectively. The herbaceous component, normally considered to be potential fuel (Kruger 1977), was reduced to about one third of the amount found in pristine fynbos following invasion by *H. sericea*, and was almost eliminated following invasion by *A. saligna*. Similarly, understorey shrubs ('other shrubs' in Table 2) were reduced following invasion by *A. saligna* to less than half the biomass in fynbos, and to less than one third by invasions of *H. sericea*. Dead material increased 1·4 times following invasion by *H. sericea*, and 3·2 times with invasion by *A. saligna*. Overall, invasion of fynbos by *H. sericea* or *A. saligna* increased the fuel mass (all biomass with diameters <6 mm) by a factor of 1·6 and 1·5, respectively. Some of these differences may be attributed to site factors, but these figures support the general observation (Kruger 1979) that invasion by vigorous alien shrubs increases biomass and fuel mass.

TABLE 2. Above-ground biomass of vegetation components (g m^{-2}) in pristine and invaded fynbos

Vegetation	Pristine* fynbos	*Hakea*-invaded fynbos	*Acacia*-invaded fynbos
Dominant shrubs†			
>6 mm	445	1808	3532
<6 mm	210	1099	498
Other shrubs			
>6 mm	46	118	130
<6 mm	232	83	145
Herbaceous plants (<6 mm)	376	130	9
Dead material			
>6 mm	71	50	358
<6 mm	404	639	1144
Total biomass	1784	3927	5816
Total fuel (<6 mm)	1222	1951	1796

* Mean of fourteen sites (van Wilgen, Le Maitre & Kruger 1985).
† Indigenous Proteaceae, *Hakea* or *Acacia*.

Size of plant parts as fuel

The mean surface area to volume ratios for the foliage of the two alien species are given in Table 3, together with a value for *P. repens* (van Wilgen 1984). The foliage of the three species is depicted in Fig. 1. The surface area to volume ratio for *H. sericea* leaves was almost double that of *P. repens*, while that of *A. saligna* was about 1·4 times that of *P. repens*. Fine fuel particles (with larger surface area to volume ratios) will increase fire behaviour parameters such as rate of spread when compared to coarser fuel particles.

Vegetation height and stratification

Profile diagrams showing the height and stratification of vegetation at the three sites are given in Fig. 2. The increase in height following invasion by *A. saligna*, the increase in

TABLE 3. Mean surface area to volume ratios and energy contents of the foliage of one indigenous and two alien invasive shrubs. The figure in parentheses is the standard deviation of the mean ($n = 20$ for surface area to volume ratios, $n = 3$ for energy contents)

Species	Surface area to volume ratio ($m^2 m^{-3}$)	Energy content ($J g^{-1}$)
Hakea sericea	8456 (735)	18 302 (525)
Acacia saligna	6460 (862)	18 198 (883)
*Protea repens**	4523 (571)	21 984 (100)

* After van Wilgen (1984).

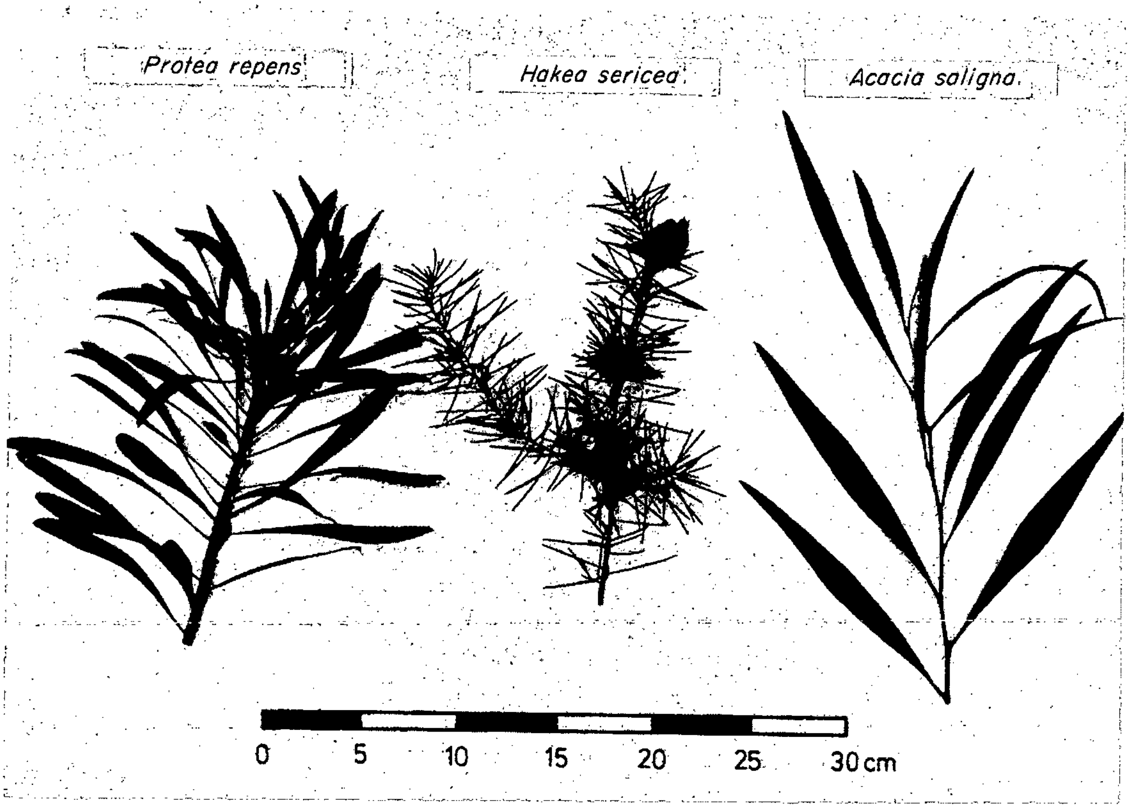

FIG. 1. Foliage of one indigenous and two alien invasive shrubs used to represent dominant species in pristine and invaded fynbos. The fruits of *Hakea sericea* were included in particles >6 mm in the biomass analysis.

foliage density following invasion by *H. sericea* and the reduction in the understorey component in both cases can clearly be seen.

Fuel moisture contents

Fluctuations in fuel moisture content of the three species sampled are depicted in Fig. 3. The moisture content of the three species differed significantly ($P < 0{\cdot}05$) on all days sampled. The moisture content of *H. sericea* remained at about 110%, while that of *P. repens* was about 155% and *A. saligna* about 270%. Differences in fuel moisture content should be taken into account when simulating fire behaviour.

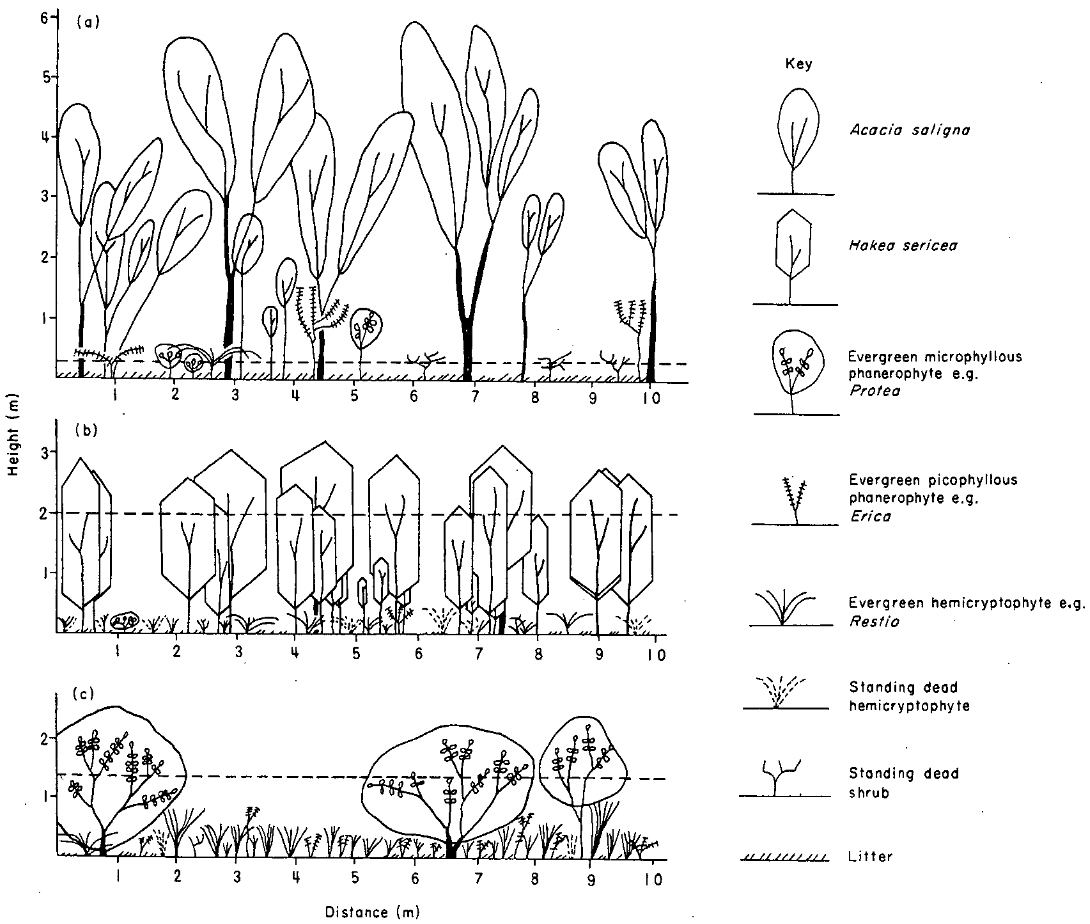

Fig. 2. Profile diagrams from 1 m-wide transects through three plant communities. (a) Fynbos invaded by *Acacia saligna*, (b) fynbos invaded by *Hakea sericea* and (c) pristine fynbos. The dashed line shows the depth of the fuel bed used in the fuel model to simulate fire behaviour.

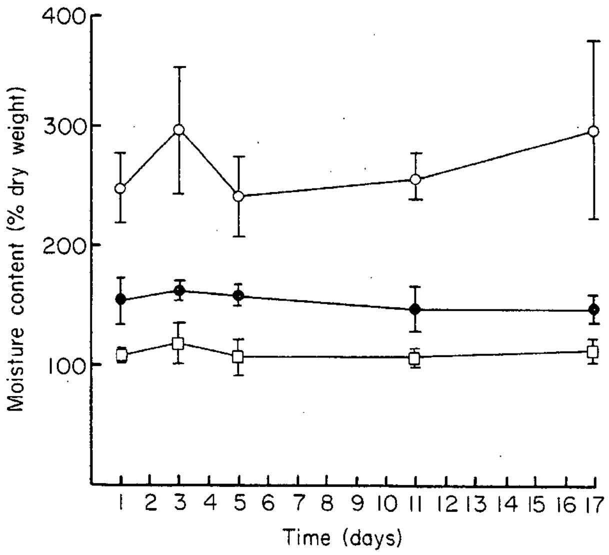

Fig. 3. Fluctuations in the moisture content of the foliage of three species growing on the same site. The species are *Acacia saligna* (○), *Protea repens* (●) and *Hakea sericea* (□). Bars are the 95% confidence intervals of the mean. The first sample was taken on 17 December 1984.

Fuel energy contents

The mean fuel energy contents of *H. sericea* and *A. saligna* are given in Table 3. These values were lower than the value for *P. repens* and fynbos species generally (van Wilgen 1984).

Simulation of fire behaviour

Parameters used in the fuel models are given in Table 4. The fuel loads and surface area to volume ratios in the fynbos fuel model have been changed to reflect changes brought about by invasion. The moisture content of *A. saligna* foliage was so high that it does not burn under average weather conditions. Most of the live shrub fuel is held aloft in stands of *A. saligna*, and fires tend to burn only in the litter layer below the canopy. Attempts to clear infestations of *A. saligna* by burning have failed for this reason (D. M. Richardson personal observation). The live shrub fuel load in the *A. saligna* fuel model was reduced to 145 g m^{-2} to exclude shrub crowns which do not burn, and the fuel bed depth estimate for the *A. saligna* model was reduced to 0·3 m (Fig. 2).

TABLE 4. Details of three fuel models used to simulate fire behaviour (using Rothermel's fire model) in pristine fynbos and sites invaded by *Hakea sericea* and *Acacia saligna*

Parameter	Pristine fynbos*	*Hakea*-invaded fynbos	*Acacia*-invaded fynbos
Fuel loads (gm^{-2})			
Dead fuel <6 mm	400	625	1150
Dead fuel 6–25 mm	95	45	314
Dead fuel >25 mm	12	12	45
Live herbaceous fuel <6 mm	500	130	9
Live shrub fuel <6 mm	224	1180	145
Surface area to volume ratios ($m^2\ m^{-3}$)			
Dead fuel <6 mm	7215	7215	6460
Dead fuel 6–25 mm	357	357	357
Dead fuel >25 mm	98	98	98
Live herbaceous fuel <6 mm	5900	5900	5900
Live shrub fuel <6 mm	4920	8450	6460
Heat content (J g^{-1})	20 000	18 500	18 700
Fuel bed depth (m)	1·4	2·0	0·3
Extinction moisture (%)	34	34	34
Midflame wind conversion factor	0·6	0·6	0·6

* After van Wilgen (1984).

Estimates of fire behaviour were made for four sets of weather conditions which represent typical days with low, moderate, high and extreme fire hazard (Table 5). Estimates of fuel moisture used in simulations are also shown in Table 5. The estimates for dead fuel were simulated by the TI-59 calculator routine. Estimates for live fuel are based on observed means, and have been adjusted to allow for differences between alien and indigenous species (Fig. 3). Simulations of rate of fire spread and Byram's (1973) fire intensity were calculated for each fuel model under the different conditions. Byram's fire intensity was estimated using the formula:

$$I = Hwr$$

where I is the fire intensity (kW m^{-1}), H is the heat yield of the fuel (kJ g^{-1}), w is the mass of available fuel (g m^{-2}), and r is the rate of fire spread (m s^{-1}). Results are shown in Figs 4

TABLE 5. Weather parameters and fuel moisture contents used in simulating fire behaviour

Degree of fire hazard	Low	Moderate	High	Extreme
Degree of cloudiness*	2	1	0	0
Air temperature (°C)	15	20	30	40
Relative humidity (%)	50	40	25	15
Windspeed (m s^{-1})	0·5	2	5	7
Slope (degrees)	0	0	0	0
Dead fuel moisture content (%)	9	8	6	4
Live fuel moisture content (%)				
(i) Pristine fynbos	180	150	140	130
(ii) *Hakea*-invaded site	130	120	110	100
(iii) *Acacia*-invaded site	180	150	140	130

* The figures for cloudiness are as follows: 0 = 0·1 cloud cover; 1 = 0·1–0·5 cloud cover; 2 = 0·6–0·9 cloud cover.

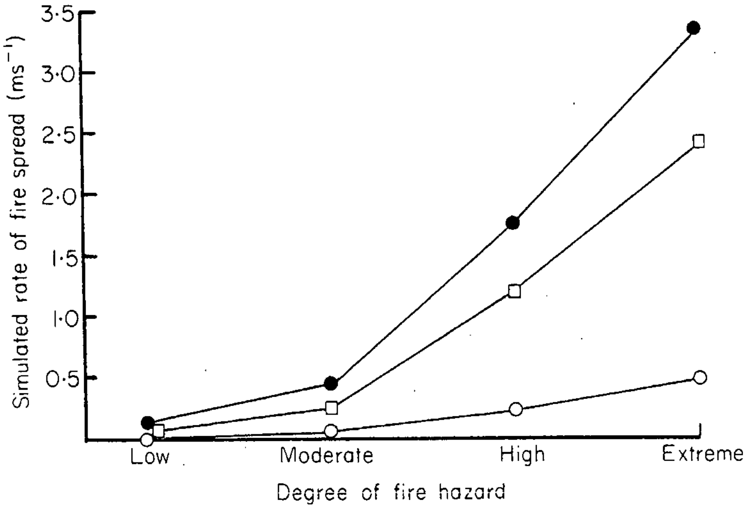

FIG 4. Simulated rates of fire spread using Rothermel's fire model and three different fuel models at four levels of fire hazard (see Table 5). The fuel models are *Acacia saligna*-invaded fynbos (○), *Hakea sericea*-invaded fynbos (□) and pristine fynbos (●).

and 5. Simulated rate of fire spread was highest in fynbos vegetation. *Hakea*-invaded areas show similar but lower rates of spread, with differences becoming larger with increasing fire hazard. Fire intensity (Fig. 5) was also slightly lower in *Hakea*-invaded sites. *Acacia*-invaded areas show low rates of fire spread ($<0·5$ m s^{-1}) and fire intensity ($<11\,000$ kW m^{-1}) under all conditions.

DISCUSSION

Invasions and fynbos vegetation structure

Invasion results in considerable changes in the natural community structure of fynbos. The mean density of dominant shrubs on the Kogelberg site was 1895 stems ha^{-1}, with a mean dominant shrub height of 1·78 m (Le Maitre 1984). The density of dominant *Protea* shrubs in fynbos at Jonkershoek was 1384 stems ha^{-1} at 21 years after fire (van Wilgen 1982). Shrub density was estimated at 8900 stems ha^{-1} for *H. sericea* and 9800 stems ha^{-1} for *A. saligna* from biomass transects. Data from stratification transects gave mean heights

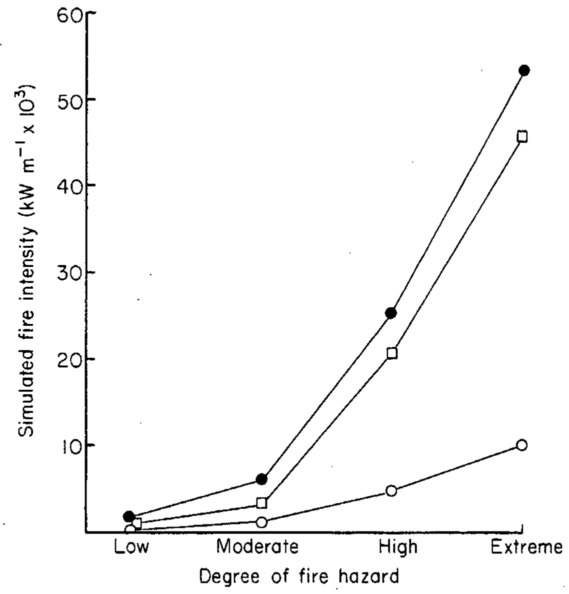

FIG. 5. Simulated rates of fire intensity using Rothermel's fire model and three different fuel models at four levels of fire hazard (see Table 5). The fuel models are *Acacia saligna*-invaded fynbos (○), *Hakea sericea* -invaded fynbos (□) and pristine fynbos (●).

of 2·6 and 3·9 m for *H. sericea* and *A. saligna*, respectively. This increase in the number and size of dominant shrubs took place at the expense of understorey herbs and shrubs (Fig. 2). The fynbos understorey is usually a species-rich assemblage, with many of the species having limited distributions. Severe infestations of alien shrubs can be expected to lead to the drastic reduction or local extinction of many species, and such infestations are therefore incompatible with the aims of nature conservation in the fynbos.

Invasions and fire behaviour

Simulations using Rothermel's model indicate that invasion of fynbos shrublands by *H. sericea* will not change potential fire behaviour markedly. Invasion should therefore not significantly increase fire hazard as was postulated by Kruger (1979), despite an increase in fuel loads, an increase in surface area to volume ratio and a decrease in live fuel moisture content of the dominant species. The major reason for this (in terms of Rothermel's model) is the increased packing density of fuel particles in the fuel bed, which effectively reduces the simulated rate of fire spread. The lower fuel energy content also contributes to the lower fire intensity. However, a large number of wildland fire phenomena still elude theoretical description (Albini 1984): 'For example, dead grass will seldom support a spreading fire when the moisture content is above 15–20%, nor will forest litter if it contains more than about 30% moisture. Yet stands of chaparral (Californian shrublands) composed predominantly of live foliage and stems, and timber stands with virtually all live foliage, can burn with great vigour at a foliar moisture content of 100%' (Albini 1984). Understorey plants in fynbos are finely divided and are important in determining fire behaviour. They are, together with dead material, responsible for carrying fires which in turn ignite the dominant shrubs. The drastic reduction of understorey plants after invasion means that fires will be more dependent on the crowns of dominant shrubs for fuel. As understorey plants have been largely eliminated, fuel in the crowns of invasive species is only ignited under extreme conditions. Fire behaviour in the elevated crowns of old *H. sericea* stands can be quite different from that in fynbos (F. J. Kruger personnal communication). These differences are not simulated by Rothermel's model. The dense foliage of the shrubs will also reduce (and in many places prevent) access (Fig. 2), which complicates the task of firefighters. In addition, *H. sericea* has recently succumbed to attacks by a fungal disease which rapidly kills large numbers of the shrubs (Richardson & Manders 1985). Fire hazard in these stands can be expected to increase dramatically as the moisture content of partly or completely dead shrubs decreases from about 110 to 10% or less.

Simulations of fire behaviour in stands of *A. saligna* showed a reduction in fire spread rate and intensity. This is because the dominant shrub did not form part of the fuel model, due to the high proportion of particles >6 mm diameter and the high moisture content of the foliage. The fuel bed was effectively reduced to the litter layer and remaining vegetation below the canopy (Fig. 2), where the high packing density of fuel particles reduces the simulated rate of fire spread and fire intensity. While field observations have shown that sites invaded by *A. saligna* do not burn easily, the above assumptions do not hold under all conditions. In a recent wildfire in the Silvermine Nature Reserve (34°10′S, 18°25′E), thickets of *A. saligna* burnt cleanly, indicating a fairly intense fire. To simulate fires in such stands, the fuel bed depth was increased to 4 m, and the woody fuel load to 650 g m^{-2} in the *Acacia* fuel model. The conditions listed in Table 5 were used, but live fuel moisture was increased by 60% to allow for observed differences (Fig. 3). Simulated rates of fire spread and intensity were slightly higher than for fynbos (3·27 m s^{-1} and 64 400 kW m^{-1} under extreme weather conditions). This fuel model will probably only apply under extreme conditions when fires burn in the shrub crowns.

The hypothesis that invasion results in increased fire hazard should be seen in the light of the above discussion. Fires will be more easily ignited in pristine fynbos, where there is an abundance of fine material in the herbaceous layers. Under moderate weather conditions, fires in fynbos will spread faster, and burn with greater intensity, than in invaded vegetation. However, under extreme weather conditions, fire intensity in invaded sites would be much higher than in pristine fynbos, although this cannot be simulated as the processes governing fire behaviour in such stands are not clearly understood. The increase in fire intensity under extreme conditions will mean that fires will be more difficult to contain and potentially more damaging to ecosystems than fires in natural vegetation. Under such conditions, the observation that invasion increases fire hazard would be valid.

ACKNOWLEDGMENTS

We thank G. M. Bailey, M. P. Brink, P. J. Brown and A. Simmers for assistance with field work, D. C. Le Maitre for some estimates of fynbos fuel mass, and the Department of Poultry Science, University of Stellenbosch for the use of a bomb calorimeter. F. J. Kruger, I. A. W. Macdonald and W. R. Siegfried provided useful comment on the manuscript. This work forms part of the conservation research programme of the Forestry Branch of the South African Department of Environment Affairs and is published by permission of the Deputy Director General.

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(*Received 27 February 1985; revision received 7 June 1985*)

Second paper: Aspects of the reproductive ecology of four Australian Hakea species (Proteaceae) in South Africa. *Oecologia*.

Oecologia (Berlin) (1987) 71:345–354

Oecologia

Aspects of the reproductive ecology of four australian *Hakea* species (Proteaceae) in South Africa

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Summary. Four shrub species of the Australian Proteaceae (*Hakea sericea*, *H. gibbosa*, *H. suaveolens* and *H. salicifolia*) were introduced to South African fynbos shrublands between 1840 and 1860. *H. sericea* is highly invasive, *H. gibbosa* and *H. suaveolens* are moderately invasive and *H. salicifolia* is not invasive. The allocation of reproductive energy, germinability, the ability to survive fires and to germinate in burnt and unburnt areas, and the nutrient content of seeds were assessed for the four species. The information was used to investigate whether the success of *H. sericea* relative to the other three species could be explained by the superior expression of any trait. The most important trait which separates *H. sericea* from the other species is its ability to produce a large seed bank in its adopted environment in the absence of seed predators. Seed production in *H. sericea* shrubs with an above-ground dry mass of 8 kg is four times greater than *H. gibbosa* and more than 16 times that of *H. suaveolens*. Although *H. salicifolia* also produces a large seed bank, its seeds are unable to survive fires due to inadequate insulation by the small follicles. The results are compared to dispersal and seed bank data for indigenous South African Proteaceae, which have low dispersal and suffer high pre-dispersal seed predation. We suggest that potential invasives in the fynbos can be identified as species that have: (i) a potentially high seed production that is limited by specialized predators; (ii) an ability to disperse over long distances; and (iii) are pre-adapted to frequent fires and low soil nutrients. The data also support the current strategy of combatting *H. sericea* using specialized insect seed predators.

Key words: *Hakea* – Invasion – Reproduction – Germination – Seed dispersal – Fire

South African fynbos shrublands occur mainly on nutrient-poor soils and comprise one of the richest floras in the world (Goldblatt 1978). A feature of fynbos shrublands is their high susceptibility to invasion by alien trees and shrubs (Macdonald and Richardson 1986). It is remarkable that invasions of this diverse vegetation type by shrubs from similar environments on other continents occur with little, if any, man-induced change to the environment. Alien trees and shrubs often form dense stands which reduce or eliminate indigenous components (Macdonald and Richardson 1986), reduce surface water resources (Versfeld and Van Wilgen 1986), and increase fire hazard (Van Wilgen and Richardson 1985).

In many areas, fynbos communities dominated by indigenous Proteaceae have been invaded by Australian Proteaceae. The family Proteaceae is concentrated in temperate Australia (about 700 species) and in the Cape Province of South Africa (about 350 species). The family is particularly prominent in fire-prone shrublands of the two regions. Proteaceous shrubs are usually the dominant woody plants on the most nutrient-poor soils in both regions (Lamont et al. 1985), but no genera of the Proteaceae are indigenous to both continents. A large proportion of successful alien plant taxa in the fynbos survive fires by virtue of possessing canopy-stored seed banks, a reproductive syndrome shared with the dominant fynbos Proteaceae (Bond 1985; Lamont et al. 1985).

Four species of evergreen perennial shrubs of the genus *Hakea* (Proteaceae) were introduced to South Africa from Australia between 1840 and 1860 (Macdonald 1984). Three species, *H. sericea* Schrad., *H. gibbosa* (Sm.) Cav., and *H. suaveolens* R. Br. invade the natural vegetation and have been declared noxious weeds. Although *H. sericea* was not widely planted, it currently occupies the greatest area of all woody invaders in the fynbos biome (Macdonald and Jarman 1984). Stands of this species occur in 42% of the 115 quarter-degree squares that constitute the fynbos biome, whereas *H. suaveolens* and *H. gibbosa* occur in only 9 and 6% of squares respectively (Macdonald et al. 1985), despite their wider dissemination by man (Neser 1978a, b). These three species all form dense thickets that substantially alter vegetation structure. A fourth species, *H. salicifolia* (Vent.) B.L. Burtt. (syn. *H. saligna* Knight), has been used extensively as a hedge plant throughout the southwestern Cape but shows no signs of invading natural vegetation.

Fires are an important feature of the fynbos environment and have aided the spread of *Hakea* species. Three of these species are dependent entirely on seed for regeneration in South Africa but *H. salicifolia* may also regenerate from stem-bases after fire (S. Neser unpublished work). *H. sericea*, *H. gibbosa* and *H. suaveolens* exhibit extreme serotiny in South Africa; all seeds produced during the life of the plant are stored in the woody follicles that open only upon death of the plant. *H. salicifolia* releases some

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Table 1. Salient features of sites at which shrubs of the genus *Hakea* were harvested for study

Site	Position	Geology	Mean annual rainfall (mm)	Altitude (m)
Vergelegen Estate	34° 56′ S; 18° 56′ E	Sandstone/granite mixtures	1,200	600
Jonkershoek Valley	33° 57′ S; 18° 54′ E	Sandstone/granite mixtures	1,100	400
Constantianek	34° 14′ S; 18° 28′ E	Sandstone	1,227	200
Millers Point	34° 01′ S; 18° 24′ E	Sandstone/granite mixtures	700	30
Blaauwklippen Valley	34° 59′ S; 18° 52′ E	Granite	1,000	180
Grabouw State Forest	34° 09′ S; 19° 01′ E	Sandstone	650	300
Wemmershoek	33° 53′ S; 19° 02′ E	Sandstone	817	140

seed intermittently but retains most seeds in the canopy. Each follicle contains two single-winged seeds (samaras) that are released following death of the parent plant. Seeds are thin-coated and germinate readily after release; there is no viable seed bank in the soil (Richardson 1985).

Several factors have been suggested to contribute to the success of *H. sericea* in South Africa. These are the ability to produce large numbers of seeds (Neser 1968; Kluge 1983), the high degree of protection afforded to the seeds by the woody follicles (Fugler 1983), high seed longevity in the canopy (Neser 1968), high germinability and rapid germination (Richardson and Van Wilgen 1984), efficient dispersal (Hall 1979) and high nutrient content of seeds (Mitchell and Allsopp 1984). Mooney, Hamburg and Drake (1986) have suggested that a valuable approach to the study of the ecological characteristics of successful invaders is a comparison of their traits with those of closely related non-invasive species.

In this study we investigated aspects of the reproductive ecology of the four *Hakea* species and related these to the relative success of each species in the fynbos. We determined differences in the allocation of reproductive energy, germinability, the ability to survive fires and to germinate in burnt and unburnt areas and the nutrient content of seeds. This information was used to investigate whether the success of *H. sericea* relative to the other three species could be explained by the superior expression of any trait. This approach could explain why certain species become invasive, and should also provide information for determining the most appropriate control strategy.

The study areas. Data for *H. sericea* were collected from populations at the Vergelegen Estate and in the Jonkershoek Valley. Data for *H. gibbosa* and *H. suaveolens* were collected from populations at Constantianek and Millers Point respectively. Data for *H. salicifolia* were collected from localities in the Jonkershoek and Blaauwklippen Valleys, from Grabouw State Forest and from Wemmershoek. Salient features of these sites are given in Table 1.

Methods

Morphology of follicles and seeds. Fifty follicles with samaras (seed plus wing) of each species were oven-dried at 80° C for 72 h and then weighed. Samaras (100) were first weighed individually with the wing intact. Wings were then carefully removed and the seed was weighed. The surface area of samaras and of seeds was determined using a leaf area meter. The samara wing loading, defined as W/A, where W is the mass (mg) and A is the surface area (mm^2) (Green 1980), was calculated for each species.

Longevity of canopy stored seeds. Two classes of follicles (the youngest and the oldest) were harvested from large shrubs of the four species. Follicles were aged by their position on the plant; old follicles were those found closest to the main stem on thick branches while young follicles were those found on the last seasons growing shoots. A 1% aqueous solution of tetrazolium bromide (International Seed Testing Association 1976) was used to test whether the viability of canopy stored seeds declines with age. One hundred seeds (five replicates of 20) of each species were used. A small section (2 mm) of the radicle of dry seeds was removed. Seeds were soaked in water for 24 h and then soaked in the tetrazolium bromide solution for 48 h. Endosperms were removed from the seed coat and opened to uncover the embryo. Seeds having a completely stained embryo in a completely stained endosperm were considered viable.

Seed release and germination characteristics. The survival of seeds in fire was determined by simulating fires burning in the crowns of the shrubs. One hundred freshly picked young follicles of each species were suspended on a wire mesh platform in the flames at 0.5 m above a fire for 90 s, the normal duration of peak temperatures in fynbos fires (B.W. Van Wilgen, unpublished work). Dry pine cones were used as fuel. The burnt follicles were placed, together with 100 freshly picked but unburnt young follicles of each species, in a dry environment. The number of open follicles was recorded daily for 11 days and then the unopened ones were forced open so that germination experiments could commence. Shade cloth (55%) was used to simulate the effects of shading by vegetation canopies on germination in unburnt vegetation for comparison with recently burnt (unshaded) sites. The treatments were as follows: (i) follicles burnt with seeds landing in recently burnt areas (unshaded); (ii) follicles burnt with seeds landing in unburnt vegetation (shaded); (iii) follicles unburnt and seeds unshaded and (iv) follicles unburnt and seeds shaded. Data from these experiments were used to test the following null hypotheses: i) Germination values of untreated seeds do not differ for the four species (seeds sown in direct sunlight); ii) Germination values of fire-treated seeds are the same for the four species; iii) The degree of protection against fire afforded by the follicle does not differ for the four species; iv) Heating the follicle does not affect the germination of each of the species individually; iv) Seeds of the four species will germinate equally well in shaded and unshaded sites (this hypothesis was tested for both fire-treated and untreated seeds). One hundred seeds of each species per treatment were planted at a depth of 5–10 mm in trays (10 seeds per tray) filled with clean river sand. Trays were watered every three days and were monitored daily for 100 days to record seedling emergence. To take both total germination and the speed of germination into account for comparison between species and treatments, "germination values" were calculated. This composite index is defined as the product of peak value (the maximum quotient derived from the cumulative germination percent on any day divided by the number of days since planting) and the mean daily germination, calculated as the percentage germination at 100 days, divided by the number of days (100) to the end of the test (Czabator 1962).

Fall velocity of samaras. Fall velocity is a good indicator of relative dispersability; seeds that fall slower have the greatest potential for dispersal. The fall velocity was determined by releasing samaras of each species individually from a height of 3.5 m in still air (<0.4 m s $^{-1}$ windspeed) and measuring the descent time.

Seed banks and allocation of reproductive energy. Eighteen *H. sericea*, 15 *H. gibbosa* and seven *H. suaveolens* shrubs were harvested from thickets of approximately equal density, while 13 solitary and unpruned *H. salicifolia* shrubs were harvested. Shrubs were selected to cover a range of size classes. Follicles (including seeds) were separated in the field and counted. Vegetative parts and follicles were weighed separately using a spring balance. Samples were collected from each shrub, placed in air-tight bottles and oven-dried at 80° C for 72 h to determine their moisture content. This was used to calculate the oven dry mass of the original material. Regression equations of total above-ground dry mass against the mass of follicles and total above-ground dry mass against number of follicles were fitted using the NONLIN procedure of the OXFORD statistical package (Commonwealth Forestry Research Institute, Oxford, England). In studies on reproductive strategies, dry mass has been used as a measure of energy allocation patterns (Harper and Ogden 1970; Hickman and Pitelka 1975; Evenson 1983; Samson and Werk 1986). This procedure is particularly appropriate in *Hakea*, where all (except in *H. salicifolia*) reproductive tissue (follicles and seeds) is retained for the life of the plant. Net reproductive effort, defined as the percentage of the total above – ground dry mass allocated to follicles and seeds was calculated for the four species.

Nitrogen and phosphorus contents of seeds. The wings were removed from the seeds and embryos were dissected from the testas after soaking in distilled water overnight. Each sample was oven-dried at 80° C for 12 h and consisted of either one seed or 0.1 g ground material (20 mesh). Phosphorus was extracted by means of the digestion method of Jackson (1958) and then assayed by the Murphy and Riley (1962) method. Standard Kjeldahl procedures with selenium catalyst and sodium thiosulphate extracted the total nitrogen and ammonium nitrogen was then determined colorimetrically using the method of Smith (1980).

Results

Morphology of follicles and seeds. The morphological characteristics of follicles, samaras and seeds are shown in Table 2. Significant differences in follicle mass were found between the four species. *H. gibbosa* has the greatest follicle mass, more than double that of *H. sericea* and 12 times greater than *H. salicifolia.* Seeds of all four species bear structures that facilitate dispersal by wind. The lateral extension of the testa to form the wing increases the mass of the structure by between 6.5% (*H. sericea*) and 15.3% (*H. gibbosa*) but increases the surface area by between 259% (*H. suaveolens*) and 349% (*H. gibbosa*). Examination of structural features of samaras of the four species suggests that samaras of *H. suaveolens* have the greatest inherent potential for dispersal.

Longevity of canopy stored seeds. No significant differences ($P<0.001$) were found between the viability of young and old canopy-stored seeds of *Hakea sericea*, *H. gibbosa* and *H. suaveolens.* The mean viability of young seeds of these three species was 99, 97 and 93% respectively. The corresponding values for old seeds were 99, 99 and 90% respectively. In the case of *H. salicifolia*, young seeds had a mean viability of 97%, while the corresponding value for old seeds was 0%. These results indicate that no decline in seed viability with increasing age occurs in any of the species other than *H. salicifolia.*

Seed release and germination characteristics. Fire-treated follicles of all species opened more rapidly than did untreated ones. All fire-treated follicles of *H. sericea* and *H. gibbosa* opened after five and seven days respectively, whereas there was a delay of 2–3 days in the opening of the untreated follicles. After 11 days, 90% and 73% of fire-treated follicles of *H. salicifolia* and *H. suaveolens* had opened whereas only 48% of untreated follicles of *H. salicifolia* had opened at this stage. No follicles of *H. suaveolens* opened without heating within 11 days after harvesting.

H. sericea and *H. suaveolens* showed similar germination patterns for both fire-treated and untreated seeds (Fig. 1). Germination commenced after 30 days and reached maximum at around 70 days for *H. sericea* and after 60 days for *H. suaveolens.* Germination of seeds of *H. gibbosa* from all treatments, except fire plus shading, commenced at 30 days and reached relatively low maxima only at the end of the test period whereas fire-treated seeds planted in the shade commenced germination only after 50 days (Fig. 1). No fire-treated seeds of *H. salicifolia* germinated. Untreated seeds of this species planted in direct sunlight and under shading showed relatively slow germination rates with maximum germination occurring at the end of the test period.

The null hypothesis that the germination value of untreated seeds does not differ for the four species (sown in direct sunlight) is refuted ($P<0.0001$ in one-way ANOVA). Untreated seeds of *H. sericea* and *H. suaveolens* showed significantly greater germination values ($P<0.0001$) than for *H. salicifolia* (Table 3). This is due to the slow germination rate of seed of *H. salicifolia* as germination percent after 100 days did not differ significantly for the three species. Germination value for *H. gibbosa* was significantly lower than for *H. salicifolia.* Germination values for fire-treated seeds were also not the same for the four species ($P<0.0005$ in one-way ANOVA). Germination values for

Table 2. Structural and morphological characteristics of samaras, seeds and follicles of four *Hakea* species. Data are mean ±S.E., with number of observations in parentheses. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; $P<0.05$)

	H. sericea	*H. suaveolens*	*H. gibbosa*	*H. salicifolia*
Follicle mass (g)	$5.28^{b}+0.16$ (50)	$3.29^{c}+0.07$ (50)	$12.86^{a}+0.31$ (50)	$1.05^{d}+0.03$ (50)
Samara mass (mg)	$31.67^{b}\pm0.46$ (100)	$13.00^{c}\pm0.29$ (100)	$42.74^{a}\pm1.13$ (100)	$12.55^{c}\pm0.36$ (100)
Follicle: samara mass ratio	$83.52^{c}\pm2.47$ (50)	$131.57^{b}\pm2.70$ (50)	$153.48^{a}\pm4.75$ (50)	$42.77^{d}\pm1.56$ (50)
Seed mass (mg)	$29.66^{b}\pm0.47$ (100)	$12.54^{c}\pm0.24$ (100)	$37.13^{a}\pm1.17$ (100)	$11.59^{c}\pm0.35$ (100)
Samara surface area X 100 (mm^2)	$1.38^{b}\pm0.02$ (100)	$0.88^{c}\pm0.01$ (100)	$2.19^{c}\pm0.02$ (100)	$0.63^{d}\pm0.01$ (100)
Seed surface area X 100 (mm^2)	$0.35^{b}\pm0.01$ (100)	$0.21^{c}\pm0.00$ (100)	$0.51^{a}\pm0.01$ (100)	$0.18^{b}\pm0.01$ (100)
Samara wing loading ($mg/100\ mm^2$)	$23.02^{a}\pm0.42$ (100)	$14.76^{d}\pm0.29$ (100)	$19.47^{c}\pm0.48$ (100)	$20.15^{b}\pm0.54$ (100)

Table 3. Mean germination values (see text) of seeds of four *Hakea* species. Fire-treated seeds were taken from follicles exposed to flames for 90 seconds. Seeds were sown in direct sunlight. Data are mean ± S.E. Number of replicates in parentheses. Means with the same superscript letter in each treatment do not differ significantly (Student-Newman-Keuls test; $P<0.05$), N.S. denotes not significant

Species	*Mean germination value*		*t*	*P*
	Fire-treated	*Untreated*		
H. sericea	$0.61^{a}\pm0.15$ (10)	$1.57^{a}\pm0.04$ (10)	6.10	<0.0001
H. suaveolens	$0.38^{a}\pm0.09$ (9)	$1.55^{a}\pm0.14$ (10)	6.98	<0.0001
H. gibbosa	$0.33^{a}\pm0.05$ (10)	$0.37^{c}\pm0.08$ (10)	0.41	N.S.
H. salicifolia	$0^{b}\ \pm0$ (10)	$0.75^{b}\pm0.14$ (10)	5.56	<0.0001

Table 4. Germination values (see text) for seeds of four *Hakea* species 100 days after planting direct sunlight and in 55% shade. Data are mean ± S.E., with number of replicates in parentheses

Species	*Treatment*	*Germination value*		*t*	*P*
		Full sunlight	*55% shade*		
H. sericea	Fire	0.61 ± 0.15 (10)	0.50 ± 0.07 (10)	0.64	N.S.
	Control	1.57 ± 0.03 (10)	1.45 ± 0.05 (10)	1.97	N.S.
H. suaveolens	Fire	0.38 ± 0.09 (9)	0.37 ± 0.05 (10)	0.10	N.S.
	Control	1.55 ± 0.14 (10)	1.46 ± 0.17 (10)	0.42	N.S.
H. gibbosa	Fire	0.33 ± 0.05 (10)	0.07 ± 0.02 (10)	4.84	<0.0005
	Control	0.37 ± 0.08 (10)	0.25 ± 0.07 (10)	1.03	N.S.
H. salicifolia	Fire	$0.0\ \pm0.0$ (10)	$0.0\ \pm0.0$ (10)	–	N.S.
	Control	0.75 ± 0.14 (10)	0.82 ± 0.11 (10)	0.42	N.S.

H. sericea, *H. suaveolens* and *H. gibbosa* were not significantly different but all *H. salicifolia* seeds were killed by exposure to heat (Table 3). Fire treatment significantly reduced germination percent in *H. salicifolia*, *H. sericea* and *H. suaveolens* but had no significant effect on *H. gibbosa* seeds (Table 3).

Shading had no significant effect on germination of seeds from fire-treated and untreated follicles of *H. sericea*, *H. suaveolens* and *H. salicifolia* and from untreated follicles of *H. gibbosa* (Table 4). Shading, however, resulted in a significantly smaller germination value for seeds from fire-treated follicles of *H. gibbosa* (Table 4).

Fall velocity of samaras. Samaras of the four species rotate when falling and all follow a single helical trajectory (Burrows 1975); the centre of mass of the samara descending in a roughly straight line in still air. The null hypothesis that fall velocities of samaras of the four species do not differ significantly is refuted ($P<0.0001$ in one-way ANOVA). Samaras of *H. gibbosa* fall more rapidly than

Table 5. Mean fall velocities (ms^{-1}) of samaras of four *Hakea* species. Samaras were released from 3.5 m under calm conditions (horizontal wind speed $<0.4\ ms^{-1}$). Means with the same superscript letter do not significantly (Student-Newman-Kuels test; $P<0.05$)

Species	*Mean fall velocity* (ms^{-1})	*Standard error*	*Sample size*
H. gibbosa	1.186^a	0.052	45
H. sericea	1.027^b	0.028	48
H. salicifolia	0.977^b	0.017	74
H. suaveolens	0.871^c	0.018	31

those of the other species. Samaras of *H. suaveolens* which have the lowest wing loading (Table 2), also have the lowest fall velocity and therefore the greatest potential for dispersal by wind (Table 5). All four species, however, have the potential for dispersal over a considerable distance.

Seed banks and allocation of reproductive energy. Regression equations of total above-ground dry mass against follicle mass and total above-ground dry mass against number of follicles are presented in Appendix 1. Equations of the form

$$Y = a + bX + cX^2$$

provided the best fit in all cases. Both *H. sericea* and *H. gibbosa* produce a relatively large mass of follicles and seeds. This is not the case for *H. suaveolens* and *H. salicifolia* (Fig. 2). Figure 3 shows the relationship between the number of follicles and the total above-ground dry mass. *H. sericea* produces a large number of follicles, even at an early stage of development. The number of follicles produced by *H. gibbosa* is lower despite it producing the same mass of tissue, as follicles are larger (Table 2). Conversely, *H. salicifolia* produces relatively numerous follicles, despite their relatively small contribution to the total above-ground dry mass. *H. suaveolens* produces few follicles and allocates

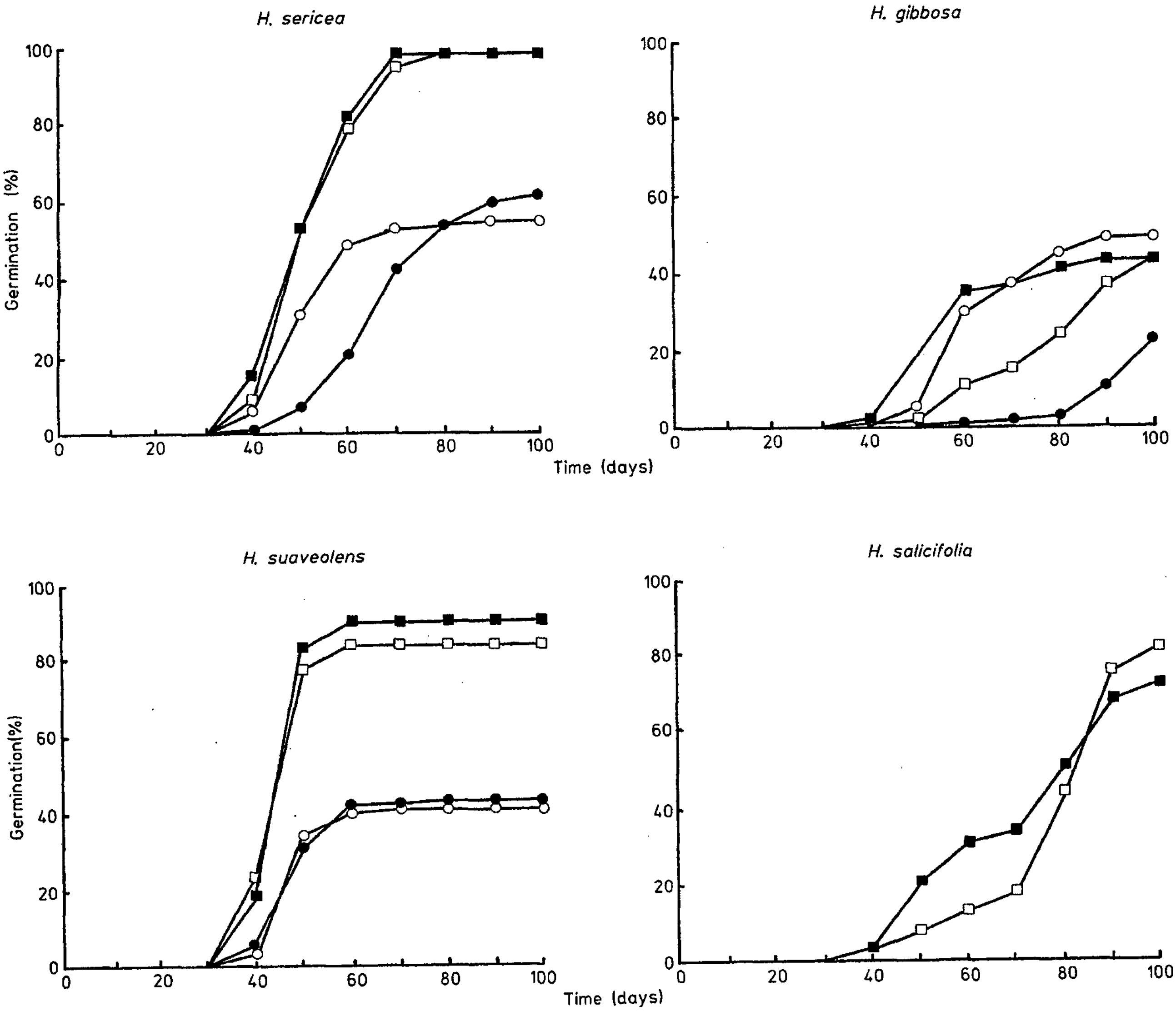

Fig. 1. Germination patterns of four *Hakea* species. Seeds from fire-treated and untreated follicles were planted in direct sunlight and in 55% shade (see text). Untreated seeds: □ = sun, ■ = shade. Fire treated seeds: ○ = sun, ● = shade

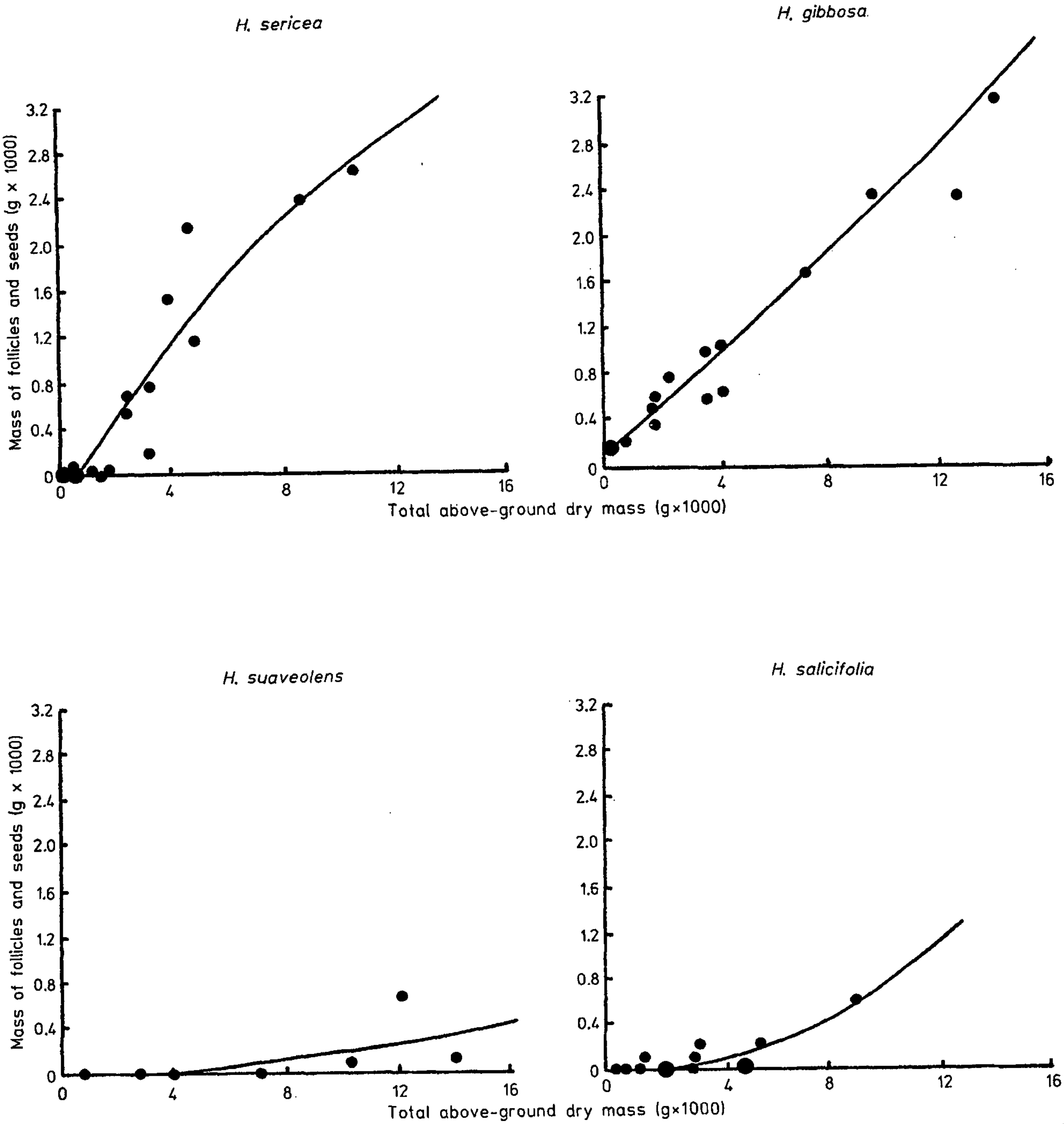

Fig. 2. The relationship between total above-ground dry mass and the mass of follicles and seeds in shrubs of four *Hakea* species in the southwestern Cape Province. Large dots represent more than one data point. The equations of the regression lines are given in Appendix 1

relatively little energy to this function. The reproductive effort (percentage of above-ground dry mass allocated to follicles and seeds) is shown in Figure 4. Differences in reproductive effort between species are significant for all comparisons except *H. salicifolia* – *H. suaveolens* as tested by the Mann-Whitney two-tailed U test. Differences between *H. gibbosa* and the remaining three species and between *H. salicifolia* and *H. suaveolens* are significant at $P < 0.001$. Differences between *H. sericea* and *H. salicifolia*, and *H. sericea* and *H. suaveolens* are significant at $P < 0.05$.

Nitrogen and phosphorus content of seeds. There were significant differences between some species in concentrations of both nitrogen and phosphorus in seeds (Table 6). Seeds of *H. suaveolens* and *H. salicifolia* contained less nitrogen and phosphorus per seed than *H. sericea* and *H. gibbosa* (Ta-

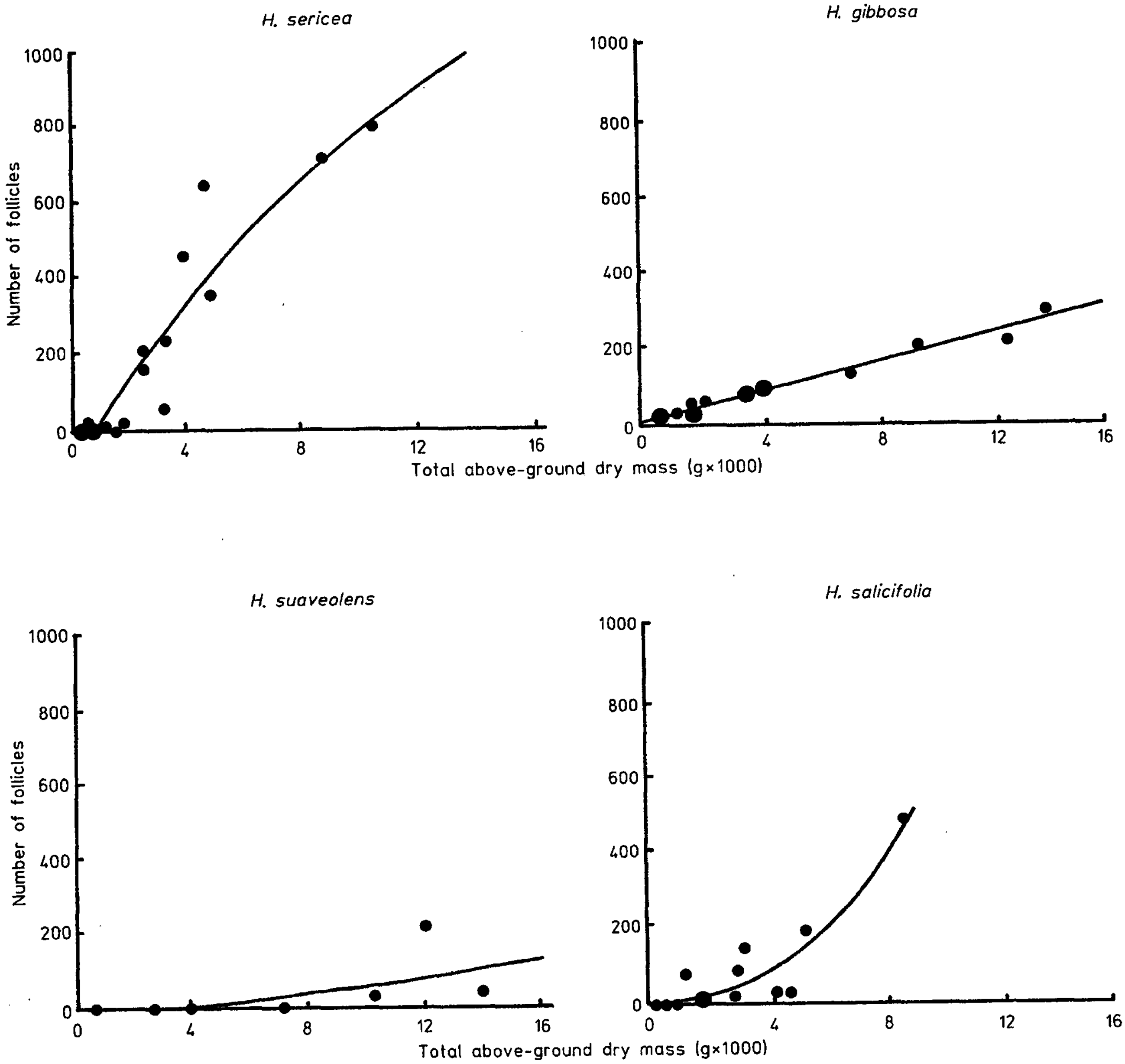

Fig. 3. The relationship between total above-ground dry mass and the number of follicles produced on shrubs of four *Hakea* species in the southwestern Cape Province. Large dots represent more than one data point. The equations of the regression lines are given in Appendix 1

ble 6). *H. sericea* seeds contained the highest concentration of nitrogen. The embryos of all four species contained more than 98% of total seed phosphorus, although there were significant differences in the phosphorus concentrations of the testas with *H. suaveolens* having the highest concentration (Table 7).

Discussion

The Australian *Hakea* species in South Africa appear to have two major advantages in reproduction over South African Proteaceae: superior dispersal abilities and much larger seed banks. Bond (1980) found that dispersal of fynbos Proteaceae with canopy-stored seed banks could be limited by minor physical barriers. Manders (1986) reports a maximum dispersal distance of 26 m for *Protea laurifolia* Thunb., with 95% of recruitment occurring within 15 m of the parent plant. Myrmecochorous (ant-dispersed) species are even less efficient at dispersal, and Slingsby and Bond (1985) found a maximum dispersal distance of less than 10 m for *Leucospermum conocarpodendron* (L.) Buek. The winged seeds of *Hakea* species, on the other hand, facilitate dispersal over several kilometers in some cases. The canopy-stored seed banks of *Hakea* species in Australia

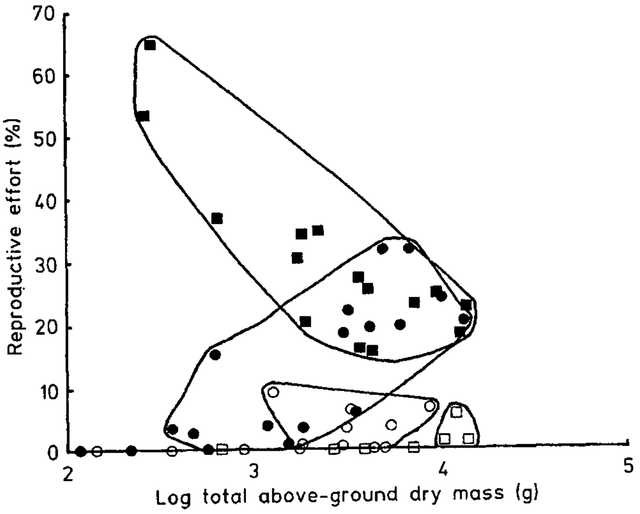

Fig. 4. Reproductive effort (ratio of dry weight of reproductive tissue to the total above-ground dry weight × 100) for four *Hakea* species. Closed curves represent all non-zero points. ● = *H. sericea*, ■ = *H. gibbosa*, ○ = *H. salicifolia* and □ = *H. suaveolens*

Table 7. Phosphorus content of testae and embryos of seed of four *Hakea* species. Data are mean ± S.E. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; $P < 0.05$).

	Testa	Embryo	
	mg g^{-1} dry mass	mg $seed^{-1}$	mg g^{-1} dry mass
H. sericea	$0.30^{c} \pm 0.02$	$0.35^{b} \pm 0.01$	$13.90^{b} \pm 0.30$
H. suaveolens	$1.09^{a} \pm 0.08$	$0.18^{c} \pm 0.01$	$16.06^{c} \pm 0.26$
H. gibbosa	$0.19^{c} \pm 0.02$	$0.63^{a} \pm 0.03$	$16.61^{a} \pm 0.49$
H. salicifolia	$0.73^{b} \pm 0.06$	$0.15^{c} \pm 0.01$	$14.64^{b} \pm 0.76$
F	60.33	187.96	9.96
d.f.	3,51	3,55	3,55
P <	0.001	0.001	0.001

suffer heavy pre-dispersal predation from insects, many of them highly specialized (Neser 1968; Gill and Neser 1984). The development of the woody follicle in Australian Proteaceae is seen primarily as a response to the presence of specialized seed predators (Johnson and Briggs 1963; Neser 1968; Lamont et al. 1985). There is virtually no pre-dispersal predation of *Hakea* seeds in South Africa (Kluge 1983), and this has led to the production of large quantities of viable seed. Seed production in *H. sericea* in South Africa is certainly much greater than in Australia (Gill and Neser 1984), but there are no data on the relative fecundity of the other three species on the two continents. The virtual absence of pre-dispersal predation in the alien *Hakea* species in South Africa is contrasted by heavy insect predation of seeds in indigenous Proteaceae. For example, more than 80% of seeds of *Protea repens* (L.) L. are destroyed by insects within two years after flowering (Coetzee 1984) and almost none remain after four years (Bond 1985).

In order to have been more successful, *H. sericea* must have displayed superiority in one or more vital trait when compared to the other three *Hakea* species. In Table 8 we compare selected attributes of the reproductive ecology of the four species. Juvenile periods range from two years in *H. sericea* and *H. gibbosa*, to four and six years for *H. salicifolia* and *H. suaveolens* respectively (Richardson 1985 and unpublished work). Although significant differences in the samara wing loadings were found between the four species, all species nonetheless possess a good ability to disperse by virtue of having a winged seed. Furthermore, while the nutrient concentrations in seeds are high compared to values for indigenous South African Proteaceae (Mitchell and Allsopp 1984), no large differences exist between the four species. The dispersability of individual samaras and the nutrient content of seeds of the four species cannot explain differences in invasive potential.

H. gibbosa shrubs produce relatively few seeds when compared to *H. sericea* but devote up to 70% of their resources to reproductive and ancillary organs (Figure 4). The very large follicles make up a greater part of the dry mass of small shrubs than in *H. sericea* (Figure 4). The greater protection afforded seeds of *H. gibbosa* is more than compensated for by the greater number of seeds produced by *H. sericea*. Slow germination and relatively low germinability of seeds of *H. gibbosa* and low germination in unburnt sites also limit the success of this species.

The relative lack of success of *H. suaveolens* as an invader may be explained by the relatively long juvenile period and low seed production. Too little energy is allocated to reproduction. Seed production commences only after

Table 6. Nitrogen and phosphorus content of seeds of four species of *Hakea*. Data are mean ± S.E. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; $P < 0.05$)

	Nitrogen		Phosphorus	
	mg $seed^{-1}$	mg g^{-1} dry mass	mg $seed^{-1}$	mg g^{-1} dry mass
Hakea sericea	$2.46^{b} \pm 0.01$	$85.87^{a} \pm 1.21$	$0.32^{b} \pm 0.01$	$10.62^{b} \pm 0.16$
Hakea suaveolens	$0.97^{c} \pm 0.03$	$78.71^{b} \pm 1.59$	$0.18^{c} \pm 0.01$	$14.46^{a} \pm 0.43$
Hakea gibbosa	$3.60^{a} \pm 0.12$	$76.14^{b} \pm 1.73$	$0.63^{a} \pm 0.03$	$11.83^{b} \pm 0.47$
Hakea salicifolia	$1.01^{c} \pm 0.07$	$75.71^{b} \pm 3.90$	$0.16^{c} \pm 0.01$	$11.79^{b} \pm 0.38$
F	220.01	3.98	141.13	18.05
d.f.	3,36	3,36	3,59	3,59
P	0.001	0.05	0.001	0.001

Table 8. Comparison of selected attributes of the seed biology and ecology of four species of Hakea. The relative values are assigned to the four species on the basis of results of this study.

Attributes	*H. sericea*	*H. gibbosa*	*H. suaveolens*	*H. salicifolia*
Juvenile period	Short	Short	Long	Moderate
Seed production	Very large	Relatively small	Relatively small	Large
Seed longevity in canopy	Long	Long	Long	Moderate?
Reproductive effort[a]	Just enough	Too much	Too little	Too little
Resistance of canopy stored seeds to fire	Resistant	Very resistant	Resistant	Intolerant
Time for follicles to open	Fast	Fast	Slow	Intermediate
Dispersability of individual samaras	Good	Good	Good	Good
Germination on burnt sites	Good	Intermediate	Good	Poor (canopy stored seeds killed)
Germination on unburnt sites	Good	Poor	Good	Poor (canopy stored seeds killed)
Nutrient concentrations in seeds	Relatively high N Normal P	Normal N Normal P	Normal N Relatively high P	Normal N Normal P

[a] Reproductive effort is defined as the ratio of dry mass of follicles and seeds to the total above-ground phytomass

6 years in *H. suaveolens* and the store of viable seeds in the canopy of large shrubs is smaller than in *H. sericea*. Seed release following fire is slow and this may lessen its competitive advantage as germination will be correspondingly slower.

Traits of *H. salicifolia* that contribute to its failure to invade fynbos are the moderately long juvenile period and the mortality of seeds during fires resulting from too little protection in small follicles. Although not shown in this study, a physiological inability to cope with the fynbos environment has probably contributed to the failure of this species to invade. Although our results show that seed viability declines in very old follicles, there is nonetheless a large seed store on individual shrubs, and the species is probably not held back by low seed numbers.

Our results suggest that the success of *H. sericea* relative to other alien *Hakea* species is due largely to the production of relatively large numbers of viable seeds. Fecundity is an important factor influencing not only the maintenance of established populations, but also the range of dispersal. A negative exponential relationship exists between seed numbers and dispersal distance (Harper 1977); such a model reveals that a 20% increase in seed numbers will increase maximum dispersal distance by 80%. The potential rate of spread is thus significantly increased by larger seed numbers (Cavers 1983). In order to refute the null hypothesis that the size of seed reserves is irrelevant in determining relative success of congeners, it is first necessary to demonstrate that the amount of seed is a limiting factor in the demography of each species (Macdonald 1984). This is demonstrated by the fact that all three invasive *Hakea* species form dense thickets, but it is only in *H. sericea* that colonization of distant areas constitutes a major problem. We ascribe the limited areal expansion of *H. gibbosa* and *H. suaveolens* populations to low seed numbers. Control measures aimed at reducing the seed bank using specialized insect seed predators (Neser 1968; Kluge 1983; Neser and Kluge in press) should provide the most effective means of combatting *H. sericea*.

Careful studies of the life history attributes of other species in their native habitats may reveal potential invaders of the fynbos. From the study of *Hakea* species, it appears that such species would: 1) have a potentially high seed production that is limited by specialized predators; 2) have an innate ability to disperse over long-distances; and 3) be pre-adapted to frequent fires and low soil nutrients.

Acknowledgements. We thank G.M. Bailey, A. Baker, P.J. Brown, K.B. Higgins, G. Hockey, Mrs C. Jacobs and A. Simmers for assistance and W.R. Siegfried for allowing us to harvest *H. salicifolia* shrubs on his property. Dr S. Neser provided us with information on *Hakea* in Australia and Dr R.M. Cowling and F.J. Kruger made useful comments on an early draft. The work of D.M.R. and B.W.v.W. forms part of the Conservation Forestry Research Programme of the South African Department of Environment Affairs (Forestry Branch). D.T.M. acknowledges the C.S.I.R. and University of Cape Town Staff Research Fund for financial assistance. This paper is part of the South African contribution to the SCOPE programme on the ecology of biological invasions.

Appendix 1. Exponential curves of the form $Y = A + BX + CX^2$ describing the relationships between total aboveground dry mass and the mass and number of follicles on shrubs of four *Hakea* spp. The curves are depicted in Figs. 2 and 3

Total dry mass in g (X) vs follicle mass in g (Y)

Species	*A*	*B*	*C*	*n*	r^2
H. sericea	−225.11	0.370	-8.318×10^{-6}	18	0.877
H. suaveolens	−52.328	0.017	8.251×10^{-7}	7	0.343
H. gibbosa	121.168	0.205	1.677×10^{-6}	15	0.954
H. salicifolia	37.501	−0.025	9.923×10^{-6}	13	0.810

Total dry mass in g (X) vs number of follicles (Y)

Species	A	B	C	n	r^2
H. sericea	−68.120	0.112	-2.518×10^{-6}	18	0.877
H. suaveolens	−16.543	0.005	2.617×10^{-7}	7	0.343
H. gibbosa	12.042	0.019	-4.018×10^{-8}	15	0.981
H. salicifolia	26.899	−0.021	8.149×10^{-6}	13	0.853

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Received February 28, 1986

Third paper: Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology*.

Journal of
Applied Ecology
1996, **33**,
161–172

Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management

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Summary

1. The invasion of fynbos shrublands by woody weed species can reduce the water yield from catchment areas dramatically. We modelled the consequences of uncontrolled invasion on water yield using a geographical information system (Arc/Info).
2. Five important processes were recognized: the occurrence of fire; the spread and establishment of alien plants after fire; rainfall-to-run-off ratios; growth and changes in biomass between fires; and effects of these changes on streamflow.
3. The simulations of water yield were modelled with the Arc/Info GRID module using a 200 × 200-m grid. It was assumed that the interval between fires was 15 years and that proliferation and dispersal of alien plants took place only after fires.
4. Between fires, the model simulated the growth of the vegetation and its effects on streamflow, using relationships between rainfall and run-off, and run-off and above-ground biomass.
5. Results for the Kogelberg area in the Western Cape Province showed that alien plants invaded about 40% of the grid cells within 50 years. Cover of alien plants increased from an initial estimate of 2·4% to 62·4% after 100 years.
6. Invasion of catchment areas would result in an average decrease of 347 m^3 of water per hectare per year over 100 years, resulting in average losses of more than 30% of the water supply to the city of Cape Town. In individual years, where large areas would be covered by mature trees, losses would be much greater.
7. In addition, invasion of fynbos by alien plants will cause the extinction of many plant species, increase the intensity of fires, destabilize catchment areas with resultant erosion and diminished water quality, and decrease the aesthetic appeal of mountain areas.
8. Control of alien weed species is necessary to avert the above impacts, and the costs of control operations could be justified by the savings achieved in maintaining adequate water run-off from stable catchments in the long term.

Key-words: catchment management, fire, fynbos, geographic information systems, hydrology.

Journal of Applied Ecology (1996) **33**, 161–172

Introduction

Fynbos, the fire-prone shrubland vegetation characteristic of the areas of the Western Cape Province of South Africa with a mediterranean climate, is prone both to periodic fire and to invasion by woody alien plants. Much of the extant fynbos vegetation occurs in mountainous areas, which are managed as water catchment areas; the most important management practices are prescribed burning and the control of alien woody weeds (van Wilgen, Everson & Trollope 1990).

Invasion of fynbos by woody weed species increases the above-ground biomass by 3–10-fold (Versfeld & van Wilgen 1986). Such increases can lead to dramatic declines in the streamflow from catchment areas, as a result of increases in transpiration and the evaporation of intercepted rainfall. One of the primary aims of the weed-clearing programme in catchment areas is to prevent such streamflow reductions, which can amount to 50% of the streamflow in some areas (van Wyk 1987).

The clearing of alien weed species from catchment areas is currently funded by the state, and funds are declining rapidly. This is not because the authorities fail to appreciate the problems that clearing alleviates, but through fierce financial competition from the various upliftment projects visualized by South Africa's new democratic government. In the worst case, where funding would be cut to the point at which clearing operations have to be suspended, it is feared that alien invasions could cover most of the catchment areas after about four fire cycles (van Wilgen, Bond & Richardson 1992). The real costs of this change, in terms of reduced water supplies to cities, agriculture and industries, could be enormous, and the question of whether such reductions can be afforded needs to be addressed urgently.

Advances in geographical information systems (GISs) and related computer technology have made the handling of large quantities of spatial data feasible. The development of a catchment management system based on GISs (Le Maitre, van Wilgen & Richardson 1993; Richardson *et al.* 1994) provided the opportunity to model the effects of invasion on water yield, using data from the Cape mountains as a basis for simulations. In this paper we describe the development of such models and present the preliminary results of the effects of catchment invasion on water yield.

Study area

Modelling was conducted using a database for the Kogelberg State Forest (35 000 ha), centred at 32°20′S; 19°03′E in the Western Cape Province, South Africa. The topography is rugged with deep ravines and steep slopes, and the geology is dominated by Cape sandstones. Soils are shallow, sandy, and nutrient-poor. Altitudes extend from sea level to 1268 m; most of the area is between 800 and 1000 m. Mean annual rainfall ranges from 600 to 1900 mm.

Predominant vegetation types include mesic and dry mountain fynbos shrublands (Moll *et al.* 1984). Northern and lower slopes are covered with low to mid-high ericoid shrublands of low to medium stature (0·1–1 m) with patchy proteoid shrublands (Boucher 1978). Upper northern slopes carry tall (1–2 m) shrublands dominated by shrubs from the families Proteaceae and Bruniaceae. Tall shrublands occur on southern slopes, with restioid herblands on peaty soils. Many endemic plant species occur in the area, making it important for nature conservation. Forests are restricted to small patches and riverine strips.

The area is managed by prescribed burning on a 12–15-year cycle. The State Forest has been kept remarkably free of alien plants compared with most other mountain catchment areas, but dense stands occur on adjacent lands and their seeds disperse into the State Forest. The most abundant aliens include *Pinus pinaster*, *Acacia cyclops*, *A. longifolia*, *A. saligna* and *Leptospermum laevigatum**.

Methods

PRINCIPLES OF THE MODEL

We recognized five distinct processes that need to be considered when calculating the spread and proliferation of alien plants and their effects on streamflow (Fig. 1), namely (i) the occurrence of a fire provides the opportunity for reproduction and dispersal; (ii) dispersal will lead both to the proliferation of existing populations and to the establishment of new populations following fire; (iii) growth during the period between fires will lead to changes in vegetation structure; (iv) the rainfall-to-run-off ratio (which varies with rainfall) must be calculated; (v) changes in the structure of vegetation will lead to changes in the streamflow. Each of these processes was modelled separately.

Modelling was conducted on spatial databases stored in a GIS. Data layers included the extent and dates of all fires, the distribution of vegetation types, the distribution of annual rainfall and the occurrence of alien plants. Each alien species was kept as a separate data layer in the database. The Arc/Info GRID module was used. In GRID each data layer was divided into rectilinear grid cells, each 200 × 200 m. Each grid cell had a single value for an attribute, for example post-fire age or vegetation type. The models were run in 1-year time steps.

Each population of an alien species was mapped onto 1:50 000-scale base maps. The species were grouped according to growth form, maturation rate and mode of dispersal (Table 1) to facilitate modelling. Population density was mapped using a qualitative scale based on the canopy-to-gap ratio, which is easily estimated by eye (Table 2). Population density classes were converted to a relative numerical abundance (Table 2) to simplify calculations of density class transitions.

The model is based on the results of a series of gauged catchment experiments, which were established to determine the effects of afforestation and fire on streamflow in the Western Cape Province (Table 3). The changes in streamflow that resulted either from removal of the vegetation by burning, or from changes brought about by afforestation, were obtained from the literature. In the case of Bosboukloof, no calibration period preceded afforestation of the catchment, precluding an estimate of virgin runoff; therefore streamflow reduction was estimated (van

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* See Table 1 for authorities for plant species names.

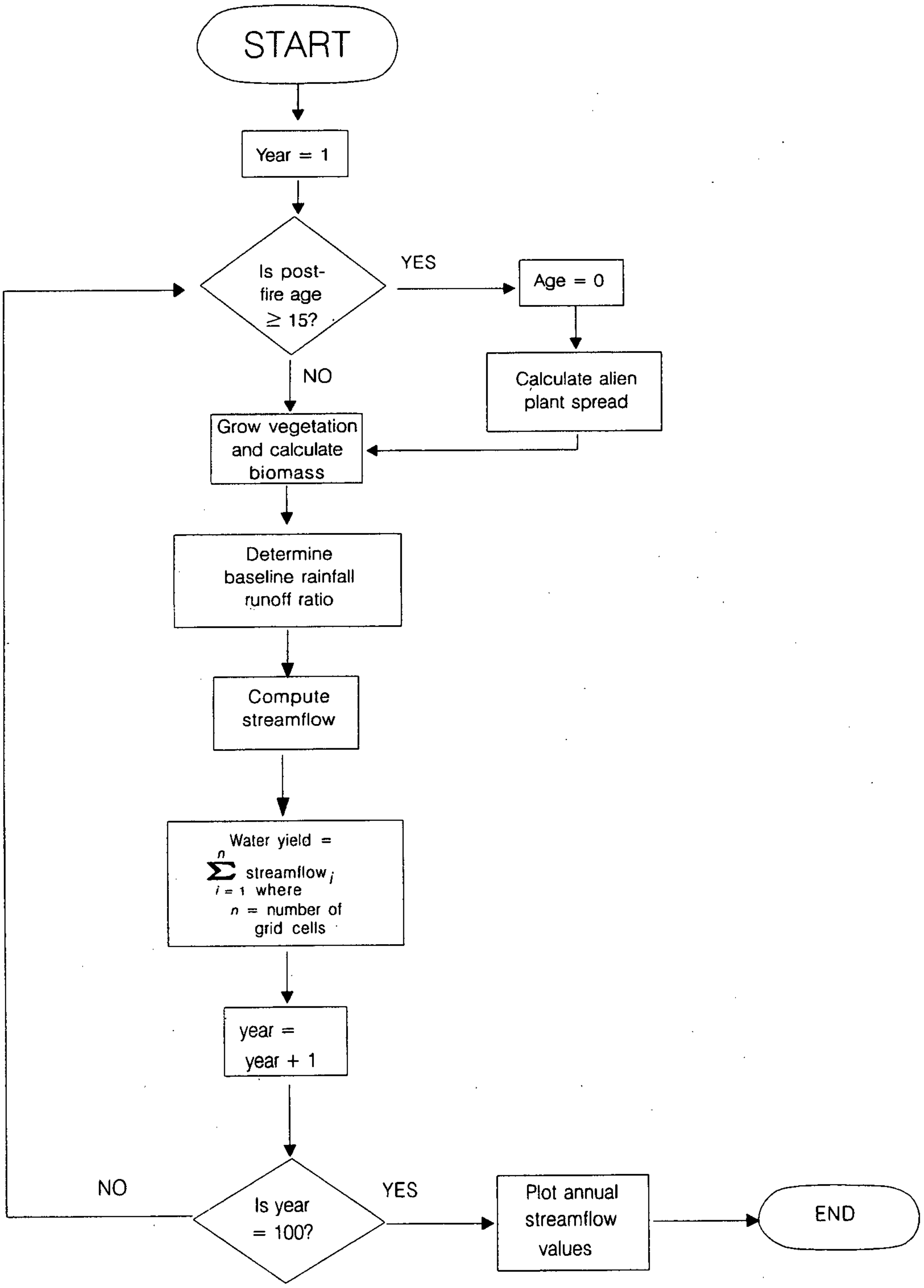

Fig. 1. Flow diagram showing the structure of a model to simulate the effects of alien plants on streamflow.

Table 1. Classification of 10 alien plant species by growth form, maturation rate and dispersal mode. For an explanation of the maturation rate see Table 4

Species	Growth form when mature	Height (m)	Maturation rate	Dispersal mode
Pinus radiata D. Don	Tall tree	> 10	Slow	Wind
Pinus pinaster Ait.	Tall tree	> 10	Slow	Wind
Hakea sericea Schrad.	Tall shrub	2–4	Fast	Wind
Hakea gibbosa (Sm.) Cav.	Tall shrub	2–4	Fast	Wind
Acacia cyclops A. Cunn. ex G. Don	Medium tree	5–10	Fast	Bird
Acacia saligna (Labill.) Wendl.	Medium tree	5–10	Fast	Bird
Acacia longifolia (Andr.) Willd.	Medium tree	5–10	Fast	Bird
Acacia mearnsii De Wild.	Tall tree	> 10	Slow	Bird
Acacia melanoxylon R. Br.	Tall tree	> 10	Slow	Bird
Leptospermum laevigatum F. Muell.	Medium tree	5–10	Slow	Wind

Table 2. Apparent density classes used in mapping populations of alien plant species

Density class	Description	Relative numerical abundance	Equivalent canopy cover (%)
None	No plants in the area	0	0
Rare	Individuals are known to occur in the area, but are few and far between	1	3
Occasional	Greater than 10 canopy diameters apart	2	6
Very scattered	6–10 canopy diameters apart	4	12·5
Scattered	3–6 canopy diameters apart	8	25
Open canopy	1–3 canopy diameters apart	16	50
Dense and closed canopy	< 1 canopy diameters apart	32	100

Wyk 1987). Biomass was calculated from published sources, taking the fraction of the catchment that had been afforested (higher biomass), or left unafforested (lower biomass) into account.

THE OCCURRENCE OF FIRE

Fires occur in fynbos at intervals of 4–40 years, with a mean of around 15 years (van Wilgen & van Hensbergen 1992). For modelling purposes we therefore assumed that a fire occurred when vegetation reached a post-fire age of 15 years (Fig. 1), and that the fire would be restricted to those areas of the vegetation with a post-fire age of 15 years.

THE SPREAD AND ESTABLISHMENT OF ALIEN PLANTS

Population increase within a grid cell

Population increase and dispersal only took place in the model after fire. We assumed that all alien plants were killed by the fire but subsequently re-established from seeds. The number of seeds depends on reproductive maturation rates, which are a function of time since the last fire (Richardson & Cowling 1992). A quantitative scale based on maturation periods and seed bank accumulation rates for different age classes was used to estimate relative seedbank sizes (Table 4). Mortality during the stages from seed to seedling, and for established populations, was included in the seed bank estimates so the 'seed bank' represents net recruitment.

The post-fire density of each species was calculated by multiplying the pre-fire relative numerical abundance (Table 2) by the relative seedbank size for that species and age (Table 4). A maximum value for the new relative numerical abundance was set at 32, equivalent to 100% canopy cover (Table 2). The relative numerical abundance values for each species (Table 2) were converted to canopy cover by expressing each as a percentage of the maximum value of 32. These cover values represented the contribution of that species to the vegetation cover in the grid cell. The total cover of alien species was calculated as the sum over the individual species, and the remainder of the grid cell was assumed to be covered by natural vegetation. The natural vegetation communities mapped by Boucher (1978) were grouped into 5 types (Table 5), with each grid cell assumed to be covered by the type that occupied the largest portion of the grid cell.

Table 3. Mean annual rainfall and run-off under conditions of minimum vegetation cover, and above-ground biomass under mature conditions with associated reductions in streamflow, in 11 gauged catchments in the Western Cape Province. Streamflow reduction is the difference in streamflow between conditions of minimum vegetation (after fire) and mature vegetation

Catchment	Treatment	Length of data record (years)	Mean annual rainfall (mm)	Runoff (mm)	Estimated above-ground biomass (g m^{-2})	Streamflow reduction (mm)	Source
Langrivier	Fynbos protected from fire for 25 years	33	1820	1360	7600	180	van der Zel & Kruger (1975); van Wilgen (1982)
Jakkalsrivier A	Fynbos protected from fire for 16 years	20	1210	544	1540	no data	Kruger (1977)
Jakkalsrivier B	Fynbos protected from fire for 16 years	20	1070	421	1540	no data	Kruger (1977)
Zachariashoek	Fynbos burnt on a 12-year cycle	14	781	290	560	0	van Wilgen & Kruger (1985); Lindley, Bosch & van Wyk (1988)
Bosboukloof	Fynbos afforested (57%) with *Pinus radiata* for 23 years	40	1300	no data	13800	330	van Laar & van Lill (1978); van Wyk (1987)
Tierkloof	Fynbos afforested (36%) with *Pinus radiata* for 16 years	40	1660	937	11500	500	van Wyk (1987)
Biesievlei	Fynbos afforested (98%) with *Pinus radiata* for 15 years	40	1310	472	18600	400	van Wyk (1987)
Lambrechtsbos A	Fynbos afforested (89%) with *Pinus radiata* for 8 years	37	1140	341	17300	350	van Wyk (1987)
Lambrechtsbos B	Fynbos afforested (84%) with *Pinus radiata* for 16 years	37	1270	399	16700	350	van Wyk (1987)
Swartboskloof	Fynbos burnt at a post-fire age of 29 years	6	2190	1060	3500	79	van Wilgen, Higgins & Bellstedt (1990); Scott & van Wyk (1992)
Kasteelkloof	Fynbos burnt on a 6-year cycle	14	1010	495	540	60	van Wilgen & Kruger (1985);Lindley, Bosch & van Wyk (1988)

Table 4. Relative seedbank sizes for different age classes of fast and slow maturing alien species

Maturation rate	Post-fire age class (years)	Relative seedbank size
Fast (*Hakea* species,	< 5	1
Acacia cyclops, A. saligna,	5–10	2
A. longifolia)	> 10	4
Slow (*Pinus* species,	< 5	0
Leptospermum species,	5–10	1
Acacia mearnsii,	11–15	2
A. melanoxylon)	> 15	4

Table 5. Above-ground biomass and growth curves for eight categories of vegetation in fynbos catchment areas

Vegetation category	Relationship between post-fire age (a, years) and biomass (b, gm^{-2})	Source for biomass figures
Ericoid–restioid fynbos	$b = 1370 \log_{10} a - 187$	Kruger (1977); van Wilgen & Richardson (1985); Richardson *et al.* (1994).
Short ericoid–fynbos	$b = 932 \log_{10} a - 108$	Kruger (1977); van Wilgen & Richardson (1985); Richardson *et al.* (1994).
Tall moist fynbos	$b = 9540 \log_{10} a - 636$	Kruger (1977); van Wilgen & Richardson (1985); Richardson *et al.* (1994).
Seeps and marshes	$b = 4820 \log_{10} a - 575$	Kruger (1977); van Wilgen & Richardson (1985); Richardson *et al.* (1994).
Low herbaceous fynbos	$b = 372 \log_{10} a + 22$	Kruger (1977); van Wilgen & Richardson (1985); Richardson *et al.* (1994).
Tall alien shrubs	$b = 5240 \log_{10} a - 415$	van Wilgen & Richardson (1985).
Medium alien trees	$b = 9610 \log_{10} a - 636$	Milton & Siegried (1981).
Tall alien trees	$b = 20000 \log_{10} a - 7060$	van Laar & van Lill (1978); van Laar (1983).

DISPERSAL TO NEW GRID CELLS

The relative number of seeds (n) available for dispersal to adjacent cells was calculated as the product of the relative numerical abundance (Table 2) and the relative seedbank size (Table 4) for an alien species of that age.

The typical dispersal curve for seeds is a negative exponential function: $y = ae^{-bx}$ where y = seed density and x = distance from source (Green 1980; Glyphis, Milton & Siegfried 1981; Auld 1988; Auld & Coote 1990). The probability that short-range dispersal will result in a grid cell having aliens in the next iteration, and their starting density, will therefore depend on the density and maturity of alien plants in neighbouring grid cells and the distance to these cells (Geritz, de Jong & Klinkhamer 1984; Auld & Coote 1990).

There are two primary modes of dispersal: bird dispersal and wind dispersal. Bird dispersal is directed largely towards suitable perches, resulting in distinct aggregations around perches (Glyphis *et al.* 1981; Gill 1985). In fynbos catchment areas, such perches are associated with riverine and forest vegetation (Manders 1990), and therefore only these sites received bird-dispersed alien plants in the model. We used the equation given by Glyphis *et al.* (1981) to describe the dispersal of bird-dispersed species:

$$f = -67{\cdot}5 \log_{10} d + 204 \qquad \text{eqn 1}$$

where f is the percentage of the relative number of seeds that would be dispersed over the distance in metres, d from the midpoint of the cell of origin to the midpoint of the target cell. (It is assumed that all seeds disperse from the centre of a cell of origin to the centre of an adjacent cell.)

Wind dispersal applies to species with winged seeds. The dispersal curves for pines and hakea were assumed to be similar because the wing loadings are similar at 18–26 g m^{-2} (van Wilgen & Siegfried 1986; Richardson, van Wilgen & Mitchell 1987). We used an equation of the type suggested by Green (1980), and derived from data (van Wilgen & Siegfried 1986) on the density of *Pinus pinaster* seeds vs. the distance from the parent plant, to describe wind dispersal as follows:

$$f = 47{\cdot}6 \log_{10} d + 149 \qquad \text{eqn 2}$$

For wind-dispersed seeds, the seed rain reaching a cell was calculated as:

$$s = \frac{nf}{100c} \qquad \text{eqn 3}$$

where s is the relative number of seeds dispersed to a given cell and c is the number of cells around the origin at that distance. For the adjacent (first order) neighbour cells the number of cells is 8, for the second order neighbours it is 16. For bird-dispersed seeds, only cells containing rivers were considered as target cells, and c would be equal to the number of adjacent cells with rivers in each order. This also reflects the fact that these species tend to spread along river courses.

If the number of seeds per cell (s) was less than unity, then the probability of a seed reaching the cell was equal to s. One seed was added to a target cell if a uniform random number was less than s. If the random number was greater than s then the target cell received no seeds. The dispersal routine was terminated after dispersal to the first order cells if s was less than unity there, otherwise it was terminated after dispersal to the second order cells. The seeds from all the cells within dispersal range were accumulated in a target cell.

The above routine had the effect of spreading seeds no further than 400 m. Field observations have shown that plants with wind-dispersed seeds are capable of dispersing a relatively small number of seeds a considerable distance (> 1–3 km, Richardson & Brown 1986; van Wilgen & Siegfried 1986). Such dispersal establishes individual trees which then provide a new focal point for proliferation after fires (Richardson & Brown 1986; Richardson 1988). We simulated this process by dispersing single seeds ($s = 1$) to four cells, each 1400 m from the cell of origin at each of the four cardinal points of the compass, after fire in scattered to dense (Table 2) stands of wind-dispersed alien trees or shrubs.

In some cases, seeds would spread from adjacent grid cells into cells already occupied by aliens. In these cases, the existing density of plants was expressed as relative numerical abundance (Table 2), and the new arrivals as a relative number of seeds. These two values were added together to provide a new estimate of the relative number of seeds present (with a maximum allowable value of 32).

To facilitate the modelling of growth and biomass (see below), the density of alien species was converted to an equivalent cover of a dense, closed canopy stand for each grid cell by expressing the relative number of seeds as a percentage of 32. Where the sum of cover values exceeded 100%, the values for each species were reduced proportionately so that the adjusted total was 100%.

RAINFALL AND RUN-OFF RATIOS

A coverage of the mean annual rainfall, which varies mainly with altitude, was included in the GIS database. The response of run-off to rainfall (Fig. 2) was based on the ratios from gauged catchments (Table 3) in the fynbos biome (run-off data in Table 3 are for periods prior to afforestation and in the year after a fire where possible). The run-off was described by the relationship ($r^2 = 0{\cdot}763$):

$$R = -368 + 0{\cdot}74\,P \qquad \text{eqn 4}$$

where R and P are the mean annual run-off and precipitation (in mm), respectively. A base ratio, representing the run-off under conditions of minimum vegetation cover, was assigned to each grid cell after fires on the basis of equation 4 above. Reductions in streamflow were calculated as changes from this base ratio (see below).

GROWTH AND CHANGES IN BIOMASS BETWEEN FIRES

The model assumed that reductions in streamflow were related to above-ground biomass in the catchment (see next section). For this reason, it was necessary to calculate biomass. After a fire, the biomass of each grid cell was set to zero. Thereafter, biomass was increased each year on the basis of predicted rates of growth for the vegetation type or species mixture concerned. The initial occupation of a grid cell after a fire was set as a percentage cover of each category of vegetation (the dominant type of fynbos, tall alien shrubs, medium alien trees and tall alien trees) using the models of increase and dispersal described above. The relationships between post-fire age and biomass (Table 5) were used to calculate an estimate of the biomass for each vegetation category. The biomass of each grid cell was then calculated as follows:

$$b_c = \sum_{i=1}^{N} \frac{z_i b_i}{100} \qquad \text{eqn 5}$$

where b_c is the biomass of the grid cell, b_i and z_i are the biomass (g m^{-2}, calculated from equations in Table 5) and cover (%) of the relevant vegetation category, respectively, and N is the number of vegetation categories (a maximum of four in this case).

EFFECTS OF BIOMASS ON STREAMFLOW

Decreases in streamflow are related to above-ground biomass (which is related to other factors influencing transpiration and rainfall interception, such as leaf area, see Fig. 3). The relationship, determined from data in Table 3, is as follows:

$$Q_r = 0{\cdot}02b + 37 \qquad \text{eqn 6}$$

where Q_r is the reduction in annual streamflow (mm) and b is the above-ground biomass (g m^{-2}). This relationship ($r^2 = 0{\cdot}765$) estimates potential

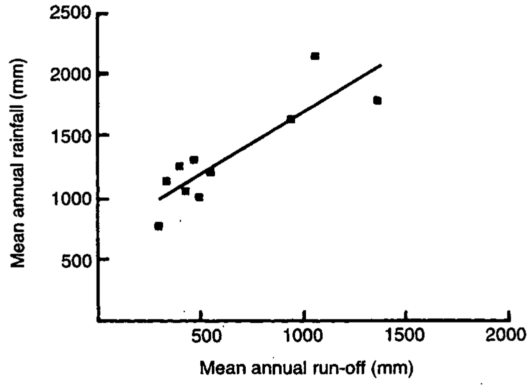

Fig. 2. Relationship between mean annual rainfall and run-off from 10 catchments with minimum vegetation cover in the Western Cape. Data are from Table 3.

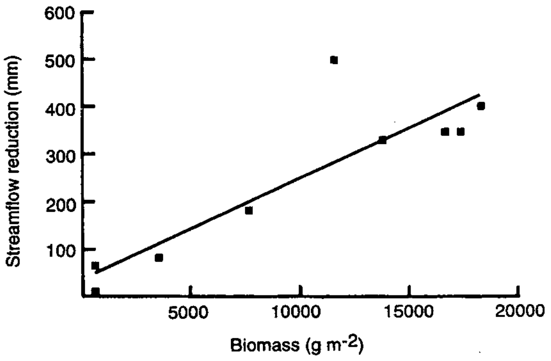

Fig. 3. Relationship between biomass and reduction in streamflow from nine gauged catchments in the Western Cape. Data are from Table 3.

reductions in streamflow based on actual gauged catchment experiments, the best available source of estimation. We used this relationship (Fig. 3), together with the rainfall, the base rainfall/run-off ratio and the calculated biomass, to calculate the run-off from each grid cell for each year of the iteration. Finally, the streamflow estimates from all of the grid cells were summed to give an estimate of the total streamflow from the area for each year.

Results

OCCURRENCE OF FIRE

At the start of the simulations, 64% of the study area had a post-fire age of less than 2 years, as a result of a recent wildfire. A further 20% had a post-fire age of 17–19 years. This resulted in large areas burning at one time in the simulations, because of the assumption in the model that fires would occur at regular intervals of 15 years. A more even distribution of post-fire ages (to be expected in larger areas), and a more stochastic simulation of the interval between fires would reduce this tendency toward regularity.

SPREAD AND ESTABLISHMENT OF ALIEN PLANTS

At the start of simulations, the distribution of alien plants was fairly sparse (Fig. 4). The cover of alien plants amounted to 2·4% (Table 6), and increased to 62·4% of the area, after 100 years (Table 6). This cover was initially distributed over 6% of the grid cells, increasing to 80% of the grid cells after 100 years (Fig. 4). Most of the cover was due to tall alien trees, represented in this case by *Pinus pinaster*. Medium alien trees, represented by bird-dispersed *Acacia* species, covered only 7% of the area after 100 years. Tall alien shrubs (*Hakea* species), which are a major problem in other areas, did not occur in the study area. The final distribution of alien plants predicted by the model ignores the possibility that interspecific competition may play a role; this is an important simplifying assumption in the model.

RAINFALL AND RUN-OFF RATIOS

The mean annual rainfall in the study area ranged from 587 to 1881 mm. Thus, the potential run-off from the study area with minimal vegetation cover would be between 67 and 1024 mm per year (equation 4). In a case where the area could become densely invaded by tall alien trees (18 000 g m^{-2}), run-off could potentially be reduced to 0–627 mm when the alien trees are mature. However, each time a fire occurs, run-off ratios would return to the base volume for minimal vegetation biomass.

GROWTH AND CHANGES IN BIOMASS BETWEEN FIRES

The changes in biomass during the simulations reflected the assumptions that fire would occur at 15-year intervals, that biomass would decrease to zero after a fire, and that it would increase according to the functions given in Table 5 between fires. This, and the bimodal distribution of post-fire ages in the area, resulted in a regular pattern of growth between fires and a large reduction in biomass when fires occurred. Where the simulations were run in the absence of alien plants, there were no long-term increases in biomass, while with alien plants, the biomass increased in accordance with the spread of alien trees and shrubs, reaching maximum values of 16 000 g m^{-2} in certain grid cells at times.

EFFECTS OF BIOMASS ON STREAMFLOW

The model produced annual estimates of streamflow in the study area for a simulation period of 100 years, for situations where alien trees and shrubs were present, and where they were absent. The streamflow from invaded and uninvaded catchment areas followed the fluctuations in biomass (Fig. 5). The cumulative streamflow over 100 years from uninvaded catchments would amount to 32 500 mm equivalent depth, or 325 000 m^3 ha^{-1}. The comparable streamflow from invaded catchments would be 290 000 m^3 ha^{-1} over 100 years, 10·6% less than from the uninvaded catchments, and equivalent to a mean reduction of 350 m^3 ha^{-1} $year^{-1}$.

Table 6. Occupation (%) by three categories of alien plants over 100 years in the Kogelberg area, as simulated by a spread model

	Years after start of simulation					
	1	20	40	60	80	100
Cover of tall alien shrubs	0	0	0	0	0	0
Cover of medium alien trees	1·2	2·2	2·3	4·7	5·1	5·4
Cover of tall alien trees	1·2	3·6	9·1	26·3	42·7	57·0

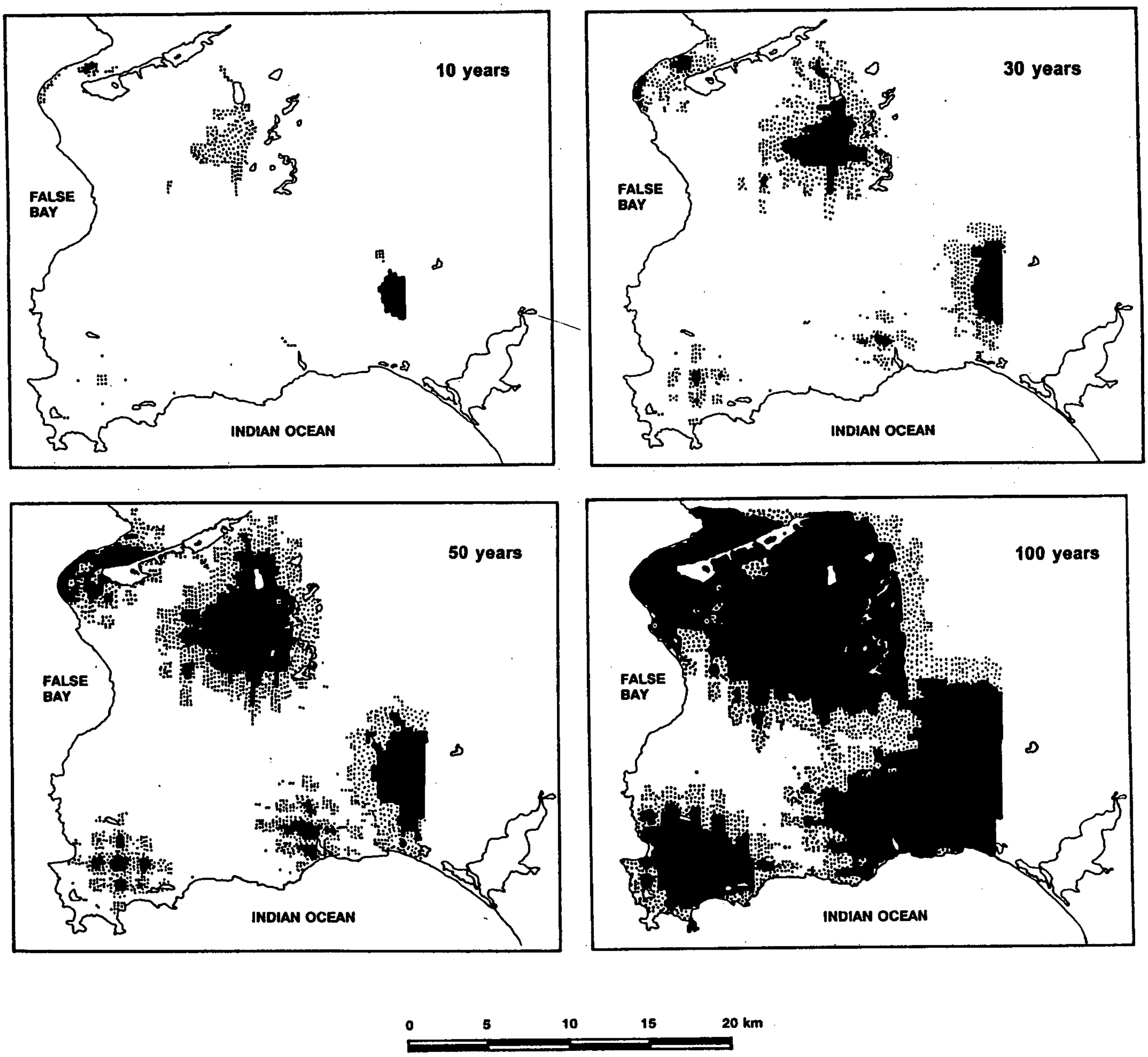

Fig. 4. Maps of the Kogelberg State Forest showing the extent of infestation by alien plants at various (top right of diagram) stages after the start of simulations of spread. Black areas represent dense (< 1 canopy diameter apart, Table 2) infestations; shaded areas represent all other density classes, while unshaded areas are free of alien plants.

Discussion

IMPLICATIONS OF INVASION FOR WATER YIELD

The catchment area which supplies the city of Cape Town with water is some 250 000 ha in extent, which means that an average of 87·0 million cubic metres of water could be lost annually if invasion were to be allowed to continue unchecked. This represents 34% of the annual water use (258 million m^3; Department of Water Affairs 1986) by the city.

However, the true impact may be greater. In the first place, the estimate of 34·7 mm per year represents the mean for the period over which the catchment became invaded. Once fully invaded, the reduction would be more. Secondly, in certain years (where fires

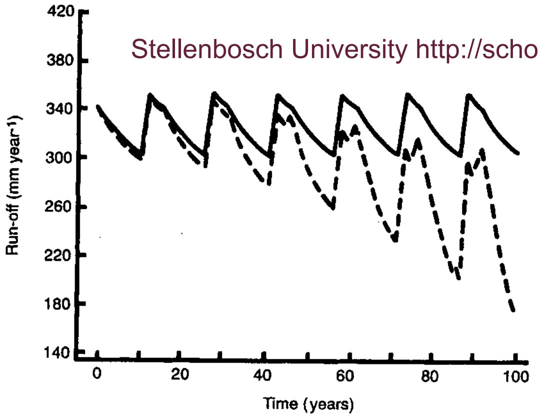

Fig. 5. Simulations of annual run-off from the Kogelberg State Forest with alien trees absent (——) with alien trees present (– – –) with a fire return interval of 15 years.

have not occurred for some time and the biomass of alien plants reaches high levels) invaded catchments would produce substantially less water. The effect would be further compounded if the year concerned had below-average rainfall. Thus, although the mean reduction would be substantial, the reduction in individual years may cause even greater problems for water supply.

The study area was also remarkably free of alien plants. Most of the remaining catchment areas that presently supply water to Cape Town are far more severely invaded. Consequently, the losses of water, and the potential for reducing these losses, would be greater than for the Kogelberg Study area reported on here.

IMPLICATIONS OF INVASION FOR OTHER CONCERNS

Invasion of catchment areas is not only of concern because of its effects on water yield. Invasion of catchments will also result in a loss of biodiversity. Fynbos is one of the world's six floral kingdoms, with 8574 plant species, of which 68·2% are endemic. Invasion of fynbos areas has already contributed to the extinction of 26 species (Hall & Veldhuis 1985). Whereas none of these extinctions can be attributed exclusively to alien plants (Richardson, McDonald & Forsyth 1989), a cascade of extinctions is virtually inevitable in the next few decades if alien invasions are not checked; *c.*750 fynbos plant species (9% of the flora) are currently at risk (van Wilgen *et al.* 1992). This level of extinction should be viewed in a serious light, given the current concern about loss of biodiversity worldwide.

Fires in mountain catchment areas, whether in the form of wildfires or prescribed burns, are events that necessitate active management. Our model has assumed a fixed fire cycle of 15 years. This assumption is of course a simplification of reality, and fires occur anywhere between once in 6 and once in 40 years. The pattern of fire frequency following invasion may be different, but it is not possible to predict this. What is certain, however, is that fire intensity increases as a result of the increased fuel loads associated with invasion (van Wilgen & Richardson 1985). This, in conjunction with the increased difficulty of access due to dense thickets of alien plants, severely complicates the fire management problem in these areas.

The increases in fire intensity associated with fires in heavily invaded mountain catchment areas can destabilize the catchments, with resultant increases in soil erosion and decreases in water quality. These changes are at least in part due to the initiation by intense fires of water-repellent layers in the soil (Scott & van Wyk 1990). In areas with a long history of invasion, chronic problems of fire and soil erosion develop (Scott, Le Maitre & van Wilgen 1991).

Finally, invasive plants alter the appearance of the landscape, thus affecting aesthetics and the potential for 'ecotourism'. Informed citizens (and international ecotourists) are well aware of the global significance of the fynbos vegetation. They will certainly not wish to visit sites that are invaded by alien plants. It is essential to take this factor into account, especially in view of the importance of ecotourism to the economy of a country like South Africa.

SOLVING THE ALIEN PROBLEM

Alien plants in catchments can be controlled through a combination of felling and burning, chemical control, and biological control (van Wilgen *et al.* 1992). The expertise exists to carry out effective control operations but funding is declining to a point where the control programmes cannot be implemented. To put this into perspective, however, the costs of clearing should be compared with the potential costs of lost water. Clearing of moderate infestations amounts to about R500 ha^{-1} prior to burning (once every 15 years). Control costs will thus average about R33 ha^{-1} year^{-1}. The potential annual gains in water of 350 m^{3} ha^{-1} would offset these costs. The pricing of water is a subject of some controversy. However, the growth of cities like Cape Town will be limited by water, making a potential saving of 30% of the water supply at a reasonable cost a powerful argument for clearing alien plants. This arrangement is strengthened by the fact that the only alternative sources of water are through recycling and desalinization, both of which are very expensive. Besides the gains to be obtained from the effective control of alien plants in terms of water, there are many other advantages. These include the conservation of biodiversity, easier fire management, increased catchment stability, a greater potential for ecotourism and direct job creation through the control programs themselves.

Acknowledgements

We thank the South African Department of Environment Affairs for funding this work, and our colleagues Greg Forsyth, Jeremy Midgley and Dirk Versfeld for useful discussion and criticism at all stages of the work. Mark Johns and Greville Ruddock supplied accurate distribution maps for alien plants in the study area.

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Received 15 June 1994; revision received 30 May 1995

Fourth paper: Valuation of ecosystem services: a case study from the fynbos, South Africa. *BioScience*.

Valuation of Ecosystem Services

A case study from South African fynbos ecosystems

Brian W. van Wilgen, Richard M. Cowling, and Chris J. Burgers

The term *ecosystem services* refers to the many conditions and processes associated with natural ecosystems that confer some benefit to humanity. Examples include the generation and maintenance of fertile soils; prevention of soil erosion; detoxification and recycling of waste products; regulation of the hydrological cycle and of the gaseous composition of the atmosphere; control of potential agricultural pests; pollination; and preservation of the earth's genetic library.

Walter Westman's classic paper "How much are nature's services worth?" (Westman 1977) raised the question of the value of conserving ecosystems for the services they provide to humanity. He pointed out nearly two decades ago that Western societies have increasingly called for the explicit quantification, in monetary terms, of the value of items formerly regarded as priceless. The trend toward valuation persists today. Yet few studies that we know of present explicit ways of evaluating ecosystem services in order to justify the allocation of funds for ecosystem maintenance and restoration. This economic justification is important where strong competition exists for the public funding needed for conservation management.

Watershed ecosystems provide quantifiable benefits that can justify management expenditure

In this article, we present a case study showing how invasion by alien plants has affected water resources in the mountain catchment areas of the Western Cape Province, South Africa. To provide an explicit accounting of the monetary value of maintenance of the ecosystem, we evaluate the benefits associated with a reliable supply of water (an ecosystem service). We compare the costs of a program of eradication of alien plants with these benefits and provide estimates of the costs of abandoning the program in the face of declining funding and competing demands for public funds.

The delivery of water from catchment areas, or watersheds, in the Western Cape Province, South Africa, serves as an example of a significant contribution from natural ecosystems to human well-being. The sustained supply of high-quality water depends on maintaining the cover of fynbos (shrubland) vegetation (van Wilgen et al. 1990). Fynbos vegetation is adapted to the summer droughts and nutrient-poor soils, as well as to the fires that occur periodically in the Cape mountains. The fynbos binds the soil, preventing erosion, while its relatively low biomass ensures conservative water use and low-intensity fires, which in turn ensure high water yields and low impacts on the soil from periodic fires.

South Africa is a dry country, and water is a resource that is likely to limit growth (Huntley et al. 1989). Catchment management is complicated by the invasion of the fynbos vegetation by nonindigenous woody trees and shrubs, which increase biomass and reduce runoff. The eradication of these weed species is seen by ecologists as a major part of catchment management (van Wilgen et al. 1990). Recent reviews have stressed that invasion of catchment areas by alien trees and shrubs would have serious effects on water supplies (van Wilgen et al. 1992, Versfeld and van Wilgen 1986). Ecologists have recognized this problem for many decades, but it has not yet received significant attention from policy makers. To justify funding for the maintenance and resto-

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ration of fynbos vegetation, it is necessary to be explicit about actual costs and benefits in monetary terms.

The importance of fynbos watersheds

The fynbos mountain watersheds are home to a major part of the Cape flora. In terms of endemic plant biodiversity, the region has been recognized as the world's "hottest" hot spot (Myers 1990). The Cape flora constitutes one of six biogeographic subdivisions, termed *plant kingdoms*, of the world. The Cape flora comprises 8574 species of vascular plants, 68.2% of which are endemic, and 989 genera of plants, 19.5% of which are endemic (Bond and Goldblatt 1984, Cowling et al. 1992). The mediterranean-type climate area of South Africa is characterized by cool, wet winters and warm, dry summers. Regular fires are considered necessary for the maintenance of the diversity of Cape flora, because fire triggers important phases of the life cycles of some plant species, such as seed release and germination. To rejuvenate the vegetation, prescribed burns are conducted at intervals of around 12–15 years in the late summer to early autumn period.

The Cape, like other mediterranean-type climate areas worldwide, is a focus of human immigration and population expansion, which makes these areas—and their associated ecosystems—disproportionately susceptible to potential environmental stress and degradation (Di Castri 1994). Cape Town, the largest city in the region, currently has a population of 2.2 million, which is projected to reach 3.5 million by the year 2000 and 6.2 million by 2020—an annual increase of between 4% and 5%. The region's other city (Port Elizabeth, 800 km to the east of Cape Town) is likely to experience similar growth, and even greater growth is predicted for the rapidly developing industrial areas at Mossel Bay (400 km east of Cape Town) and Saldanha Bay (120 km north of Cape Town). In addition, the region supports extensive irrigated croplands, producing deciduous fruit, wine, and wheat for local consumption and export.

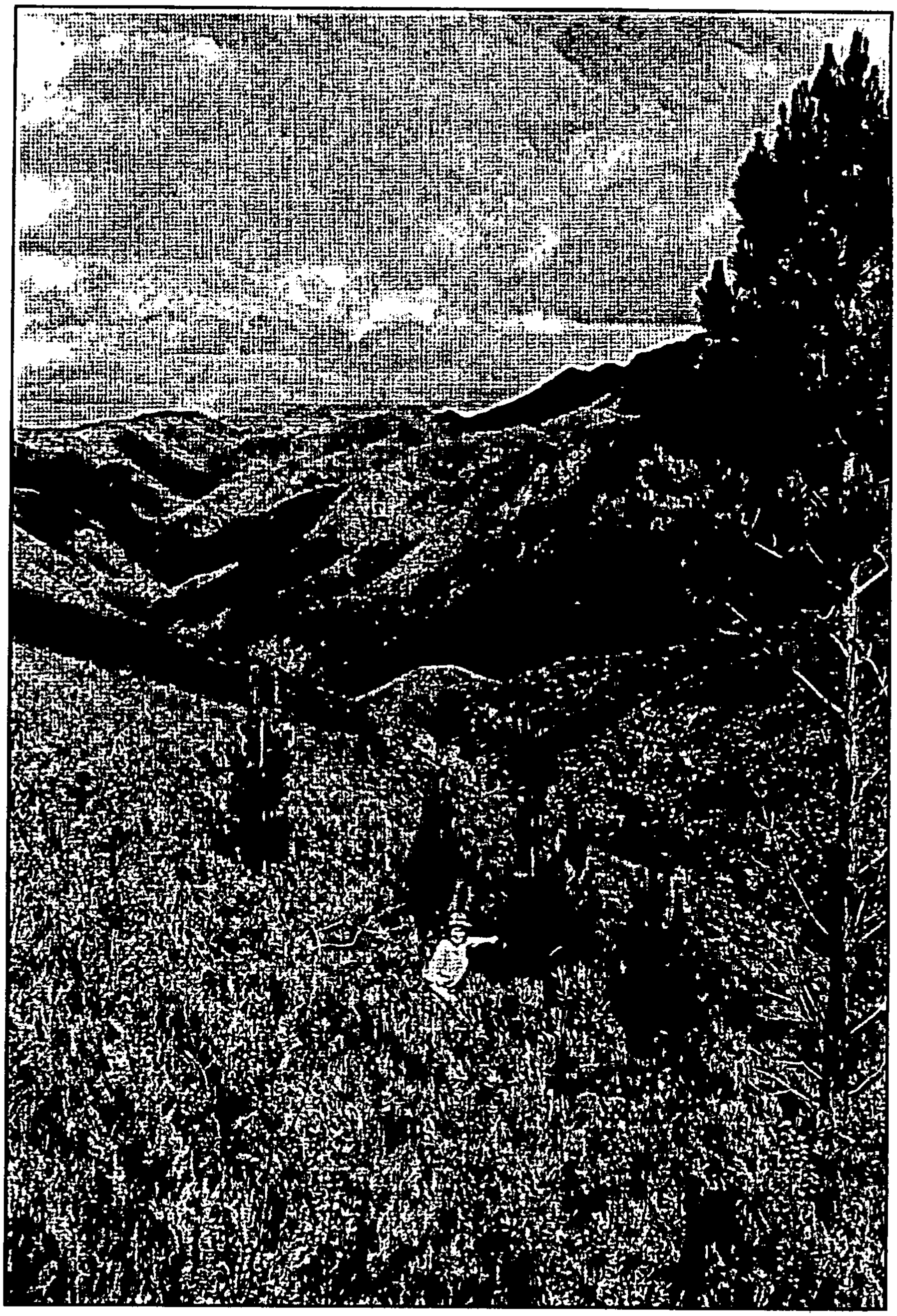

Figure 1. *Pinus pinaster* invading a fynbos mountain watershed. The increases in biomass and structure are striking. Following several fire cycles, closed canopy stands can develop and completely replace the native fynbos. Photo: G. G. Forsyth.

Fynbos-clad mountain catchments fulfill approximately two-thirds of the Western Cape's water requirements. This ecosystem service plays a crucial role in the region's economy and contributed a gross domestic product of US$15.3 billion in 1992 (Bridgeman et al. 1992). The continued growth of the industries that make up the Western Cape Province's economy, which will be necessary to support the growing population of the region, is limited by the availability of water. For example, the deciduous fruit industry is entirely dependent on water derived from adjoining mountain catchments; in 1993 this industry generated a gross export earning of $560 million and provided employment for approximately 250,000 people.

The Western Cape is also home to

large and rapidly growing numbers of economically marginalized people who live in informal settlements on the periphery of urban centers. The Reconstruction and Development Programme of South Africa's Government of National Unity (African National Congress 1994) endorses the principle that all South Africans have a right to "convenient access to clean water." Yet most of these poorer communities currently do not have access to reliable sources of clean water. Optimal catchment management is necessary to ensure that this water is made available and delivered in the most cost-effective manner possible.

Although the sustained delivery of water alone should justify the expenditure of public funds on optimal catchment management, alien-free catchments provide a wide range of additional ecosystem services and economic opportunities. The fynbos flora is widely harvested for cut flowers, dried flowers, and thatching grass (van Wilgen et al. 1992). The combined value for 1993 of these enterprises, much of which was made up of export earnings, was $18–$19.5 million and provided a livelihood for 20,000–30,000 people (Cowling and Richardson 1995). Many fynbos plants have been developed as food and drug products (Donaldson and Scott 1994). Foremost amongst these is rooibos tea (*Aspalathus linearis*), one of the 245 species of this genus in the Cape flora. The rapidly growing exports of this tea generated foreign exchange of $2.1 million in 1993. Research is currently underway to develop species of *Cyclopia*, an endemic fynbos genus in the Fabaceae, as a high-quality health tea. Several other plants, including horticultural and medicinal crops, are currently used commercially; undoubtedly many as yet undiscovered plants would provide similar opportunities.

Many of these services are based on the phenomenal biodiversity of fynbos ecosystems. Alien plants are recognized as the greatest threat to this biodiversity (Richardson et al. 1992) and are largely responsible for the extraordinarily high number of endangered and threatened taxa (1406, or 16.4% of all plant species) among the Cape flora (Cowling and Hilton-Taylor 1994).

The unique and spectacularly beautiful fynbos flora is an internationally recognized ecotourist resource (Bridgeman et al. 1992). Tourism in the region is substantial; for example, approximately 400,000 tourists visit the Cape of Good Hope Nature Reserve each year, an area of enormous plant biodiversity immediately south of Cape Town. A major growth industry in the Western Cape, ecotourism has great potential to provide employment and fuel economic growth in an economically and ecologically sustainable way (McNeely 1988, Swanson 1991). Uncontrolled alien plant invasions are a significant threat to the ecotourism resources of the Western Cape.

Alien plants in fynbos watersheds

Fynbos ecosystems are remarkably prone to invasion by alien woody weeds (trees and shrubs; Figure 1). These weeds displace the native fynbos and increase biomass by between 50% and 1000% (Versfeld and van Wilgen 1986), resulting in significant decreases in runoff from catchment areas. The weeds are also fire-adapted species, which complicates the program of prescribed burning. Whereas weed-free areas can easily be subjected to prescribed burns, areas infested by weeds first have to be cleared if their spread after fire is to be prevented. Therefore, an active program aimed at the eradication of alien trees and shrubs is carried out in catchment areas (van Wilgen et al. 1990).

The invasive plants were introduced to South Africa to provide a source of fast-growing timber in the relatively treeless landscape and also as hedge plants, as agents for binding shifting dunes along the coast, and as ornamental plants. The introductions began with European settlement of the area in the mid-seventeenth century and gained momentum in the early nineteenth century. Not all introduced plants have become invasive. The most important invasive species originated in Australia and the mediterranean-type climate areas of Europe and North America (Stirton 1978).

In fynbos, alien woody weeds fall into two broad groups. The most important group includes serotinous plants (plants with seeds stored in cones or persistent fruits) such as *Hakea sericea* and *Pinus pinaster*, which are killed by fire and then release the seeds held in closed serotinal cones. To eliminate these plants, they are felled before burning. The seeds of the alien plants are then released, after which they either germinate or are consumed by rodents. Approximately one year after felling, the area is burned and the seedlings of alien plants are killed. However, regular follow-up weeding operations are required to eliminate the few individuals that inevitably escape the fire. These follow-up operations are usually carried out 2.5 and 10 years after burning (Macdonald et al. 1985).

The second group of weeds includes those species with continual seed release (e.g., Australian *Acacia* species). Large quantities of hard-coated seeds accumulate in the soil (Richardson et al. 1992). In this case, control is more problematic. Felling and burning results in abundant seedlings, which need to be cleared by hand-pulling—a time-consuming and labor-intensive process.

Invasion of fynbos watershed areas by alien plants results in changes to vegetation structure that fundamentally alter the nature of the fire management problem. Increases in aboveground biomass result in increases in fuel loads and therefore in fire intensity. Access to affected areas becomes difficult, and the construction and maintenance of fire breaks becomes onerous, expensive, and largely ineffective. These changes are difficult to quantify in monetary terms. In some areas, however, these changes have led to the deterioration of the ecological integrity of watersheds to the point that they become a financial burden rather than an asset. For example, on the slopes of Table Mountain, above the city of Cape Town, invasion by alien plants has increased fire intensities, leading to severe soil erosion (Scott and van Wyk 1990, Scott et al. 1991). At the same time, the elimination of indigenous plants

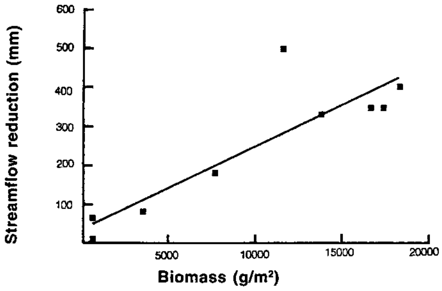

Figure 2. Relationship between biomass and reduction in streamflow from nine gauged catchments in the Western Cape with varying degrees of invasion by alien trees (from Le Maitre et al. in press). This relationship was used to simulate reductions in streamflow in invaded catchments.

has further favored erosion through a reduced capacity to cover and protect the soil after fires. As a result, enormous sums of money have had to be spent after each fire to remove sediment from the city's stormwater drains, roads, and houses. Similar problems could develop elsewhere in the region as the population encroaches on mountain areas.

Currently, funding for watershed management in South Africa is under pressure, especially in view of the competition for funds from social projects in the postapartheid era. The new democratic government is not likely to allocate enough funding to catchment management unless the expenditure of public funds can be justified in terms of the betterment of human well-being. The South African situation is not unique. Governments elsewhere, especially in the developing world, find themselves in similar situations, in which the conservation and maintenance of ecosystems is difficult to justify in the absence of a sound economic evaluation. Such evaluations are difficult to find, but they include the Amazonian rain forests, where exploitation of nonwood resources would provide profits while conserving the forests (Peters et al. 1989).

The impacts of alien plants on water resources

Le Maitre et al. (in press) have developed a model to simulate the effects on water yield of invasion of watersheds by alien plants, using the results from watershed experiments in the Cape mountains as a basis. These experimental watersheds, many of which have continuous records of streamflow and rainfall covering more than a half a century, have clearly shown that afforestation with alien plants can decrease streamflow (van Wyk 1987). In the experimental watersheds, the biomass of natural and alien vegetation had been determined, and the growth rates of invasive plants and natural vegetation between fires were known.

The model, which runs on a geographic information system, is initiated with a known mixture of natural vegetation and alien plants. It assumes an interval of 15 years between fires (the mean return interval calculated from fire records). After each fire, the aboveground biomass of the area is assumed to be reduced to zero; alien plants increase in density and also spread to adjacent areas (these simulations were based on known rates of proliferation and spread for the species concerned). The biomass of the watershed between fires was simulated using the known rates of growth for both alien plants and native vegetation. Because of the higher growth rates of alien plants, the biomass of watersheds increased in the simulations as the watersheds became invaded.

Le Maitre and his coworkers (in press) established a statistically significant relationship between aboveground biomass and reductions in streamflow, based on the long-term watershed experiments described above (Figure 2). Although the exact mechanisms of the reductions are not clearly understood, they are undoubtedly a function of both increased transpiration and interception of rainfall by alien trees. Both of these variables are increased by increases in the leaf area as the vegetation becomes dominated by tall alien trees instead of short shrubs; these increases are easily described using biomass, a surrogate measure of leaf area.

The relationship between simulated biomass and streamflow reductions was used to calculate the water yield between fires, using scenarios with and without alien plants.

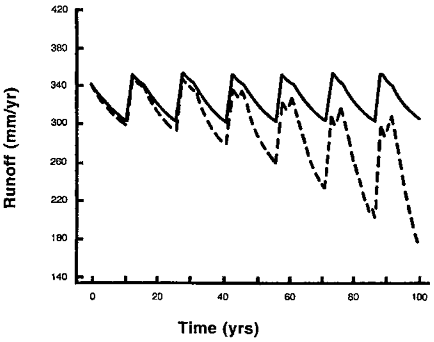

Figure 3. Simulations of annual runoff from the Kogelberg area in the Western Cape Province with alien trees absent (solid line) and with alien trees present (dashed line) with a fire return interval of 15 years (from Le Maitre et al. in press).

In their simulations, Le Maitre et al. (in press) used a study area in the Kogelberg Mountains, to the east of Cape Town, that was relatively free of alien plants (cover of 5.4%) when simulations were initiated. The model indicated that alien plants would invade approximately 40% of the area within 50 years and 80% after 100 years, with a corresponding increase in biomass of 150% or more. This invasion would result in an average decrease of 347 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ of water over 100 years, resulting in average losses of more than 30% of the water supply to the city of Cape Town. In individual years, when large areas would be covered by mature trees, losses would be much greater, exceeding 50% of the runoff from similar uninvaded areas (Figure 3).

Economics of water and catchment management

We examined the economics of water and catchment management in two ways. First, we compared the costs of developing water supply facilities (dams and water distribution networks) in two identical catchments, with and without the management of alien weed populations. Second, we compared the cost-effectiveness of optimal catchment management to alternative means of securing water supplies, such as recycling or desalinization of seawater.

The assumptions made for the two identical catchments (Table 1) were derived from established relationships between rainfall, runoff, and the aboveground biomass of vegetation, as modeled by Le Maitre et al. (in press). A 10,000-hectare catchment, with 1500 mm of rainfall annually, would support around 3800 g/m^2 of fynbos vegetation at 15 years postfire. The same catchment, if fully invaded by alien trees and shrubs, would support a biomass of around 11,000 g/m^2 at the same stage. The catchment would yield 742 mm (rainfall equivalent) of streamflow under conditions of no aboveground vegetation (as found immediately after fire), or 74.2×10^6 m^3/yr.

The costs of management of alien plants can be divided into the clearing of existing stands of alien plants and the subsequent follow-up operations required to keep these areas free of new invaders. The costs of initial clearing amount to between $140 and $830 per hectare, depending on the density of invasion; annual follow-up operations are estimated to cost $8 per hectare over large watershed areas.

A report on the potential water supply facilities in the Western Cape (DWAF 1994) lists 20 remaining sites for the development of water supply facilities in the province. The capital costs of building these facilities range from $0.83–$215 million, with a mean of $1.08 per cubic meter of water. We used this mean to estimate the cost of a theoretical water supply scheme from a 10,000-hectare catchment yielding 62.7×10^6 m^3/yr at $67.7 million. The mean operating costs amount to 2.1¢ per cubic meter, or $1.29 million per year for a 10,000-hectare catchment (Table 1).

The unit cost of water for the two hypothetical catchments can be calculated by assuming an annual interest cost on capital outlays (the building of a water supply facility in both cases, and the initial clearing of alien plants in one) and combining this cost with the annual operating costs (Table 1). We used 8% inflation as a conservative estimate, because inflation in South Africa over the past ten years has ranged between 10% and 16%. Although total annual costs are 11% higher for the case in which alien trees are managed, the unit cost of water production is 14% lower because of the larger volumes of water that would be produced from a watershed where alien trees are cleared and managed. Furthermore, such a watershed would yield an additional 14.1×10^6 m^3/yr of water, almost 30% more water than an unmanaged catchment. This last point is particularly important in view of the

Table 1. Assumptions for parameters, together with costs and water yields, in two identical catchments, with and without the management of alien weed populations. Vegetation classes are from Le Maitre et al. (in press). Biomass and streamflow reductions were calculated from relationships given in Le Maitre et al. (in press).

Catchment descriptor	With the management of alien plants	Without the management of alien plants
Area (ha)	10,000	10,000
Mean annual rainfall (mm)	1500	1500
Postfire age (years)	15	15
Vegetation cover	70% short ericoid-restioid fynbos; 30% tall moist fynbos	33% tall alien shrubs; 33% medium alien trees; 33% tall alien trees
Capital cost of clearing initial infestations ($/ha)	830	0
Capital cost of developing water supply facility (millions of $)	67.7	67.7
Capital cost of building water supply facility plus initial clearing of aliens (millions of $)	76	67.7
Annual interest on capital cost at 8% (millions of $)	6.1	5.4
Cost of alien plant management (an operating cost, $ $\cdot$ ha^{-1} $\cdot$ yr^{-1})	8	0
Operating cost of water supply facility (millions of $ per year)	1.29	1.29
Total operating costs (alien plants plus water supply facility; millions of $ per year)	1.37	1.29
Total annual costs (interest plus operating, millions of $ per year)	7.47	6.69
Aboveground biomass (g/m^2)	3867	10,964
Streamflow from catchment without vegetation (mm rainfall equivalent)	742	742
Reduction in streamflow due to plant biomass at 15 years postfire (mm rainfall equivalent)	114	256
Water yield ($\times 10^6$ m^3/yr)	62.7	48.6
Unit cost of water (¢/m^3)	11.9	13.8

limited opportunities for establishing new water supply facilities.

The alternatives to obtaining water from optimally managed catchments are not attractive. A sewage effluent exchange plant that would deliver the same volume of water as a well-managed catchment of 10,000 ha (62.7×10^6 m^3/yr) would cost $135 million to build and would operate at $2.6 million per year. Using the assumption of 8% interest on capital outlay, this example equates to a unit cost of $0.21/$m^3$. Direct reuse of sewage would cost $0.25/$m^3$, whereas desalinization would deliver water at $0.80/$m^3$. Thus these alternatives would deliver water at a cost between 1.8 and 6.7 times more than optimal catchment management.

Conclusions

Optimal catchment management provides three tangible benefits in terms of ecosystem services: It delivers water at the cheapest rate, it delivers more water, and it provides additional ecosystem services such as economic exploitation of fynbos plants and ecotourism opportunities. Our analysis has concentrated on the first two benefits by examining the direct costs of delivering water, but this analysis needs to be viewed in the greater context of its contribution to the economy of the region.

Many arguments for the conservation of ecosystems rely on their existence value—the value attached to a resource regardless of its actual or potential use. One way of measuring existence values would be to assess how much people would be willing to pay to ensure that an area continues to exist undisturbed, whether or not those people make use of such an area. However, existence values are becoming increasingly difficult to quantify and to defend, particularly in developing countries, where basic human needs and economic growth are the overriding concerns. Our analysis shows that in terms of the cost-effective and sustainable delivery of clean water, well-funded management of fynbos-clad catchments by removing and preventing alien plant invasions makes sound economic sense. This practice would also restore and sustain biodiversity in catchment areas and thus enable the maintenance and growth of economic enterprises based on fynbos plants. The challenge we and other Western Cape scientists face is to convince policy makers of the wisdom, for the long term, of allocating public funds for the optimal management of fynbos catchments. Doubtless, many other scientists in many other nations face similar challenges.

Acknowledgments

Van Wilgen acknowledges CSIR and the South African Department of Environment Affairs and Tourism for supporting this work. Cowling acknowledges the Pew Charitable Trust for financial support.

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Fifth paper: Invasive alien plants and South African rivers: A proposed approach to the prioritization of control operations. *Freshwater Biology*.

Freshwater Biology (2007) **52**, 711–723 doi:10.1111/j.1365-2427.2006.01711.x

Invasive alien plants and South African rivers: a proposed approach to the prioritization of control operations

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SUMMARY

1. A number of parallel initiatives in South Africa have been addressing the prioritization and management of invasive alien plant species, the prioritization of rivers for the conservation of biodiversity, and broad-scale planning for water resource management. This paper has combined aspects of these approaches to develop a composite index of prioritization of quaternary catchments for alien plant control purposes.
2. We calculated, for each quaternary catchment, a simple composite index that combined estimates of (i) the number of invasive alien plant species present; (ii) the potential number of invasive alien plant species that would be present if they occupied the full range as determined by climatic envelope models; (iii) the degree of habitat loss in rivers; and (iv) the degree of water stress. Each of the four components contributed between one and four to the combined index, which had a range of values between four and 16.
3. We used a geographic information system to map the distribution of priority catchments for invasive alien plant control. Of the 1911 quaternary catchments in South Africa and Lesotho, just over one-third (650) were in the highest priority category with an index of 13 or more. A relatively small proportion (273, or 14%) of the catchments had the maximum scores of 15 or 16.
4. The approach identified priority areas that have not currently been identified as such, and should provide decision makers with an objective and transparent method with which to prioritize areas for the control of invasive alien plants. We anticipate debate about the way in which components of the index are calculated, and the weight given to the different components, and that this will lead to the transparent evolution of the index. Improvements would also come about through the addition of a more comprehensive list of species, and through the addition of further components.

Keywords: catchment management, conservation planning, Lesotho, water stress, Working for Water programme

Introduction

Rivers are globally threatened by the development of impoundments, flow regulation and pollution (Dudgeon *et al.*, 2006). In addition to these pressures, invasive alien species pose a significant threat to the ecological integrity of river ecosystems, and are often cited as the second most pressing threat (after direct habitat destruction) to global biodiversity (Mooney & Hobbs, 2000). The focus of attention with regard to alien species and rivers has often fallen onto faunal elements, notably alien fish (Rahel, 2000, 2006), and floating aquatic weeds (van Wyk & van Wilgen, 2002), while terrestrial ecologists have focussed largely on

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the impacts of invasive alien plants away from river ecosystems. River ecosystems are nonetheless very important, and several studies have found riparian zones to be more invaded by alien species than other plant communities, and rivers may function as dispersal corridors for the rapid spread of invasive alien plants across landscapes (Thébaud & Debussche, 1991; Pysěk & Prach, 1994; Planty-Tabacchi *et al.*, 1996). It is also widely recognised that river ecosystems cannot be managed in isolation of their catchments (Tinley, 1991; Allan, Erickson & Fay, 1997), but ecological studies that explicitly seek to integrate terrestrial and aquatic aspects of ecosystem management are rare (Dudgeon *et al.*, 2006).

While it is often the case that parallel initiatives aimed at aspects of river or water conservation are attempted in isolation, the fact that they exist offers promising potential for integration. In South Africa, for example, ecologists and water resource planners have focused on a number of aspects relating to the conservation of rivers and water resources in a number of parallel yet largely unrelated initiatives. One of these relates to the impact of terrestrial invasive alien plant species, where the impact of these species on water resources has clearly been demonstrated (Le Maitre *et al.*, 1996, 2002; van Wilgen, Cowling & Burgers, 1996; Dye & Jarmain, 2004), leading to the establishment of one of the largest invasive alien plant clearing programmes globally (van Wilgen, Le Maitre & Cowling, 1998). Provisional estimates indicate that between 1400 and 3300 million m^3 of surface runoff, or between 3% and 7% of the national mean annual runoff, is used by invading alien vegetation. This is in excess of the volume used by native vegetation (Görgens & van Wilgen, 2004). If the spread of such vegetation is not controlled, the impact is likely to increase. Through the government's interventions, large areas are being cleared of alien vegetation. Current policy recognises that the removal and containment of such vegetation should, where applicable, form part of catchment management strategies (Department of Water Affairs and Forestry, 2002).

In a second set of initiatives in South Africa, aquatic ecologists have been developing approaches towards the prioritization of river ecosystems for the conservation of biodiversity. This work (King, Tharme & de Villiers, 2000; Roux, 2001) has been driven by (and even preceded) a number of newly-adopted policies. In particular, South Africa's new water legislation, adopted in 1996, requires that the ecological integrity of river ecosystems be maintained to protect their capacity to deliver goods and services to people on a sustainable basis. South Africa has also ratified the Convention on Biodiversity, and in terms of this is developing a national biodiversity strategy and action plan, which will include an explicit prioritization of river ecosystems for conservation (Driver *et al.*, 2005). Finally, several large-scale initiatives, funded by the Global Environmental Facility, have resulted in the introduction and development of systematic conservation planning to underpin the national biodiversity strategy and plan (Gelderblom *et al.*, 2003; Driver *et al.*, 2005).

A third group of initiatives has arisen under the auspices of studies seeking to secure a reliable supply of water (Department of Water Affairs and Forestry, 2004). South Africa is a dry country, and like many others the demand for water resources often exceeds the capacity of ecosystems to provide them. South Africa's ambitious new water legislation has stretched the managerial capacity to implement the law's new requirements, and has required that catchments be defined in terms of the water stress that they experience to prioritize interventions. Water stress can be quantitatively defined as the difference between water availability and requirements.

The existence of these parallel initiatives offers the opportunity to combine approaches to achieve the maximum positive impacts. The concurrent prioritization of invasive alien species and areas for control operations aimed at conserving water resources, the broad-scale (national) conservation planning, and the prioritization of rivers for conservation, clearly invites a co-ordinated approach. Given advances in processing technology of spatial data, and the growing realisation that holistic solutions to environmental problems are necessary, it is now possible to develop pragmatic and practical approaches that can guide policy and implementation aimed at conserving rivers and water resources.

In this paper, we propose an approach that will enable managers to prioritize river systems and their catchments for the purposes of invasive alien plant control. The approach we propose will combine results from recent work on the spatially explicit predictions of range expansions in important invasive alien plant species (Rouget *et al.*, 2004) with that of conservation planners who have sought to prioritize river ecosystems in terms of the degree of habitat loss, and that of water resource planners who have calculated the water balance of catchments. Our aim was not to conduct an exhaustive analysis of the problem. Rather, we wish to demonstrate the feasibility of an approach that will lead to the prioritization of catchments for alien plant control operations, thus ensuring that such operations can be directed at priority areas in terms of conservation importance, the risk of invasion, and a positive impact on water resources.

Methods

Selection of invasive alien species

We selected 13 invasive alien plant species to illustrate our prioritization exercise. The species were selected from a recently developed list of invasive alien plants in South Africa (Nel *et al.*, 2004), and are found in one or more of the major terrestrial biomes of South Africa (including savannas, grasslands, Mediterranean-climate shrublands, and arid-zone shrublands). This list differentiates between species that have invaded riparian zones, and those that have invaded upland areas away from riparian zones. The species selected are those that invade and dominate riparian areas, plus the most important species, in terms of their impact on hydrology, that invade upland areas. We did not consider riparian invaders that are not major ecosystem 'transformers' (i.e. species that form extensive, monospecific stands, dominating or replacing native vegetation), or invaders of uplands whose impacts on evapotranspiration were small. We also did not consider invasive alien species under effective biological control (Zimmermann, Moran & Hoffmann, 2004). The list used here is not intended to be comprehensive, but was chosen to demonstrate the principle.

Establishing the current and future distribution of alien species

The current distribution of the 13 selected invasive alien plant species was determined from the South African Plant Invaders Atlas (SAPIA) database. This atlas comprises nearly 50 000 records for more than 500 species of invasive alien plants, incorporating records from roadside surveys carried out between 1979 and 1993, and the SAPIA project (1994–98), as well records collected on an *ad hoc* basis from 1999 onwards (Henderson, 1998; Nel *et al.*, 2004). Records are entries that note the presence, and abundance, of a species in quarter-degree squares (15′ latitude × 15′ longitude, hereafter grid cells). Nel *et al.* (2004) related the range of a species to the number of grid cells in the SAPIA database in which the species was recorded. The categories of range were: very widespread = found in >350 grid cells; widespread = found in 70–350 grid cells; and localised = found in <70 grid cells. The SAPIA database also notes the abundance of species that are recorded in a grid cell in the following categories: rare (one sighting of one or a few plants); occasional (a few sightings of one or a few plants); frequent (many sightings of single plants or small groups); abundant (many sightings of clumps or closed stands); and very abundant (forming extensive stands). Nel *et al.* (2004) used these records to define categories of abundance as follows: abundant = recorded in the SAPIA database as 'very abundant' or 'abundant' in 16% or more of grid cells where it occurred; and common = recorded as 'very abundant' or 'abundant' <16% of grid cells where it occurred.

The potential future distributions of 71 major invasive alien plant species were modelled using a variant of climatic envelope models (Rouget *et al.*, 2004). This technique produces spatial estimates of future distribution at a scale of 1′ latitude × 1′ longitude, i.e. a much finer resolution than the estimates of present distribution. We recognise that climate envelope modelling can produce large over estimates of the potential area to be invaded, and that invasive species are limited by many other factors besides climate. Riparian areas would provide an additional 'filter' for habitat suitability for those species that invade such areas. This provides an additional degree of confidence in predictions of future distribution for at least some of the species used in this study.

Establishing the degree of habitat loss in rivers

Important rivers were defined using data on the conservation status and importance of river ecosystems, as identified by the national spatial biodiversity assessment (Driver *et al.*, 2005). The data were in the form of river 'signatures', which were derived from geomorphological and hydrological characteristics, including flow variation and baseflow, the key physical drivers of river heterogeneity. Characterising river heterogeneity in this way over time and space is key to predicting pattern and the distribution of river biota (Montgomery, 1999; Rogers & O'Keefe, 2003). River signatures have been used as a basis for characterising river ecosystems that share the same biological response potential and similar biodiversity. Although the results of Driver *et al.*'s (2005) recently-completed study are preliminary and subject to several data limitations, the study has identified broad priorities for the conservation of freshwater biodiversity within mainstem rivers. Mainstem rivers are defined as the longest river segments within quaternary catchments, and did not include any further tributaries. Quarternary catchments are nested subdivisions of primary, secondary and tertiary catchments, where primary catchments refer to the drainage areas of major rivers. Quarternary catchments were delineated as areas of similar total surface runoff for the purposes of water resource planning (Department of Water Affairs and Forestry, 2002). There are 1911 such quarternary catchments in South Africa and Lesotho, and they are larger in arid areas than in wetter areas.

Driver *et al.*'s (2005) assessment identified threatened ecosystems by evaluating habitat loss in each river, using the following definitions:

Critically endangered. River ecosystems that had lost >90% of their original natural habitat, leading to a breakdown of ecosystem functioning (loss of connectivity and/or disruption of flow regimes) and a loss or potential loss of species.

Endangered. River ecosystems that had lost 60–90% of their original natural habitat, and whose functioning was compromised.

Vulnerable. River ecosystems that had lost 40–60% of their original natural habitat, and whose functioning is likely to be compromised if further natural habitat is lost.

Least threatened. River ecosystems that had lost <40% of their original natural habitat, and are therefore relatively intact (although they may be degraded to varying degrees).

Establishing the degree of water stress

A comparison of the available water and the total water requirements for the year 2000 was calculated for 87 sub-water management areas in South Africa (Department of Water Affairs and Forestry, 2004) for the purposes of water resource planning. The data for this comparison were obtained from country-wide situation assessments, and included data on transfers between water management areas and to neighbouring countries. The data enabled a comparison of demand (the sum of all current demands on water, including requirements for meeting ecological targets and international obligations) and supply (available water supplies in the form of river flow, the capacity of impoundments, and interbasin transfers). The statistics enabled a broad perspective of the water situation to be gained at a national scale. We overlaid the estimates for the 87 areas on the 1911 quaternary catchments to derive estimates of water stress or availability (defined here as the difference between water supply and demand) at a quaternary catchment level, assuming that water stress was evenly distributed among all quaternary catchments in a sub-water management area.

Developing priorities for management action

We used quaternary catchments as a basis for prioritization. We calculated, for each quaternary catchment, four indices that provide estimates of (i) the number of invasive alien plant species present; (ii) the potential number of invasive alien plant species that would be present if they occupied the full range as determined by climatic envelope models; (iii) habitat loss in rivers; and (iv) the degree of water stress. We calculated these indices as follows:

Current distribution of invasive species. We overlaid the coverages for grid cells and quaternary catchments using a geographic information system, and recorded the number (out of 13) of species that occurred in overlapping catchments and grid cells. We scored the catchments in terms of the number of species that occurred in the catchments as follows: one = no species present; two = one to three species present; three = four to six species present; and four = seven or more species present. This scaling of the index was aimed at placing a higher priority on those river systems that were invaded by higher numbers of species. This approach assumed that more alien species will have higher impacts than fewer species, as each additional species could both have unique impacts and occupy vacant habitats within the landscape.

Potential distribution of invasive species. We overlaid the modelled coverages for potential plant distributions based on climatic models and recorded the number (out of 13) of species that occurred in overlapping catchments, as above. We scored the catchments in terms of the number of species that would potentially occur there using the same categories as above. This scaling of the index was aimed at placing a higher priority on those river systems that would potentially become invaded by higher numbers of species, for the same reasons as outlined above.

Habitat loss in rivers. We determined in each quaternary catchment the length of rivers that were classified as either endangered or critically endangered, and expressed this length as a percentage of the total length of rivers occurring in the catchment. We scored the catchments as follows: one = 0–25%; two = 26–50%; three = 51–75%; and four = 75–100% of the combined length of rivers in the endangered or critically endangered categories, respectively. This scaling of the index was aimed at placing a higher priority on those river systems that had lost more habitat than others (see Discussion).

Degree of water stress. The difference between water availability and requirements for the year 2000 for each of the 87 areas was used to obtain an index of the degree of water stress experienced within each quaternary catchment. A surplus indicated that all current demands could be met, and that supply exceeded demand, while a zero or negative water balance indicated that current demands balanced or exceeded supply (in these cases, water required for ecosystem maintenance cannot be assured). We scored the catchments as follows: one = lowest water stress (≥11 million m^3 $year^{-1}$ surplus); two = 6–10 million m^3 $year^{-1}$ surplus; three = 1–5 million m^3 $year^{-1}$ surplus; and four = highest water stress (≤0 million m^3 $year^{-1}$). This scaling of the index was aimed at placing a higher priority on those river systems that were experiencing higher degrees of water stress. The highest priority would go to those rivers where demand exceeded supply, and where clearing invasive alien plants would have direct benefits for water supplies and ecosystem protection.

We calculated a simple composite index that combines the four individual indices. We assumed that each of the four estimates above was of equal importance, and we added the individual scores to arrive at the composite index. This gave 13 possible scores for quaternary catchments, ranging from 4 to 16. We then determined the number of catchments in each category, and mapped these in three categories of combined scores: lowest priority (4–8), intermediate priority (9–12), and highest priority (13–16).

Results

Selection of invasive alien species

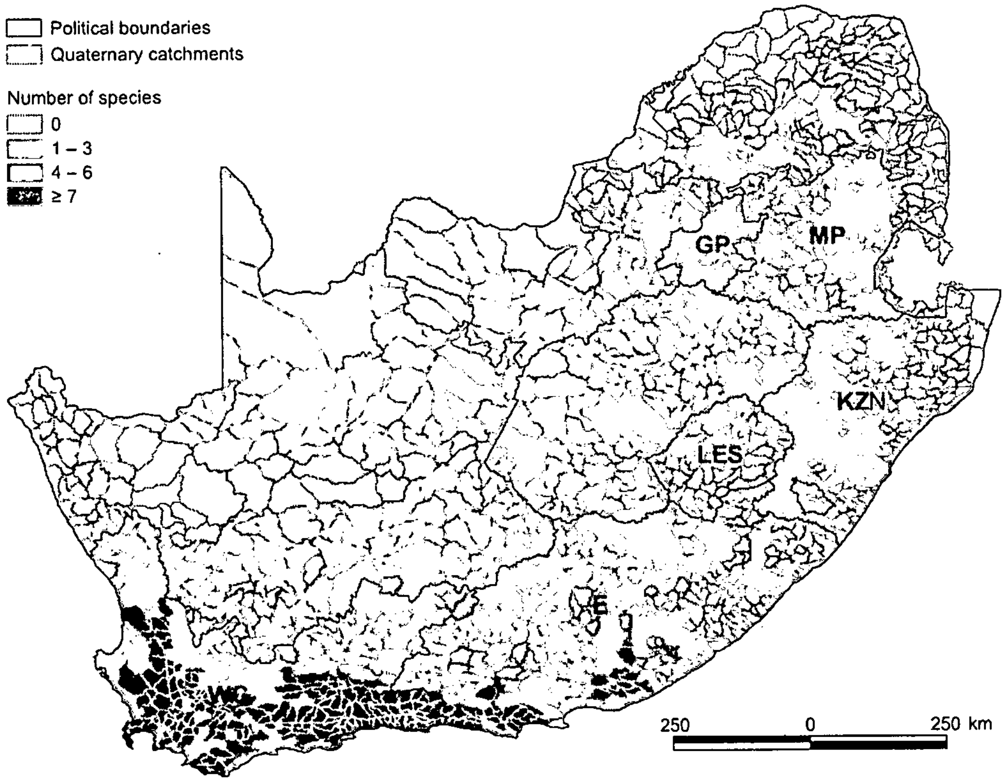
Of the 13 species of invasive alien plants selected for this study (Table 1), five were major invaders in the riparian zones of perennial rivers, five were major invaders in terrestrial upland environments, one was important in both of these zones, and the remaining two were invaders of ephemeral river beds in arid environments. Table 1 also shows the number of quarter-degree squares in which the species has been recorded, and the range abundance category assigned to it by Nel *et al.* (2004). The five species recorded as 'very widespread' were distributed over the whole country. 'Widespread' species tended to be concentrated in particular regions; four of these (red river gum, cluster pine, Monterey pine and sweet hakea) were in Mediterranean-climate shrubland areas, one (tamarisk) was in arid shrublands, and one (patula pine) in grassland areas. Of the localised species, rock hakea invades Mediterranean-climate shrublands and oleander invades arid shrublands.

Current and future distribution of alien species

The species selected in this study are currently found in 24–557 of a total of 1995 grid cells in South Africa and Lesotho (Table 1). Most of the species were recorded in the south-western extremity of the country, with significant numbers also occurring in the eastern half of the country (Fig. 1). When the potential plant distribution was taken into account, the analysis

Table 1 Selected invasive alien plant species that impact on rivers and their catchment areas in South Africa

Invasive alien plant species	Habitats invaded	Typical impacts on river systems	Range and abundance	Number of quarter-degree squares
Black wattle (*Acacia mearnsii* De Wild.)	Riparian zones of perennial rivers; uplands	Increases total evaporation and decreases streamflow; displaces riparian vegetation and destabilises river banks	Very widespread and abundant	432
Grey poplar (*Populus canescens* [Aiton] Sm.)	Riparian zones of perennial rivers and streams	Increases total evaporation and decreases streamflow; displaces riparian vegetation	Very widespread and abundant	557
Spanish reed (*Arundo donax* L.)	Riparian zones of perennial rivers and streams	Displaces riparian vegetation	Very widespread and common	377
Red river gum (*Eucalyptus camaldulensis* Dehnh.)	Riparian zones of perennial rivers	Increases total evaporation and decreases streamflow; displaces riparian vegetation and destabilises river banks	Widespread and common	123
Weeping willow (*Salix babylonica* L.)	Riparian zones of perennial rivers	Probably increases total evaporation and decreases streamflow; displaces riparian vegetation	Very widespread and common	475
Tamarisk (*Tamarix chinensis* Lour.)	Ephemeral rivers	Potentially depletes groundwater	Widespread and common	92
Mesquite (*Prosopis glandulosa* Torr.)	Ephemeral rivers	Depletes groundwater	Very widespread and abundant	453
Oleander (*Nerium oleander* L.)	Rocky water courses in semi-arid mountain areas	Displaces native streambank vegetation; poisonous	Localised and abundant	24
Cluster pine (*Pinus pinaster* Ait.)	Uplands	Increases total evaporation and decreases streamflow; increases fuel loads and fire intensity, leading to severe erosion after fire.	Widespread and abundant	86
Monterey pine (*Pinus radiata* D. Don.)	Upper catchments	Increases total evaporation and decreases streamflow; increases fuel loads and fire intensity, leading to severe erosion after fire	Widespread and common	71
Patula pine (*Pinus patula* Schltdl. & Cham.)	Uplands	Increases total evaporation and decreases streamflow; increases fuel loads and fire intensity, leading to severe erosion after fire	Widespread and common	90
Sweet hakea (*Hakea sericea* Schrad. & J.C. Wendl.)	Uplands	Probably increases total evaporation and decreases streamflow; increases fuel loads and fire intensity, leading to severe erosion after fire	Widespread and common	78
Rock hakea (*Hakea gibbosa* [Sm.] Cav.)	Uplands	Probably increases total evaporation and decreases streamflow; increases fuel loads and fire intensity, leading to severe erosion after fire	Localised and abundant	18



indicated that a far greater proportion of the country is at risk from invasion by alien plants in riparian zones and their upland catchments (Fig. 2). In particular, many more species of invasive alien plants are likely to establish in the eastern portions of the country, especially along the southern and eastern escarpment where rainfall is highest.

Ranking habitat loss in rivers

Of South Africa's 120 individual river signatures, 44% were assessed by Driver *et al.* (2005), in terms of habitat loss, as being critically endangered, 27% as endangered, 11% as vulnerable and 18% as least threatened. Rivers in the critically endangered and endangered categories were concentrated in the south, in the central north-west, and in the arid north-west (Fig. 3). Rivers in the remainder of the arid north-west, and along most of the eastern seaboard, were largely assigned to the categories 'vulnerable' or 'least threatened'.

Demand for water resources

Water deficits were identified in more than half of the water management areas in South Africa and Lesotho (Fig. 4), although the results of the National Water Resource Strategy show that a surplus still exists for the country as a whole.

Developing priorities for management action

Of the 1911 quaternary catchments in South Africa and Lesotho, just over one-third (650) had a composite index of 13 or more on our scale from 4 to 16 (Fig. 5). A relatively small proportion of the catchments (273 or 14%) had the highest scores of 15 or 16. The higher priority catchments were concentrated in a number of distinct areas (Fig. 6). These included the southern and south-western parts of the country; a group of catchments in the KwaZulu/Natal province in the east; a group in the centre of the country, around the developed and highly populated areas in the Gauteng

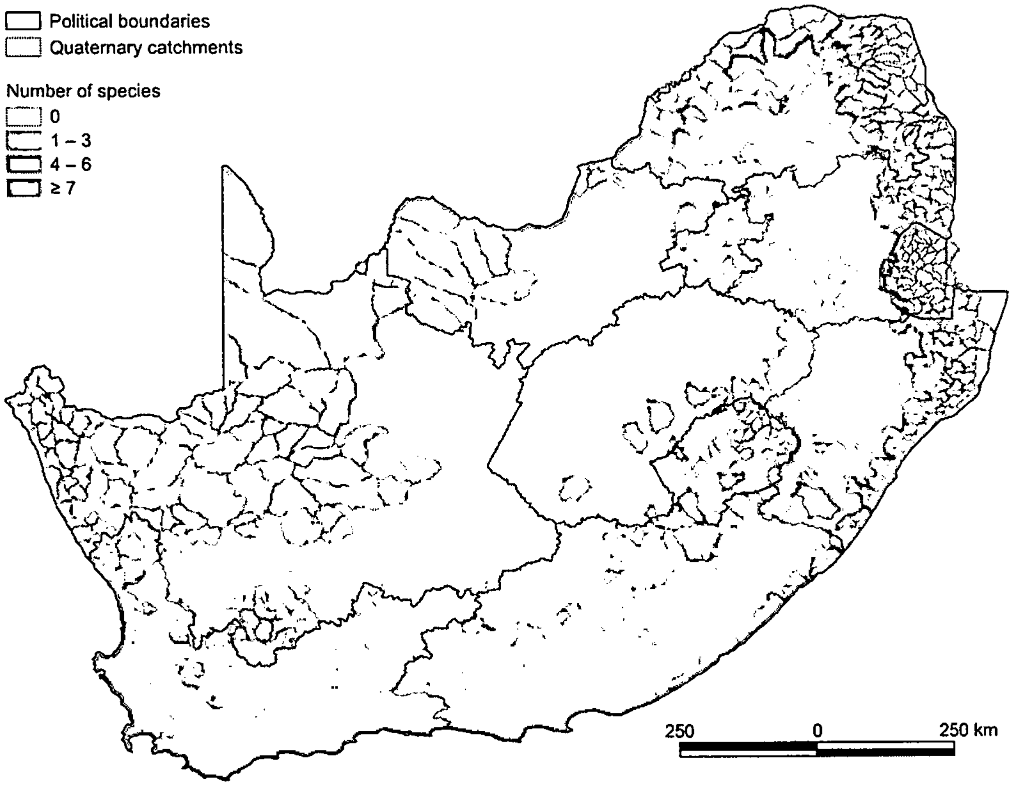


Fig. 2 The potential distribution of 13 invasive alien plant species by quaternary catchments in South Africa and Lesotho.

province; and a group in the mid-northern areas. Catchments with the lowest priorities were those in the extreme west and north-west, and along the eastern seaboard in the Eastern Cape province.

Discussion

Options for prioritization

Alien plant control operations are carried out for a number of reasons. The most important of these in South Africa are to reduce the impacts of invasive alien plants on scarce water resources, and to ensure that biodiversity conservation targets are met. The approach that we propose here seeks to place the highest priorities on river systems that are either currently or potentially invaded by the highest numbers of alien species, that have experienced the highest degree of habitat loss, and that are experiencing the highest degree of water stress. However, the achievement of biodiversity conservation goals on the one hand, and water conservation goals on the other, may require different approaches. For example, it could be argued that rivers who have lost >75% of their original natural habitats should not get the highest priority, and that a focus on rivers that are more intact would be a better option for the conservation of biodiversity. Relatively intact systems would arguably harbour more valuable biodiversity than less intact systems, and should therefore be assigned a higher priority. On the other hand, river systems that have experienced a high degree of habitat loss are probably also the systems where water stress will be high, calling for a higher prioritization. Our rationale for placing a higher priority on rivers that have experienced a high degree of habitat loss is related to the goal of achieving targets with regard to biodiversity conservation. In South Africa, river systems have been grouped into categories based on their 'signatures' (Driver *et al.*, 2005), and targets have been set to conserve a representative sample of each category. If such targets are to be achieved, then it would be necessary to place a higher priority on those systems where a high degree of loss had already been

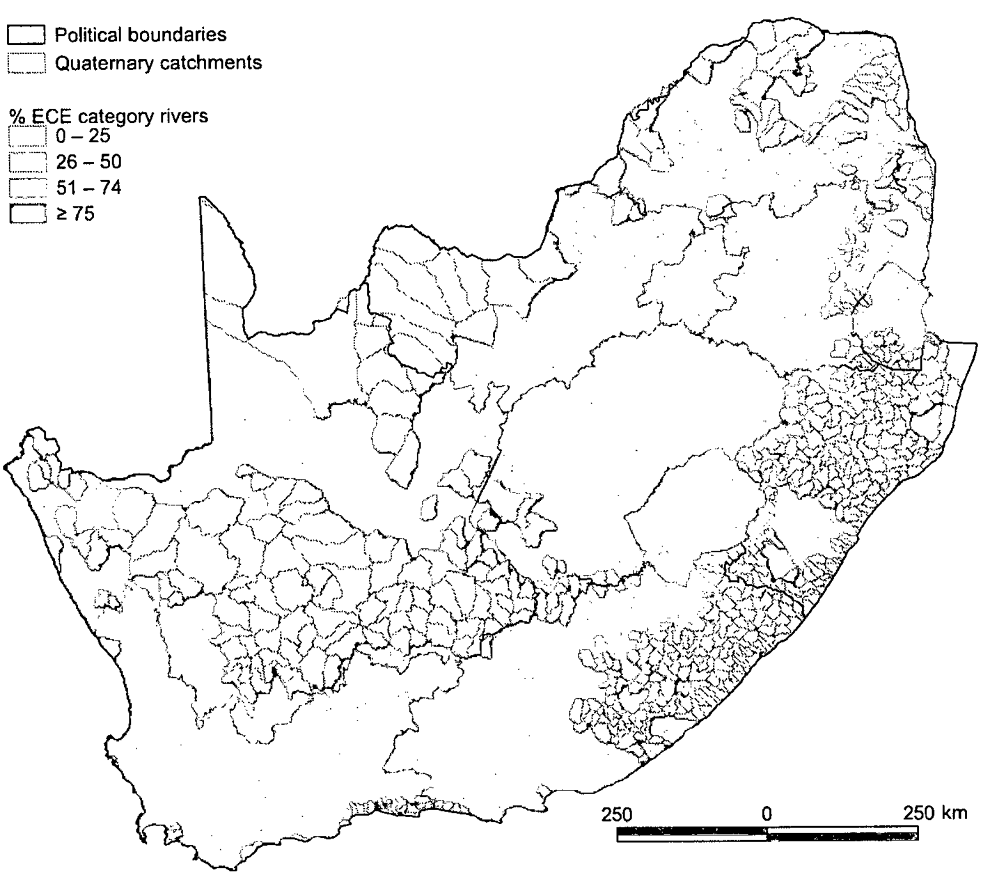


Fig. 3 The distribution of quaternary catchments in South Africa and Lesotho in terms of four categories of habitat loss, based on the proportion of river length in the categories 'endangered' and 'critically endangered' (ECE).

experienced, and where the options for conservation of what remains are limited.

The value of prioritization

This study, although preliminary, has identified emergent priority areas for the clearing of invasive alien plants with a view to conserving rivers and water resources. Results of the analysis show that current priorities in the allocation of funds to clearing projects are not always in line with the priorities defined here. For example, some of South Africa's nine provinces should receive higher priority than others (Fig. 6). If the allocation of funds to provinces was performed on an equal basis, then each province would receive about 11% of the budget. Currently, the Western Cape province receives the largest share (25%) of the budget (Anonymous, 2003), and this is in line with its high priority as assessed in this study. However, our study indicates that the Eastern Cape province was less of a priority, but it receives 15% of the budget. On the other hand, the Gauteng and Free State provinces, which our study has indicated are priority provinces, receive only 3.4 and 1.5% of the budget, respectively. If the approach suggested here is adopted, refined, and applied with diligence, we believe that it will ultimately lead to improved conservation outcomes at national level through an ability to better identify priority areas.

Use and limitations of the approach

The approach described in this paper will provide decision makers with an objective and transparent method with which to prioritize areas for the control of invasive alien plants. It brings together four important considerations in such a way that their individual contributions to an overall list of priorities

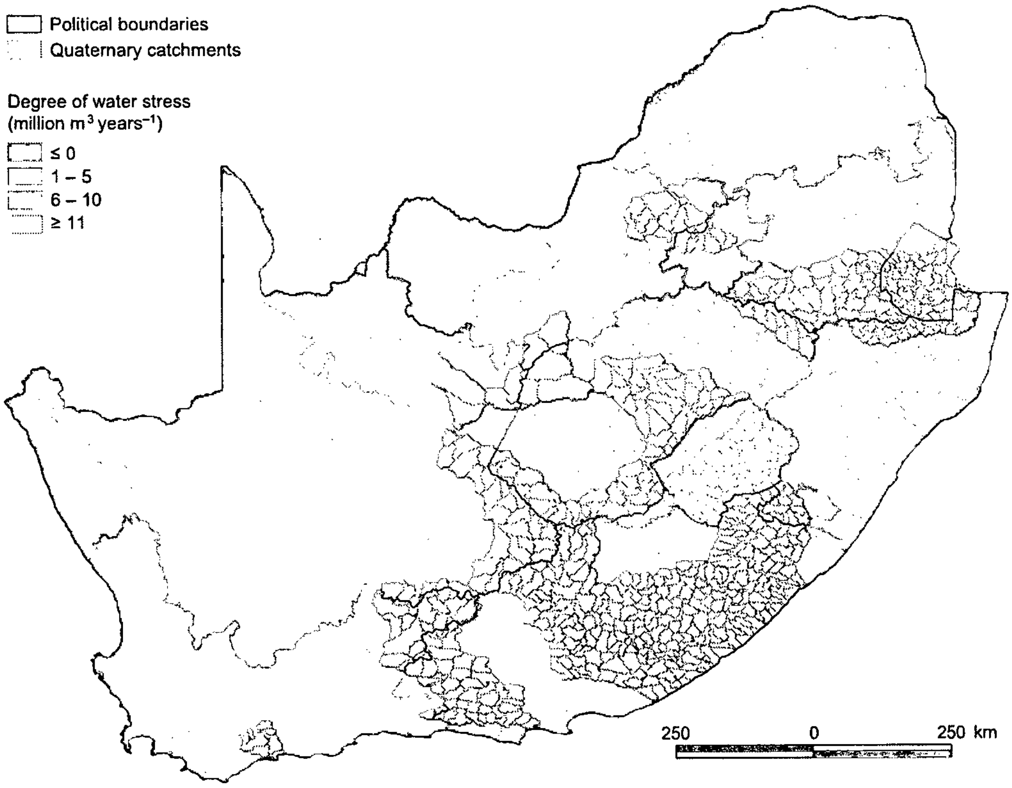


Fig. 4 The distribution of quaternary catchments in South Africa and Lesotho in terms of four categories of water surplus or stress, calculated as the difference between estimated available water and estimated demand in 2000.

becomes evident. If the method is adopted, it will make a contribution to the achievement of diverse goals, including the protection and/or restoration of water resources, and the conservation of river ecosystems and their biodiversity. How components of the index are calculated and how the four different components are weighted was arbitrary and can therefore be debated. As a consequence, the proposed

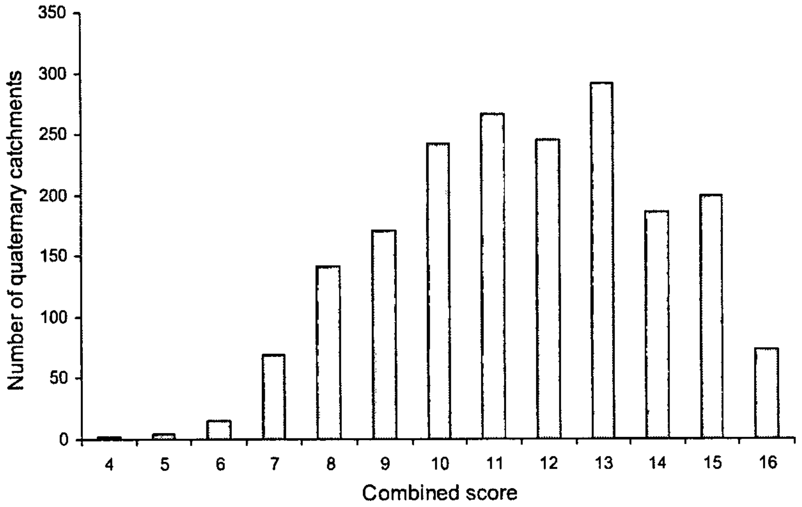


Fig. 5 The number of quaternary catchments in South Africa according to an index of priority for the control of invasive alien plants. The index is a composite of (1) the number of invasive alien plant species present; (2) the potential number of invasive alien plant species; (3) the degree of habitat loss in rivers; and (4) the degree of water stress, and increases with increasing priority relative to these four factors.

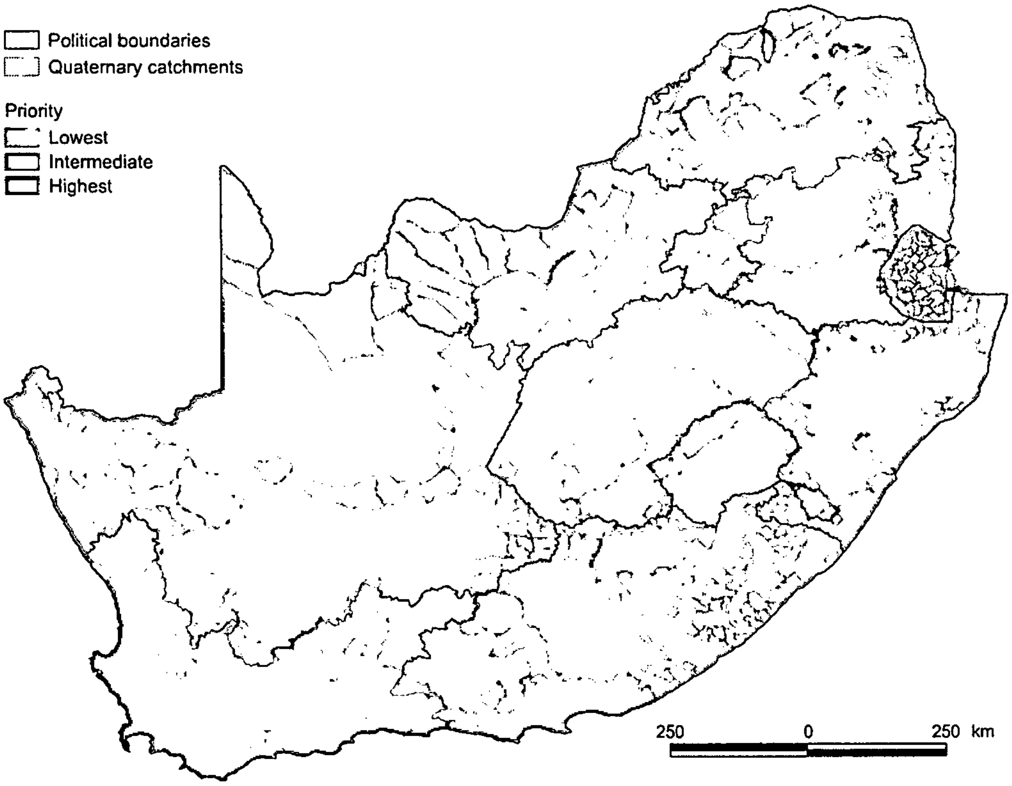


Fig. 6 Distribution of quaternary catchments in South Africa and Lesotho in terms of their priority for the control of invasive alien plants. Priorities are shown in terms of a combined index assigned to individual catchments (see text), grouped as follows: lowest priority (4–8), intermediate priority (9–12), and highest priority (13–16).

composite index may evolve. Improvements would also come about through the addition of a more comprehensive list of species. For example, the inclusion of the potential for future invasions (Nel *et al.*, 2004; Olckers, 2004) would allow for the selection of areas to ensure that they are well managed in terms of preventing invasions, rather than by waiting until they become heavily invaded before action is taken. Further improvements could come about through additional components to the index. For example, invasive alien plant clearing programmes in South Africa have gained political support and funding largely because of their potential to provide employment in poverty stricken and economically depressed areas (van Wilgen *et al.*, 1998; Magadlela & Mdzeke, 2004). In the case of South Africa, therefore, it is almost certain that the potential for poverty alleviation would be added to the list of factors to be included in a prioritization index. Other refinements that could be made would be to include priorities for the conservation of terrestrial biodiversity, and the potential impacts on agriculture; and to improve the determinations of water stress by calculating this at a quaternary catchment level. Finally, the index described in this paper has been applied at a national scale. The concept could also be applied at finer scales, and this may require input data at a correspondingly finer scale. Such data are only likely to be available for limited areas at this stage.

Priority areas and priority species

The method described here will allow managers and policy makers to prioritize areas for action in terms of invasive alien plant clearing programmes. However, the most successful operations in the history of invasive alien plant control have been those that have targeted species rather than geographical areas. Successful alien plant control operations must be based on a sound understanding of the biology and ecology of the target species, and control interventions should be aimed at the most vulnerable aspects of the species' life cycle (van Wilgen, Richardson & Higgins, 2000). While the prioritization of areas for control intervention is important, it is of equal importance that a means for prioritizing species is also developed, to guide policy and research. In this regard, research into the potential for biological control of invasive alien species is important. Biological control has underpinned the successful control of many invasive alien plant species in South Africa (Zimmermann *et al.*, 2004), and, when successful solutions can be found, it arguably provides the best means for the long term, sustainable control of invasive alien plant species. The two approaches of prioritization of areas, and research into the ecology, life cycles and biological control of major and emerging weeds (*sensu* Olckers, 2004) should be used jointly to achieve the maximum beneficial impact on invasive alien plant populations.

Acknowledgments

We thank the DST/NRF Centre for Invasion Biology, the CSIR, and the South African National Biodiversity Institute for funding this work.

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Zimmermann H.G., Moran V.C. & Hoffmann J.H. (2004) Biological control in the management of invasive alien plants in South Africa, and the role of the Working for Water Programme. *South African Journal of Science*, **100**, 34–40.

(Manuscript accepted 17 April 2006)

Part III.

Full list of published papers, and analysis of citations.

Part III. Full list of published papers, and analysis of citations.

Introduction

This section provides a list of 100 publications in the fields of (1) fire ecology and management of fynbos ecosystems; (2) fire ecology and management of savanna and grassland ecosystems; (3) the broader field of fire ecology; and (4) invasive alien plant ecology and management. Evaluating the research output of scientists is becoming increasingly common, for the purposes of appointments, research grant awards and promotions (Hirsch 2005; Egghe 2006; Lehmann, Jackson and Lautrup 2006; Lovegrove and Johnson 2008). Hirsch (2005) proposed an index (the *h*-index) as a measure of both research productivity and impact. Hirsch's measure is obtained by ranking papers in order of decreasing citations with paper i having $C(i)$ citations and solving the equation $h = C(h)$. In other words, an *h*-score of 10 indicates10 papers, each of which has been cited at least 10 times. Hirsch argued that the h-index "may provide a useful yardstick with which to compare, in an unbiased way, different individuals competing for the same resource when an important evaluation criterion is scientific achievement". Egghe (2006) introduced the *g*-index as an "improvement of the *h*-index of Hirsch to measure the global citation performance of a set of articles" (Egghe 2006). If this set is ranked in decreasing order of the number of citations that they received, the *g*-index is the (unique) largest number such that the top g articles received (together) at least g^2 citations. Egghe (2006) maintained that the *g*-index "inherits all the good properties of the *h*-index and .... yields a better distinction and order of the scientists from the point of view of visibility". The full list of publications, and an analysis of the relevant bibliometric indices, is provided in the sections below.

Lovegrove and Johnson (2008) used the publication records of 163 South African biologists who had been rated as researchers by the National Research Foundation to examine the relationship between the *h*- and *g*-indices (Figure 1). The *h*- and *g*-indices produced by the set of publications listed in Part III of this thesis ($h = 23$ and $g = 41$) are at the upper end of the distribution for South African biologists (Figure 1).

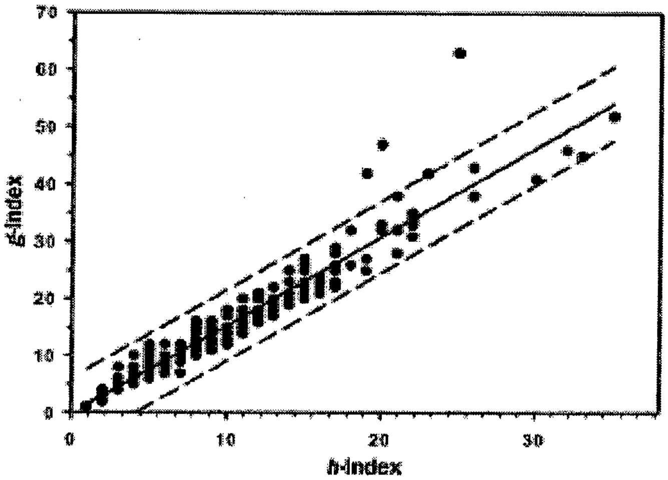

Figure 1. *The correlation between the* h- *and* g-*indices of 163 South African biologists who have been rated as researchers by the National Research Foundation (from Lovegrove and Johnson 2008).*

Detailed list of publications

Table 1 indicates (1) the involvement of co-authors (the roles of others are recorded in the acknowledgements in each paper); (2) which papers arose from work submitted for a higher degree; and (3) which papers are included in the sample of 15 selected papers presented in Part II of this thesis. The number of citations for each paper is given as on the 30th of October 2008.

Table 1. *List of 100 publications in the fields of fire ecology and management, and the ecology and management of invasive alien plants. Notes provide an indication of the involvement of authors, whether or not the paper has been used as part of another degree, and which papers have been included in Part II of this thesis. The number of citations was assessed on the 15th of March 2008.*

Publication	**Notes**	**Number of citations**
FIRE ECOLOGY AND MANAGEMENT (FYNBOS ECOSYSTEMS)		
1. van Wilgen, B.W. (1980). Assessment of the effects of burning on populations of the Clanwilliam cedar using aerial photography. *South African Forestry Journal* 114, 72-74.	Sole author.	0
2. van Wilgen, B.W. and Kruger, F.J. (1981). Observations on the effects of fire in mountain fynbos at Zachariashoek, Paarl. *Journal of South African Botany* 47, 195-212.	Work shared equally with co-author.	12

3. van Wilgen, B.W. (1981). Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. *South African Forestry Journal* 118, 42-55.	Sole author. This paper arises from work that was submitted for an MSc degree.	16
4. van Wilgen, B.W. (1981). An analysis of fires and associated weather factors in mountain fynbos areas of the southwestern Cape. *South African Forestry Journal* 119, 29-34.	Sole author.	3
5. van Wilgen, B.W. and Le Maitre, D.C. (1981). Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *South African Forestry Journal* 119, 24-28.	Lead author. David Le Maitre arranged for collection and analysis of some of the samples.	6
6. van Wilgen, B.W. (1982). Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *Journal of Ecology* 70, 217-225.	Sole author. This paper arises from work that was submitted for an MSc degree. Included in sample of selected papers.	15
7. van Wilgen, B.W. (1984). Fire climates in the southern and western Cape Province and their potential use in fire control and management. *South African Journal of Science* 80, 358-362.	Sole author. This paper arises from work that was submitted for a PhD degree.	10
8. van Wilgen, B.W. (1984). Adaptation of the United States Fire Danger Rating System to fynbos conditions. I A fuel model for fire danger rating in the fynbos biome. *South African Forestry Journal* 129, 61-65.	Sole author. This paper arises from work that was submitted for a PhD degree.	4
9. van Wilgen, B.W. and Burgan, R.E. (1984). Adaptation of the United States Fire Danger Rating System to fynbos conditions. II Historic fire danger in the fynbos biome. *South African Forestry Journal* 129, 66-78.	Lead author. Bob Burgan assisted with interpretation. This paper arises from work that was submitted for a PhD degree.	6
10. van Wilgen, B.W., Le Maitre, D.C. and Kruger, F.J. (1985). Fire behaviour in South African fynbos (macchia) vegetation and predictions	Lead author. David Le maitre was responsible for the collection of data in the Cederberg. Fred Kruger	18

from Rothermel's fire model. *Journal of Applied Ecology* 22, 207-216.	designed the original experimental layout. This paper arises from work that was submitted for a PhD degree.	
11. van Wilgen, B.W. and Viviers, M. (1985). The effect of season of fire on serotinous Proteaceae in the western Cape and the implications for fynbos management. *South African Forestry Journal* 133, 49-53.	Lead author. Mike Viviers collected the field data. This paper arises from work that was submitted for a PhD degree.	8
12. van Wilgen, B.W. and Richardson, D.M. (1985). Factors influencing burning by prescription in mountain fynbos catchment areas. *South African Forestry Journal* 134, 22-32.	Lead author. Dave Richardson conducted some data analysis. This paper arises from work that was submitted for a PhD degree.	3
13. van Wilgen, B.W. and Kruger, F.J. (1985). The physiography and fynbos vegetation communities of the Zachariashoek catchments, southwestern Cape Province. *South African Journal of Botany* 51, 379-399.	Lead author. Fred Kruger initiated the study, and completed or participated in 40% of the field work.	1
14. van Wilgen, B.W. (1986). A simple relationship for estimating the intensity of fires in natural vegetation. *South African Journal of Botany* 52, 384-385.	Sole author.	1
15. Bosch, J.M., van Wilgen, B.W. and Bands, D.P. (1986). A model for comparing water yield from fynbos catchments burnt at different intervals. *Water S.A.* 12, 191-196.	This model was developed jointly with Jan Bosch. Don Bands provided minor inputs.	4
16. van Wilgen, B.W. and Lamb, A.J. (1986). The flower picking industry in relation to mountain catchment management in the fynbos. *Acta Horticulturae* 185, 181-188.	Lead author. Alan Lamb assisted with field data collection.	3
17. Van Wilgen, B.W. (1986). Swartboskloof - Twenty years on. *African Wildlife* 40, 244-249.	Sole author.	0
18. van Wilgen, B.W. (1987). Fire regimes in the fynbos biome. *Disturbance and the dynamics of fynbos biome communities*. (Ed by	Sole author.	16

R.M. Cowling, D.C. le Maitre, B. McKenzie, R.P. Prys-Jones and B.W. van Wilgen). South African National Scientific Programmes Report No. 135, CSIR, Pretoria, pp 6-14.		
19. Higgins, K.B., Lamb, A.J. and van Wilgen, B.W. (1987). Root systems of selected plant species in the Jonkershoek Valley, Southwestern Cape Province. *South African Journal of Botany* 53, 249-258.	Kevin Higgins did most of the field work, assisted by Alan Lamb. I was responsible for interpretation and writing of the paper.	10
20. Worth, S.W. and Van Wilgen, B.W. (1988). The Blushing Bride: Status of an endangered species. *Veld & Flora* 74, 123-124.	Steve Worth collected the data, and I wrote the article.	2
21. van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. (1990). The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78, 210-222.	Lead author. Kevin Higgins assisted with data collection. Dirk Bellstedt conducted chemical analyses. Included in sample of selected papers.	24
22. van Wilgen, B.W., in collaboration with Breytenbach, G.J., Brown, P.J., Forsyth, G.G., Kromhout, C., Kruger, F.J., Lamb, A.J., Le Maitre, D.C., Manders, P.T. and Moll, E.J. (1988). Fynbos terrestrial ecosystems. *Long-term data series relating to southern Africa's renewable natural resources*. (Ed by I.A.W. Macdonald and R.J.M. Crawford). South African National Scientific Programmes Report No. 157, CSIR, Pretoria.	I was convenor of this review and responsible for drawing together and reporting on inputs of others.	0
23. van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. (Editors) (1992). *Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof.* Ecological Studies Series, number 93. Springer Verlag, Heidelberg, Germany.	Lead editor of this book. Dave Richardson shared editing duties (about 33%). Fred Kruger played a leading role in shaping terms of reference for chapters. Bertie van Hensbergen negotiated publication with Springer.	34
24. van Wilgen B.W., Bond, W.J. and Richardson, D.M. (1992) Ecosystem management. The Ecology of Fynbos: Nutrients, Fire and diversity	Lead author, in close collaboration with William Bond. Dave Richardson responsible for the section	58

Ed: Cowling, R.M. Oxford University Press, Cape Town, pp 345-371.	on aliens. Included in sample of selected papers.	
25. van Wilgen, B.W. & McDonald, D.J. (1992). The Swartboskloof experimental site. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof. Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 1-20	Lead author. Dave McDonald provided the section describing the vegetation.	3
26. Versfeld, D.B., Richardson, D.M., van Wilgen, B.W., Chapman, R.A. & Forsyth, G.G. (1992). The climate of Swartboskloof. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 21-36	Dirk Versfeld was lead author. Other inputs shared equally.	6
27. van Wilgen, B.W. & van Hensbergen, H.J. (1992). Fuel properties of vegetation in Swartboskloof. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof. Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 37-53	Lead author. Bertie van Hensbergen developed the fire occurrence model.	10
28. van Wilgen, B.W. & Forsyth, G.G. (1992). Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof. Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 54-80	Lead author. Greg Forsyth shared field work equally, but did not participate in interpretation or writing. Included in sample of selected papers.	18
29. Smith, R.E., van Wilgen, B.W., Forsyth, G.G. & Richardson, D.M. (1992). Co-existence of seeders and	Joint lead author with Rose Smith. Other inputs shared equally.	0

sprouters in a fire-prone environment: the role of ecophysiology and soil moisture. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 108-122.		
30. Richardson, D.M. & van Wilgen, B.W. (1992). Ecosystem, community and species response to fire in mountain fynbos: Conclusions from the Swartboskloof experiment. Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof. Eds: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen, H.J. Springer-Verlag, Heidelberg, pp 273-284.	Work shared equally with co-author.	3
31. Richardson, DM and van Wilgen, BW (1992) Swartboskloof - Major study of effects of fire in mountain fynbos completed. *African Wildlife* 46, 160 - 164.	Work shared equally with co-author.	0
32. Le Maitre, DC, van Wilgen, BW and Richardson, DM (1993). A computer system for catchment management: background, concepts and development. *Journal of Environmental Management* 39, 121 - 142.	Work shared equally with co-authors.	4
33. van Wilgen, BW, Richardson, DM and Seydack, A (1994). Managing fynbos for biodiversity: constraints and options in a fire-prone environment. *South African Journal of Science* 90, 322 - 329.	Lead author. Dave Richardson provided inputs relating to alien plant management. Armin Seydack contributed options for fire management fron the southern Cape.	11
34. Richardson, DM, van Wilgen, BW, Le Maitre, DC and Higgins, KB, and Forsyth, GG (1994) A computer-based system for fire management in the mountains of the Cape Province, South Africa. *International Journal of Wildland Fire* 4, 17 -32.	Work shared equally with co-authors. Included in sample of selected papers.	20
35. Richardson, DM, van Wilgen, BW,	Dave Richardson was lead	47

Higgins, SI, Trinder-Smith, TH, Cowling, RM and McKelly, DH (1996). Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation* 5, 607 - 647	author. Remaining work shared equally with co-authors.	
36. van Wilgen, BW (1996). Management of the natural ecosystems of the Cape Peninsula: Current status and future prospects. *Biodiversity and Conservation* 5, 671 - 684.	Sole author.	0
37. Richardson, DM, Caroline Gelderblom, Brian W. van Wilgen and Terry H. Trinder-Smith (1998) Managing biodiversity on the Cape Peninsula, South Africa: a hotspot under pressure. In: Rundel, P.W., Montenegro, G. & Jaksic, F. (eds). Landscape Degradation and Biodiversity in Mediterranean-Type Ecosystems, pp 189 - 204. Berlin, Springer-Verlag.	Dave Richardson was lead author. Remaining work shared equally with co-authors.	0
38. van Wilgen, BW and Scott, DF (2001). Managing fires on the Cape Peninsula: Dealing with the inevitable. *Journal of Mediterranean Ecology* 2, 197 - 208.	Lead author. Dave Scott provided data on soil water repellency.	6
39. Gelderblom, CM, van Wilgen, B.W., Nel' J, Sandwith' T, Botha' M, and Hauck' M (2003). Turning strategy into action: implementing a conservation plan for the Cape Floral Kingdom. *Biological Conservation* 112, 291 – 297	Work carried out largely by Caroline Gelderblom, Jeanne Nel and myself. I was responsible for drafting the paper for publication.	19
40. Heelemann, S., Procheş, Ş., Cowling, R.M., Rebelo, A.G., van Wilgen and Porembski, S. (2008). Fire season effects on the recruitment of non-sprouting serotinous Proteaceae in the eastern (bimodal-rainfall) fynbos biome, South Africa. *Austral Ecology* 32, 119 – 127.	I provided data on the fire climatic differences between eastern and western parts of the biome.	0
41. Forsyth, GG and van Wilgen, B.W. (2008). The recent fire history of the Table Mountain National Park, and implications for fire management. *Koedoe* 50, 3 - 9.	Greg Forsyth collated the database and conducted analyses with my guidance. I was responsible for interpretation, and writing the paper.	0

FIRE ECOLOGY AND MANAGEMENT (SAVANNA AND GRASSLAND ECOSYSTEMS)		
42. Everson, T.M., van Wilgen, B.W. and Everson C.S. (1988). Adaptation of a model for rating fire danger in the Natal Drakensberg. *South African Journal of Science* 84, 44-49.	Terry Everson was lead author. I played a leading role in the research design and interpretation.	5
43. van Wilgen, B.W. and Wills, A.J. (1988). Fire behaviour prediction in savanna vegetation. *South African Journal of Wildlife Research* 18, 41-46.	Lead author. Alf Wills assisted with field work and data collection.	11
44. Stocks, BJ, van Wilgen, BW, Trollope, WSW, McRae, DJ, Mason, JA, Weirich, F and Potgieter, ALF (1996). Fuels and fire behaviour dynamics on large-scale savanna fires in Kruger National Park, South Africa. *Journal of Geophysical Research* 101 (D19), 23541 - 23550.	Brian Stocks was lead author. Remaining work shared equally with co-authors. Included in sample of selected papers.	23
45. Lindesay, J.A., Andreae, M.O., Goldammer, J.G., Harris, G., Annegarn, H.J., Garstang, M., Scholes, R.J. and van Wilgen, B.W. (1996). International Geosphere-Biosphere Programme/International Global Atmospheric Chemistry SAFARI-92 field experiment: Background and overview. *Journal of Geophysical Research* 101 (D19), 23521 - 23530.	Janette Lindesay was lead author; other authors were members of the project steering committee.	49
46. van Wilgen, BW, Andreae, MO, Goldammer, GJ, and Lindesay, JA (1997). *Fire in Southern African Savannas: Ecological and Atmospheric Perspectives.* Witwatersrand University Press, Johannesburg.	In practice, I was sole editor of this book.	25
47. Stocks, BJ, van Wilgen, BW and Trollope, WSW (1997). Fire Behaviour and the Dynamics of Convection Columns in African Savannas. In: van Wilgen, BW, Andreae, MO, Goldammer, GJ, and Lindesay, JA (eds). Fire in Southern African Savannas: Ecological and Atmospheric Perspectives. Wits University Press, pp 47 - 55.	Brian Stocks was lead author. Remaining work shared equally with co-authors.	5
48. van Wilgen, BW, Biggs, HC, and	Lead author. Thresholds	25

Potgieter, ALF (1998). Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe* 41, 69 - 87.	developed in discussion with co-authors. Included in sample of selected papers.	
49. van Wilgen, BW, Biggs, HC, O'Regan, S and Mare, N (2000). A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. *South African Journal of Science* 96 167 - 178.	Lead author. Harry Biggs assisted with statistical analyses, Sean O'Regan with editing and compiling the fire database, and Naledi Mare with GIS analysis. Included in sample of selected papers.	32
50. H.C.Eckhardt, B.W. van Wilgen and H.C. Biggs (2000). Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology* 38 108 - 115.	Holger Eckhardt was lead author. Remaining work shared equally with co-authors.	36
51. Brockett, B.H., Biggs, H.C. & van Wilgen, B.W. (2001). A patch mosaic burning system for conservation areas in southern Africa. *International Journal of Wildland Fire* 10, 169 – 183.	This work formed part of Bruce Brockett's MSc thesis, which I co-supervised. Work on this paper was jointly shared between the authors.	32
52. van Wilgen, B.W., Trollope, W.S.W, Biggs, H.C., Potgieter, A.L.F. and Brockett, B.H. (2003). Fire as a driver of ecosystem variability. In: The Kruger experience: Ecology and management of savanna heterogeneity (ed by J. du Toit, K.H Rogers and HC Biggs), Island Press, New York, pp 149 – 170.	I was sole author of this paper, which drew on experience and publications of the co-authors.	22
53. van Wilgen, BW, N. Govender, H.C. Biggs, D. Ntsala and X.N. Funda (2004). Response of savanna fire regimes to changing fire management policies in a large African national park. *Conservation Biology* 18, 1533 - 1540.	Lead author. Navashni Govender and Don Ntsala assisted with data analysis. Nicholus Funda completed the analysis of spatial heterogeneity. Harry Biggs made valuable conceptual inputs. Included in sample of selected papers.	26
54. Govender, N, Trollope, WSW and van Wilgen, BW (2006). The effect	Winston Trollope collected the bulk (80%) of the data.	17

of fire season, fire frequency, rainfall and management on fire intensities in savanna vegetation in South Africa. *Journal of Applied Ecology* 43, 748 - 758.	Navashni Govender also collected data and conducted analyses. I was responsible for data interpretation and writing the paper.	
55. van Wilgen, B.W., Govender, N., Biggs, H.C. (2007). The contribution of fire research to fire management: A critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16, 519 – 530.	Lead author. Navashni Govender collated information on historic studies, and Harry Biggs made valuable conceptual inputs. Included in sample of selected papers.	2
56. Van Wilgen, BW, Govender, N and MacFadyen, S. (2008). An assessment of the implementation and outcomes of recent changes to the fire management of the Kruger National Park. *Koedoe* 50, 22 - 31.	Lead author. Navashni Govender assisted with data analysis. Sandra MacFadyen conducted GIS analyses.	0
FIRE ECOLOGY (GENERAL)		
57. van Wilgen, B.W., Everson, C.S.and Trollope, W.S.W. (1990). Fire management in southern Africa: Some examples of current objectives, practices and problems. In: Goldammer, J.G. (ed.). Fire in the tropical biota: ecosystem processes and global challenges. Springer, Berlin, pp179 - 209.	Lead author of this review paper. Colin Everson and Winston Trollope contributed inputs on grassland and savanna sites respectively.	32
58. van Wilgen, B.W. and Manders, P.T. (1990) Adoption of United States fire technology in South Africa: a technology transfer exercise. *Technology transfer in the South African Forestry Industry*. Southern African Institute of Forestry.	Lead author. Pat Manders provided valuable inputs.	0
59. Binkley, D, Becker-Heidman, P, Crutzen, PJ, Frost, P, Gill, AM, Granstrom, A, Mack, F, Menaut, J-C, van Wilgen, BW and Wein, RW (1993). Impacts of fires on ecosystems. In GJ Goldammer and PJ Crutzen (eds). Fire in the environment: Its ecological, climatic and atmospheric chemical importance. Wiley, Chichester, pp 359-374.	Dahlem conference report. I was part of the working team.	0
60. Andreae, MO, Fishman, J, Garstang,	Andy Andreae was lead	15

M, Goldammer, JG, Justice, CO, Levine, JS, Scholes, RJ, Stocks, BJ, Thompson, AM and van Wilgen, BW (1994). Biomass burning in the global environment: First results from the IGAC/BIBEX field campaign STARE/TRACE-A/SAFARI-92. In R.G. Prinn (ed). Global Atmospheric-Biospheric Chemistry, Plenum Press, New York and London.	author; other authors were members of the project steering committee.	
61. Bond, WJ and van Wilgen, BW (1996). *Fire and Plants*. Chapman & Hall, London.	Lead author of the chapters on fuel and on management, co-author of the chapter on competition, and reviewer of remaining 6 chapters.	481
62. van Wilgen, BW and Scholes, RJ (1997). The vegetation and fire regimes of southern hemisphere Africa. In: van Wilgen, BW, Andreae, MO, Goldammer, GJ, and Lindesay, JA (eds). Fire in Southern African Savannas: Ecological and Atmospheric Perspectives. Wits University Press, pp 27 -46.	Work shared equally with co-author.	26
63. Geldenhuys, C.J., van Wilgen, B.W., Bond, W.J., van der Vijver, C.A.D.M. and De Ronde, C. (2004). Fire effects on the maintenance of biodiversity, soil and nutrients. In: Wildland fire management handbook for sub-Saharan Africa (ed by J.G. Goldammer and C. De Ronde). Global Fire Monitoring Centre, Freiburg, pp. 88 – 113.	Co-contributor to this review paper.	0
64. van Wilgen, BW (2005). Managing fires: the science behind the smoke. *Quest* 1(3), 26 – 33.	Sole author.	0
INVASIVE ALIEN PLANT ECOLOGY AND MANAGEMENT		
65. Richardson, D.M. and van Wilgen, B.W. (1984). Factors affecting the regeneration of Hakea sericea. *South African Forestry Journal* 131, 63-68.	Work shared equally with co-author.	3
66. van Wilgen, B.W. and Richardson, D.M. (1985). The effect of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *Journal of Applied*	Lead author, and work shared equally with co-author. This paper arises from work that was submitted	43

Ecology 22, 955-966.	for a PhD degree. Included in sample of selected papers.	
67. Richardson, D.M. and van Wilgen, B.W. (1986). Effects of thirty-five years of afforestation with Pinus radiata on the composition of mesic mountain fynbos near Stellenbosch. *South African Journal of Botany* 52, 309-315.	Work shared equally with co-author.	14
68. van Wilgen, B.W. and Siegfried, W.R. (1986). Seed dispersal properties of three pine species as a determinant of invasive potential. *South African Journal of Botany* 52, 546-548.	Lead author. Roy Siegfried provided valuable inputs	13
69. Richardson, D.M. and van Wilgen, B.W. (1986). The effects of fire in felled Hakea sericea and natural fynbos and the implications for weed control in mountain catchments. *South African Forestry Journal* 139, 4-14	Work shared equally with co-author.	8
70. Kruger, F.J., Richardson, D.M. and van Wilgen, B.W. (1986). Processes of invasion. The ecology and control of biological invasions in South Africa. (Ed. by I.A.W. Macdonald, F.J. Kruger and A.A. Ferrar). Oxford University Press, Cape Town, pp 145-155.	Co-contributor to this review paper.	20
71. Versfeld, D.B. and van Wilgen, B.W. (1986). Impacts of woody aliens on ecosystem properties. The ecology and control of biological invasions in South Africa. (Ed. by I.A.W. Macdonald, F.J. Kruger and A.A. Ferrar). Oxford University Press, Cape Town, pp 239-246.	Work shared equally with co-author	38
72. Richardson, D.M., van Wilgen, B.W. and Mitchell, D.T. (1987). Aspects of the reproductive ecology of four Australian Hakea species (Proteaceae) in South Africa. *Oecologia* 71, 345-354.	Work shared equally with Dave Richardson; Derek Mitchell provided chemical analyses for data in Tables 6 and 7. Included in sample of selected papers.	15
73. van Wilgen, BW, Cowling, RM and Burgers, CJ (1996). Valuation of	Lead author, with some inputs from co-authors.	81

ecosystem services: a case study from the fynbos, South Africa. *BioScience* 46, 184 - 189.	Included in sample of selected papers.	
74. Le Maitre, DC, van Wilgen, BW, Chapman, RA and McKelly, D. (1996). Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology* 33, 161 - 172.	I developed the models on which this paper was based, with help from David Le Maitre. Arthur Chapman and David McKelly provided technical support, and David Le Maitre assumed responsibility for drafting the paper. Included in sample of selected papers.	83
75. Allen, DG, Harrison, JA, Navarro, RA, van Wilgen, BW and Thompson, MW (1997). The impact of commercial afforestation on bird populations in Mpumalanga province, South Africa - insights from bird atlas data. *Biological Conservation* 79: 173-185.	I conceptualised this paper, and brokered the combination of forestry data (from Mark Thompson) with bird atlas data supplied by the other authors.	33
76. van Wilgen, BW, Little, PR, Chapman, RA, Görgens, AHM, Willems, T and Marais, C (1997). The sustainable development of water resources: History, financial costs and benefits of alien plant control programmes. *South African Journal of Science* 93, 404 – 411	Lead author of this paper. Other authors provided varying components necessary to estimate benefits.	28
77. van Wilgen, BW, Le Maitre, DC, Cowling RM (1998). Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water programme. *Trends in Ecology and Evolution* 13, 378.	Lead author of this paper, which was conceptualised in discussions with co-authors.	48
78. van Wilgen, BW and van Wyk, E (1999). Invading alien plants in South Africa: Impacts and solutions. In: *People and rangelands: Building the future*. Proceedings of the VI International Rangeland Congress, Townsville, Australia (Edited by David Eldridge and David Freudenberger), pages 566 - 571.	Lead author of this review. Ernita van Wyk assisted with the assembly of information.	11
79. Holmes, PM, Richardson, DM, van Wilgen, BW and Gelderblom, C (2000). The recovery of South	Pat Holmes was lead author, and all authors contributed equal inputs.	11

African fynbos vegetation following alien tree clearing and fire: implications for restoration. *Austral Ecology* 25 631 – 639.		
80. van Wilgen, BW, van der Heyden, F, Zimmermann, HG, Magadlela, D and Willems, T (2000). Big returns from small organisms: developing a strategy for the biological control of invasive alien plants in South Africa. *South African Journal of Science* 96 148 - 152.	Lead author, with significant inputs from Francois van der Heyden. Other authors contributed minor comments.	6
81. Moran, VC, Hoffmann, JH, Donnelly, D, Zimmermann, HG, and van Wilgen, BW (2000). Biological control of alien invasive pine trees (*Pinus* species) in South Africa. *Proceedings of the Xth International Symposium on Biological Control of Weeds*, (ed by Neal R. Spencer), pp 941 – 953.	I was responsible for initiating a programme of research on the biocontrol of invasive pine trees. Cliff Moran used a number of my reports to illustrate the motivation for targeting pines in this paper.	4
82. Van Wilgen, BW, Richardson, DM and Higgins, S (2000). Integrated control of alien plants in terrestrial ecosystems. In: *Best management practices for preventing and controlling invasive alien species* (edited by G Preston, G Brown and E van Wyk), Working for Water Programme, Cape Town, pp 118 – 128.	Lead author of this paper, which was conceptualised in discussions with co-authors. Steve Higgins computed some of the control scenarios.	2
83. De Wit, M, Crookes, D and van Wilgen, BW (2001). Conflicts of interest in environmental management: Estimating the costs and benefits of a tree invasion. *Biological Invasions* 3, 167-178.	This paper is based on research that I conceptualised, but was carried out by the co-authors. I was responsible for writing the paper.	25
84. van Wilgen, BW, Richardson, DM, Le Maitre, DC. Marais, C and Magadlela, D (2001). The economic consequences of alien plant invasions: Examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability* 3, 145 - 168.	I reviewed available material and wrote the paper. Dave Richardson provided the table of impacts, and other co-authors supplied relatively minor information.	27
85. Le Maitre, DC, B.W. van Wilgen, C.M. Gelderblom, C. Bailey, R.A. Chapman and J.A. Nel (2002). Invasive alien trees and water	I developed the research on which this paper was based. Co-authors were responsible for various	36

resources in South Africa: Case studies of the costs and benefits of management. *Forest Ecology and Management* 160, 143 - 159.	case studies. David Le Maitre assumed responsibility for drafting the paper.	
86. Rouget, M, Richardson, DM, Nel, JA and van Wilgen, BW (2002). Commercially important trees as invasive aliens – towards spatially explicit risk assessment at a national scale. *Biological Invasions* 4, 397 – 412.	I participated in the design and commissioning of this research, and provided minor inputs to the paper.	19
87. Van Wyk, E and van Wilgen, BW (2002). The control of water hyacinth (Eichhornia crassipes): A case study approach to compare the costs of three control options in South Africa. *African Journal of Aquatic Science* 27, 141 – 149.	Work shared equally with co-author	3
88. van Wilgen, BW, Marais, C, Magadlela, D, Jezile, N and Stevens, D (2002). Win-win-win: South Africa's Working for Water programme. In Mainstreaming biodiversity in development: Case studies from South Africa (ed by S.M. Pierce, R.M. Cowling, T. Sandwith and K. MacKinnon), pp. 5 - 20. The World Bank, Washington D.C.	I wrote this paper with minor inputs from Christo Marais and Dumisani Magadlela. Nosipho Jezele and Desmond Stevens supplied material for the two boxes.	8
89. van Wilgen, BW, M.P. de Wit, H.J. Anderson, D.C. Le Maitre, I.M. Kotze, S. Ndala, B. Brown and M.B. Rapholo (2004). Costs and benefits of biological control of invasive alien plants: case studies from South Africa. *South African Journal of Science* 100, 113 -122.	I conceptualized and led this research, with economic analyses being done by de Wit, Anderson and Rapholo. Le Maitre, Kotze, Brown and Ndala provided technical support.	1
90. Richardson, D.M. and van Wilgen, B.W. (2004). Invasive alien plants in South Africa: How well do we understand the ecological impacts? *South African Journal of Science* 100, 45 - 52.	Work shared equally with co-author.	22
91. Görgens, A.H.M. and van Wilgen, B.W. (2004). Invasive alien plants and water resources: an assessment of current understanding, predictive ability and research challenges. *South African Journal of Science* 100, 27 - 34.	Work shared equally with co-author	3

92. Nel, J.L., Richardson, D.M.,Rouget, M., Mgidi, T, Mdzeke, N.P., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., and Neser, S. (2004). A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science* 100, 53 - 63.	This research was led by Jeanne Nel. Supporting inputs were provided equally by co-authors.	25
93. Forsyth, G.G., Richardson, D.M., Brown, P.J. and BW van Wilgen, B.W. (2004). A rapid assessment of the invasive status of Eucalyptus species in two South African provinces. *South African Journal of Science* 100, 75 - 77.	Field work was conducted by Greg Forsyth and Pat brown. Write-up shared equally with co-authors	0
94. Marais, C., van Wilgen, B.W. and Stevens, D. (2004). The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science* 100, 97 - 103.	Work shared equally with co-authors	9
95. van Wilgen, B. W. (2004). Scientific challenges in the field of invasive alien plant management. *South African Journal of Science* 100, 19 - 20.	Sole author	8
96. van Wilgen, B.W. (2004). A South African perspective on plant introductions: motivations, problems and processes. 14th Australian Weeds Conference, Papers and Proceedings (ed by B.M. Sindel and S.B. Johnson). Weed Society of New South Wales, Wagga Wagga, pp 39 – 41.	Sole author	0
97. van Wilgen, B.W., Nel, J.L. and Rouget, M. (2007). Invasive alien plants and South African rivers: A proposed approach to the prioritization of control operations. *Freshwater Biology* 52, 711 – 723.	Lead author. Jeanne Nel provided data layers, and Matheu Rouget did the GIS analysis. Included in sample of selected papers.	3
98. Van Wilgen, B.W. and Moran, V.C. (2007). Integrated management of invasive alien plants in South Africa: A case for biological control. Working for Water Programme, Cape Town, 22 pp.	Lead author. Cliff Moran provided valuable guidance and minor inputs.	0

99. van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M. and Schonegevel, L. (2007). A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management* 89, 336 – 349.	Lead author. Belinda Reyers and David Le Maitre did analysis on biodiversity and groundwater, and Lucille Schonegevel did technical GIS work.	0
100. Richardson, DM, van Wilgen, BW and Nuñez, MA (2007). Alien conifer invasions in South America: short fuse burning? *Biological Invasions* 10, 573-577.	Work shared equally with co-authors	1

Calculation of h- *and* g-*indices*

Table 2 provides an analysis of the *h*- and *g*-indices of the papers listed in Table 1. The h-index is calculated as the number of papers (*h*) that each have *h* or more citations. The g-index is calculated as the (unique) largest number such that the top *g* articles received (together) at least g^2 citations.

Table 2. *Papers that contributed to the* h- *and* g-*scores of B.W. van Wilgen. Full references for the papers listed here can be found in Table 1.* <u>*Underlined*</u> *shows the h-score (= 23), and* ***bold*** *shows g-score (= 41).*

Paper	Total citations	Rank (r)	Cumulative citations	r^2
Fire and plants (book, 1996).	481	1	481	1
Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology* (1996)	83	2	564	4
Valuation of ecosystem services: a case study from the fynbos, South Africa. *BioScience* (1996)	81	3	645	9
Ecosystem management (book chapter, 1992)	58	4	703	16
International Geosphere-Biosphere Programme/International Global Atmospheric Chemistry SAFARI-92 field experiment: Background and overview. *Journal of Geophysical Research* (1996)	49	5	752	25
Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water programme. *Trends in Ecology and Evolution* (1998)	48	6	800	36
Current and future threats to plant biodiversity on the Cape Peninsula, South	47	7	847	49

Africa. *Biodiversity and Conservation* (1996)				
The effect of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *Journal of Applied Ecology* (1985)	43	8	890	64
Impacts of woody aliens on ecosystem properties. The ecology and control of biological invasions in South Africa. (book chapter, 1986).	38	9	928	81
Invasive alien trees and water resources in South Africa: Case studies of the costs and benefits of management. *Forest Ecology and Management* (2002)	36	10	964	100
Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology* (2000)	36	11	1000	121
Fire in South African Mountain Fynbos: Species, community and ecosystem response in Swartboskloof (book, 1992).	34	12	1034	144
The impact of commercial afforestation on bird populations in Mpumalanga province, South Africa - insights from bird atlas data. *Biological Conservation* (1997)	33	13	1067	169
Fire management in southern Africa: Some examples of current objectives, practices and problems. (book chapter, 1990).	32	14	1099	196
A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. *South African Journal of Science* (2000)	32	15	1131	225
A patch mosaic burning system for conservation areas in southern Africa. *International Journal of Wildland Fire* (2001)	32	16	1163	256
The sustainable development of water resources: History, financial costs and benefits of alien plant control programmes. *South African Journal of Science* (1997)	28	17	1191	289
The economic consequences of alien plant invasions: Examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability* (2001)	27	18	1218	324
The role of vegetation structure and fuel	24	19	1242	361

chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* (1990)				
The vegetation and fire regimes of southern hemisphere Africa (book chapter, 1997).	26	20	1268	400
Response of savanna fire regimes to changing fire management policies in a large African national park. *Conservation Biology* (2004)	26	21	1294	441
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