The evolution of fire and invasive alien plant management practices in fynbos

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The history and development of fire and invasive alien plant management policies in fynbos during the 20th century are reviewed. Fire was initially condemned outright as a destructive force, but as its vital role became better understood, management policies switched from protection to active burning in 1968. During the 1970s, large, coordinated research programmes were established, resulting in a solid basis of knowledge on which to develop fire management policies. Despite policies of prescribed burning, wild fires remain the dominant feature of the region, fortunately driving a variable fire regime that remains broadly aligned with conservation objectives. The problem of conserving fire-adapted fynbos is complicated by invading alien trees that are also fire-adapted. Research results were used to demonstrate the impacts of these invasions on water yields, leading to the creation of one of the largest alien plant control programmes globally. Despite improvements in control methods, alien trees, notably pines, continue to spread almost unchecked. Biological control offered some hope for controlling pines, but was ruled out as too high a risk for these commercially-important trees. Failure to address this problem adequately will almost certainly result in the severe degradation of remaining fynbos ecosystems.

Key words: biological control, conservation, pines, prescribed burning

Introduction

The fynbos shrublands of the nutrient-poor areas of the Western and Eastern Cape provinces in South Africa have high levels of endemism, with over 6 200 (69%) of the over 9 000 plant species being endemic.[1] The fynbos region is one of the world's six floral kingdoms,[2] and several nature reserves were recently proclaimed as world heritage sites in recognition of their global importance as centres of endemism. Fire is an important process in fynbos, which is both fire-adapted and fire-dependent. Fires are necessary, but they also damage crops, plantations and buildings that encroach on natural ecosystems, and 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 social importance of fires, fynbos managers have long sought to influence the occurrence, timing and extent of fires.

The invasion of fynbos by alien plants is also an increasingly important aspect of ecology. In fire-prone ecosystems, successful alien species are fire-adapted themselves, and they come to dominate as a result of superior growth rates and pre-adaptation to frequent fires. 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.

This paper traces the evolution of fire management, and related invasive alien plant management policies in fynbos conservation areas during the 20th century and beyond. Over the years, management practices have changed in response to 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 document the role that research has played in informing these changes. I conclude by sketching the challenges facing ecosystem managers today.

Fire management in fynbos ecosystems

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

Early botanists regarded fires as a destructive force in fynbos, and agitated for protection from fire.[3–7] There were also concerns about the possible detrimental effects of fire on water supplies. For example, the 1926 Drought Investigation Commission stated that veld burning was harmful, especially in important watershed areas, and they recommended that such areas should be protected from both grazing and fire.[8] 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 tasked with 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.[8]

Against this background, there was also growing evidence that fire was not necessarily always detrimental,[9] and later that fire was probably necessary. A leading ecologist at the time, C.L. Wicht (Fig. 1) 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'.[10] P.G. Jordaan demonstrated in 1949 that fires in summer, at intervals of at least eight years, were 'safe' for *Protea repens,* and

Fig. 1. C.L. Wicht, who made the first serious suggestion of prescribed burning as a management option in fynbos vegetation in 1945.

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pointed out that safe fire frequencies would almost certainly apply to other fynbos plant species.[11] He later (1965) extended the notion of safe and unsafe fire periods to fire seasons as well.[12] A further study in 1966 demonstrated that all of the 448 species identified in the mountains near Stellenbosch survived fire, either by sprouting or by regeneration from seed.[13] However, the realisation 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 their rapid recovery following unplanned fires, which stimulated soil-stored seed reserves to regenerate *en masse.*[14–16] These realisations, combined with observations that protection of fynbos from fire could lead to declines in streamflow,[17] led to the introduction in 1968 of a policy of prescribed burning.[8]

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.*[18] 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'.[8] The change from fire protection to prescribed burning was based on the assumption that maintaining healthy fynbos by regular burning was the best way of protecting the soil, and thus ensuring a sustained yield of water from catchment areas.[19] On public land, the goal of nature conservation enjoyed equal status with the goals of water and soil conservation.[8]

Policy documents at the time[20] indicated that prescribed burning had three 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 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 unstated assumption behind this goal was that large, harmful wildfires were the result of fuel accumulation, and were likely only to occur in large, continuous tracts of vegetation that had not been burnt for some time. The third purpose 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.

Research to support fire management

The South African Department of Forestry initiated a fynbos ecological 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 Council for Scientific and Industrial Research (CSIR), with the purpose of funding and coordinating research.[21] 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,[22, 23] of how fire protection led to senescence and poor regeneration after long fire-free intervals,[24,25] and of how to define acceptable, as well as unacceptable, seasons for burning.[26–28] On the termination of the Fynbos Biome Project[29] in 1990, it was possible to provide fairly detailed prescriptions regarding the management of fynbos by means of prescribed burning. These included acceptable inter-fire periods, seasons, and weather conditions under which fires would achieve the desired ecological outcomes, and systems for their management.[30–32]

The practical implementation of prescribed burning

During the 1970s, managers of fynbos ecosystems made good progress with the implementation 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 firebreaks, and the area in which a burning operation could be completed in a single day. By 1981, approximately 40 burns were carried out in the fynbos biome per year.[33]

However, a steady decline in prescribed burns followed policy directives that restricted 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,[26, 28] thus eliminating the possibility of burning in September and October, the months with the safest weather for burning.[33, 34] This change in policy resulted in a decline by 1988 of 75% in the area burnt in prescribed burns.[33]

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.[35] In addition, an increasing focus on the conservation of biodiversity led to calls for variation in fire regimes.[18] 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.[18] The approach also incorporated inevitable wildfires into planning and monitoring,[33] and was formalised in the development of a GIS-based system for the management and monitoring of fires in fynbos areas.[31]

Effects of prescribed burning on fynbos fire regimes

One of the 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 practised) with records from 1973–1986 (when prescribed burning was practised).[36] 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 five years, and were thus not reliant on large, continuous areas of older vegetation. The 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 that prescribed burning reduced wildfire occurrence.

A similar detailed analysis of a 70-year fire record was recently completed for the Swartberg Mountains.[37] 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'. [37]

The latest comprehensive analysis of fire records from 10 large nature reserves in the Western Cape over the past 40–50 years[38,39] showed that modern fynbos fire regimes are in fact dominated by wildfires, which account for more than 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 wildfires. For example, of the 150 fires on record in the Cedarberg between 1945 and 2006, the 10 largest were responsible for 66% of the total area burnt.[38] Finally, some concern has been expressed that, in some areas, fires are becoming more frequent. For example, the area subjected to short (less than six years) intervals between fires covered >16% of the Table Mountain National Park in the last two decades, compared to about 4% in the previous two decades.[39]

The above findings prompt the following conclusions:

(1) The assumption that prescribed burning would be necessary to prevent vegetation senescence and loss of species is not supported by evidence. Prescribed burning plays a minor role in modern fire regimes, and wildfires alone should provide sufficient opportunities for 'rejuvenation'.
(2) 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 evidence. Reductions in fuel do not consistently prevent the spread of wildfires, which can burn through five-year post-fire vegetation provided that hot, dry, and windy conditions prevail.
(3) It appears that fire return periods are decreasing in some areas (possibly as a result of increasing human population densities and access), leading to increased opportunities for ignitions.[39] This suggests that fynbos fires are not fuel limited (except when the vegetation is very young), but rather triggered by the co-occurrence of weather conducive to wildfires and a source of ignition.
(4) Increases in fire frequency could arise as a result of increased human populations leading to a higher number of ignition opportunities. This would be exacerbated if changes in climate lead to hotter and drier weather, leading to more fires and further reductions in fire return periods. Such trends would be difficult to reverse, and therefore represent a significant threat to fynbos ecosystems.

Current ecological understanding of the role of fire in fynbos

Current understanding of the role of fire in fynbos is relatively robust. Most plant species are resilient to a wide range of fire return intervals. For example, a study of 210 co-occurring fynbos species showed that most were able to resprout after fire, and 200 out of the 210 species could survive fire return intervals of between 10 years and 40 years.[40] 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.[26] While only a small proportion of the total number of species fall into this category,[40] they can be the dominant component 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.[25] As a result, they are usually the species that are used to determine acceptable fire return intervals.[30] For example, one rule proposed a minimum interval between fires that would allow at least 50% of 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.[41] Application of this rule normally suggests a minimum period of 10 years 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 an important determinant of recruitment. 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.[26,28] In 1985 this led to recommendations to restrict management fires to this time of the year.[30] While these restrictions applied to the western and inland zones, it was recognised that fire season was less critical in the eastern coastal zone.[42] Recent work[43] in the eastern coastal areas of the fynbos biome in 2007 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 in the eastern fynbos biome. Flowering shifts 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.[44,45] Variation in the intervals between fires, in fire season, or fire intensity will induce variation in the density of proteaceous overstorey shrubs; and this variation is in turn associated with the maintenance of diversity in understorey species.[44,45] Pre-fire stand densities may also affect the density of post-fire recruitment,[46] resulting in alternating densities and species diversity on the same site between different fires. Recurrent fires will therefore buffer plant populations from extinction,[44] by ensuring stable coexistence over time, despite localised extirpation by individual fires. However, it is well known that repeated frequent burning can eliminate important overstorey shrubs in fynbos.[25,47] Should large areas be subjected to repeated frequent burning, recolonisation would depend on a species' ability to disperse seeds from adjacent areas, sometimes over long distances.[48,49] While this may be possible for some of the wind-dispersed Proteaceae, a large number of fynbos plant species that rely on soil-stored and ant-dispersed seeds[50] may not be able to effectively recolonise large areas from which they have been extirpated. 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.[51] 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.

Invasive alien plant management in fynbos ecosystems

Invasive alien plants in fynbos ecosystems

There are over 150 species of alien plants that are invasive in the fynbos biome.[52] However, many of these are not (currently) of major ecological significance, and only 30 species (17 trees, 8 shrubs, 3 grasses, 1 succulent and 1 annual) occupy at least 10% of the biome.[53] Of these the most important groups of species include the pines (*Pinus* species), wattles (*Acacia* and *Paraserianthes* species), hakeas (*Hakea* species), and gums (*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. 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 across the biome. They can, and do, form dense and impenetrable stands (Fig. 2). The second group is the wattles. These species typically produce copious amounts of seeds, but these are released on ripening. The seeds are hard-coated and accumulate in the soil. The seeds are spread along rivers, by moving soil around, or by birds. Soil-stored seed banks are stimulated to germinate in dense stands by fire. Gums 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.

A range of methods are available to control invasive alien plants, including mechanical, chemical and biological control. While the first two methods can be used to contain infestations, neither provides a permanent or sustainable solution to the problem.[54,55] Biological control options provide more sustainable solutions, but are only available for some of the invasive alien plant species in the fynbos.[56] Hakeas and several wattles have a suite of seed-feeding and gall-forming insects which can reduce seed loads. A promising project, seeking seed-destroying insects for pines,[57] was terminated because of fears that the proposed insect would assist the infection of commercially-important pine trees by pitch canker.[58]

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. Early botanists, including Peter MacOwan (in 1888) and Rudolf Marloth (in 1908), raised concerns that alien plants would replace natural vegetation.[59] In a landmark publication in 1945, Wicht stated[10] 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'.

In 1982, the General Assembly of the Scientific Committee on problems of the Environment (SCOPE) identified the invasive spread of plants, animals and microorganisms, 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 reviewing and improving understanding of biological invasions and their implications. The South African component of this work led in 1986 to a synthesis

Fig. 2. Pines, originating from forestry plantations, are spread by fire and can dominate mountain watersheds after a few fire cycles. Fires in areas where invasive pines have been cleared can lead to extensive soil damage: (**a**) pines spreading from a forest plantation in the Eastern Cape; (**b**) initial stages of invasion in the Kogelberg Biosphere Reserve; (**c**) extensive invasions in remote parts of the Tsitsikamma mountains; and (**d**) initial stages of soil damage following fire in felled stands of invading pines, Stellenbosch.

volume,[60] in which the current understanding was set out. Work 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 biological control), and a good deal of useful work was done. For example, research initiated by SAFRI examined the underlying reasons for differences in the invasive potential of closely-related plant species.[61,62] This work ultimately led to the development of the first robust model of invasive potential in a large group of plants.[63]

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. The idea that invasive alien trees could have negative impacts on streamflow (in much the same way as commercial forestry did) was first raised in 1977 by Kruger.[64] It was raised again during the SCOPE synthesis,[65] and at the conclusion of the Fynbos Biome project.[30,66] This led 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.[67] 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-riparian streamflow reduction conditions. 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 annual water supply to the city of Cape Town). Based on this work, the costs of 'generating' water from catchments where alien plants were either controlled, or not, were estimated.[68] 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[69] 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 programmes would pay off, rather than leaving them for control at a later date.

Subsequently, several other papers have estimated the economic consequences of alien plant invasions in fynbos ecosystems and elsewhere. All of these papers[70–73] provide estimates showing that clearing invasive alien plants makes economic sense (in that they deliver positive cost–benefit ratios). These findings rely heavily on 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.[74]

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 and extent of infestation. It is necessary to control these flushes of seedlings to prevent them becoming dominant over the next few years. Extensive unplanned fires will precipitate the need for additional effort in the form of 'follow-up' operations. CapeNature estimated in 2006 that these additional costs would amount to R17.5 million[75] following fires on 40 000 ha. Alternatively, 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, control costs would rise almost four-fold to an estimated R65 million on the same 40 000 ha.[75] On average therefore, if control operations were carried out within five years of an unplanned fire, additional costs could amount to around R1 000 per ha. Finally, if the problem is not dealt with (because of a lack of capacity or funds), then the environmental impacts (for example, water losses) would represent a cost attributable to wildfires. The 4.3 million hectares of extant fynbos is subjected to a mean fire return period of 15 years, so about 286 000 ha burns every year. About 33% of the three major catchments in the Western Cape are invaded to some degree,[76] 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* (eight species), *Paraserianthes, Leptospermum, Sesbania,* and *Hakea* (two 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.[56] Many of these releases have resulted in the target invasive species being brought under substantial or complete control.[56]

Management responses

Attempts to control invasive alien plants began in the fynbos biome as early as the 1930s. Control efforts in the second half of the 20th century 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, 47 years of control attempts on the southern Cape Peninsula, were 'almost totally ineffective for the first 35 years'.[77] The early, erratic control efforts were replaced later by coordinated control programmes[78] in the 1970s and 1980s. 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 lost in the late 1980s, due to many factors. The seasonal restrictions on burning meant that many prescribed fires, necessary for the control of seedlings after felling operations, could not be carried out. The government also

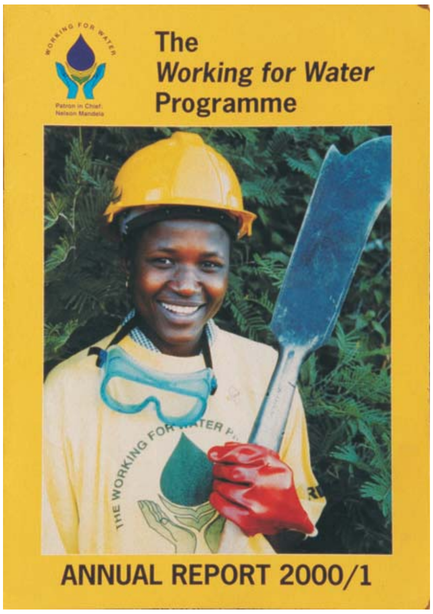

Fig. 3. Cover of the annual report of the Working for Water programme, for the 2000/2001 financial year. Most promotional material for the programme stresses employment and development opportunities as well as ecological benefits.

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 fragmentation, and loss of capacity and experience. The government of the day cut funding, resulting in further loss of capacity. The net result was that invasive alien plant control programmes fell behind, and cleared areas were under threat of re-invasion.

The development of economic arguments, based 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 (Fig. 3). The events that led to the formation of this programme are documented elsewhere,[79] 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.[77]

The programme has attracted funding and gained local and international acclaim, but it relies heavily on political support and remains vulnerable for this reason. Political support for this programme stems almost entirely from 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.

The benefits of alien plant control, especially those in natural (rather than agricultural) environments are '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 large.

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). People find it difficult to appreciate (or gain political benefit or advantage from) the avoidance of future impacts that are not yet manifesting themselves.

The predicted benefits of clearing invasive alien plants on water yields are based on plantation forestry, and there have been no rigorous attempts to quantify the actual gains from land cleared of invasive alien plants, rather than of clearfelling plantations. This is a serious weakness, and it makes the programme vulnerable in terms of its ability to compete for funding against other projects which may be supported by more tangible evidence of benefits.

The fact remains, however, 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.

Prognosis for invasive alien plant control

Whether or not control attempts are having real impacts on the status of alien plant invasions is an important question. The Working for Water programme was initially proposed as a 20-year activity,[80] but clearing major infestations within that timeframe will not be possible. At current rates of clearing, infestations of several important species would be cleared only within 30–85 years.[54] This estimate is based on a number of assumptions, each of which reduces the estimate of time needed to clear existing infestations; the estimates are therefore probably serious underestimates. These assumptions include: (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. 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 also underscores the importance of biological control, which is seen by its proponents[57] as a particularly attractive option because it is cost-effective and safe compared to the expense and risks associated with herbicides; it can be successfully integrated with other management practices; and, most compelling of all, it is self-sustaining. There are counter-arguments to the use of biological control.[81,82] Those who hold these views believe that the outcomes of an introduction cannot be predicted precisely enough *a priori* to know that the benefits will outweigh the environmental costs. Examples of unintended consequences include impacts on non-target species, and the disruption of food webs. The evidence suggests that these concerns are often groundless, but they are nevertheless responsible for serious barriers to biological control.[83] A resolution to this debate remains an important challenge.

Integrating prescribed burning and alien weed control operations is also important. Fire regimes are difficult to manage, and wildfires are inevitable. There is therefore an urgent need to become more flexible with regard to follow-up operations after fires, 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, may ultimately determine the fate of the unique fynbos vegetation.

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.[84] Each individual fire event contributes to the regime, but ecosystem managers tend to focus on 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.[85] 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 described by 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).[86] With the advent of modern geographic information system 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.[84] Plant populations may fluctuate considerably over time, with local extinctions and recolonisations taking place within a much larger landscape.[45] 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.

At the close of the Fynbos Biome Project in 1992, reviews of the fire management of fynbos ecosystems[30,87] concluded that prescribed burns, combined with wildfires, firebreak burns in spring, and occasional longer periods between fires would provide sufficient stochasticity to ensure the survival of coexisting species. The same reviews also concluded that dealing with invasive alien plants presented a greater challenge than fires for managers of fynbos ecosystems. The reviews proposed four scenarios relating to the future of fynbos ecosystem management, based on different levels of funding (unchanged, increased, decreased and curtailed). They predicted that funding would probably decline, and that invasion would therefore continue largely unchecked. This was especially so in the case of pines, for which no biological control agents were available. In reality, the creation of the Working for Water programme[80] has significantly increased the funding available for invasive alien plant control. However, in the first decade of operations, the programme cleared only 4.5% of the estimated area invaded by pines,[55] a rate that will not prevent the spread and eventual domination of pines. The termination of research into the biological control of pines[58] means that the prospect of bringing pine invasions under control has been further reduced. Solving the problem of controlling fire-adapted invasive alien pines in the fynbos remains the largest challenge to managers concerned with the conservation of fynbos ecosystems. Failure to address this problem adequately will almost certainly result in the severe degradation of remaining fynbos ecosystems.

This paper is dedicated to Fred Kruger, pioneer fynbos fire ecologist and exceptional mentor.

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1. Goldblatt P. and Manning J. (2002). Plant diversity of the Cape region of South Africa. *Annals of the Missouri Botanical Garden* **89**, 281–302.
2. Takhtajan A. (1969). *Flowering Plants: Origin and Dispersal.* Oliver and Boyd, Edinburgh.
3. Levyns M.R. (1924). Some observations on the effects of bush fires on the vegetation of the Cape Peninsula. *S. Afr. J. Sci.* **21**, 346–347.
4. Pillans N.S. (1924). Destruction of indigenous vegetation by burning on the Cape Peninsula. *S. Afr. J. Sci.* **21**, 348–350.
5. Marloth R. (1924). Notes on the question of veld burning. *S. Afr. J. Sci.* **21**, 342–345.
6. Compton R.H. (1926). Veld burning and veld deterioration. *S. Afr. J. Nat. Hist.* **6** (1), 5–19.
7. Compton R.H. (1934). The results of veld burning. *Educ. Gaz.* **33**, 644–655.
8. Bands D.P. (1977). Prescribed burning in Cape Fynbos. In *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems,* General Technical Report WO-3, eds H.A. Mooney and C.E. Conrad, pp. 245–256. USDA Forest Service, Washington D.C.
9. Phillips J.F.V. (1930). Fire: its influence on biotic communities and physical factors in South and East Africa. *S. Afr. J. Sci.* **27**, 352–367.
10. Wicht C.L. (1945). *Report of the Committee on the Preservation of the Vegetation of the South Western Cape.* Special Publication of the Royal Society of South Africa, Cape Town.
11. Jordaan P.G. (1949). Aantekeninge oor die voortplanting en brandperiodes van *Protea mellifera* Thunb. *J. S. Afr. Bot.* **15**, 121–125.
12. Jordaan P.G. (1965). Die invloed van 'n winterbrand op die voortplanting van vier soorte van die Proteaceae. *Tydskrif vir Natuurwetenskappe* **5**, 27–31.
13. Van der Merwe P. (1966). Die flora van Swartboskloof, Stellenbosch en die herstel van die soorte na 'n brand. *Annals of the University of Stellenbosch* 41, Series A, Number 14.
14. Boucher C. (1981). Autecological and population studies of *Orothamnus zeyheri* in the Cape of South Africa. In *The Biological Aspects of Rare Plant Conservation,* ed. H. Synge, pp. 343–353. John Wiley & Sons, New York.
15. Voigts M. (1982). *South Africa's Proteaceae: Know Them and Grow Them.* Struik, Cape Town.
16. Worth S.W. and van Wilgen B.W. (1988). The Blushing Bride: status of an endangered species. *Veld & Flora* **74**, 123–124.
17. Van der Zel D.W. and Kruger F.J. (1975). Results of the multiple catchment experiments at the Jonkershoek Research Station, South Africa. II. Influence of protection of fynbos on stream discharge in Langrivier. *Forestry in South Africa* **16**, 13–18.
18. Van Wilgen B.W., Richardson D.M. and Seydack A. (1994). Managing fynbos for biodiversity: constraints and options in a fire-prone environment. *S. Afr. J. Sci.* **90**, 322–329.
19. Kruger F.J. (1977). Ecology of Cape fynbos in relation to fire. In *Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems,* General Technical Report WO-3, eds H.A. Mooney and C.E. Conrad, pp. 230–244. USDA Forest Service, Washington D.C.
20. Van Wilgen B.W. (1984). *Prescribed Burning in Fynbos.* Information Leaflet 11. Department of Environmental Affairs and Tourism, Pretoria.
21. Huntley B.J. (1987). Ten years of cooperative ecological research in South Africa. *S. Afr. J. Sci.* **83**, 72–79.
22. Kruger F.J. and Bigalke R.C. (1984). Fire in fynbos. In *Ecological Effects of Fire in South African Ecosystems,* eds P. de V. Booysen and N.M. Tainton, pp. 67–114. Springer, Berlin.
23. Van Wilgen B.W., Richardson D.M., Kruger F.J. and van Hensbergen H.J. (1992). *Fire in South African Mountain Fynbos: Species, Community and Ecosystem Response in Swartboskloof.* Springer Verlag, Heidelberg.
24. Bond W.J. (1980). Fire and senescent fynbos in the Swartberg, Southern Cape. *S. Afr. For. J.* **114**, 68–74.
25. Van Wilgen B.W. (1982). Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *J. Ecol.* **70**, 217–225.
26. Bond W.J., Vlok J. and Viviers M. (1984). Variation in seedling recruitment of Cape Proteaceae after fire. *J. Ecol.* **72**, 209–221.
27. Bond W.J. (1984). Fire survival of Cape Proteaceae – influence of fire season and seed predators. *Vegetatio* **56**, 65–74.
28. 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. *S. Afr. For. J.* **133**, 49–53.
29. Cowling R.M. (1992). *The Ecology of Fynbos: Nutrients, Fire and Diversity.* Oxford University Press, Cape Town.
30. Van Wilgen B.W., Bond W.J. and Richardson D.M. (1992). Ecosystem management. In *The Ecology of Fynbos: Nutrients, Fire and Diversity,* ed. R.M. Cowling, pp. 345–371. Oxford University Press, Cape Town.
31. Richardson D.M., van Wilgen B.W., Le Maitre D.C., Higgins K.B. and Forsyth

G.G. (1994). A computer-based system for fire management in the mountains of the Cape Province, South Africa. *Int. J. Wildl. Fire* **4**, 17–32.
32. Juhnke S.R. and Fuggle R.F. (1987). Predicting weather for prescribed burns in the south-western Cape, Republic of South Africa. *S. Afr. For. J.* **142**, 41–46.
33. 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 *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges,* ed. J.G Goldammer, pp. 179–209. Springer, Berlin.
34. Van Wilgen B.W. and Richardson D.M. (1985). Factors influencing burning by prescription in mountain fynbos catchment areas. *S. Afr. For. J.* **134**, 22–32.
35. Seydack A.W.H. (1992). Fire management options in fynbos mountain catchment areas. *S. Afr. For. J.* **161**, 53–58.
36. Brown P.J., Manders P.T., Bands D.P., Kruger F.J. and Andrag R.H. (1991). Prescribed burning as a conservation practice: A case study from the Cedarberg mountains, Cape Province, South Africa. *Biol. Cons.* **56**, 133–150.
37. Seydack A.H.W., Bekker S.J. and Marshall A.H. (2007). Shrubland fire regime scenarios in the Swartberg Mountain Range, South Africa: implications for fire management. *Int. J. Wildl. Fire* **16**, 81–95.
38. Forsyth G.G. and van Wilgen B.W. (2007). *Analysis of the fire history records from protected areas in the Western Cape.* Report CSIR/NRE/ECO/ER/2007/0118/C, CSIR, Stellenbosch.
39. Forsyth G.G. 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.
40. Van Wilgen B.W. and Forsyth G.G. (1992). Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In *Fire in South African Mountain Fynbos: Species, Community and Ecosystem Response in Swartboskloof,* eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen, pp. 55–80. Springer-Verlag, Heidelberg.
41. Kruger F.J. and Lamb A.J. (1979). *Conservation of the Kogelberg State Forest. Preliminary assessment of the effects of management from 1967 to 1978.* Report 79–02, Jonkershoek Forestry Research Centre, Stellenbosch.
42. Van Wilgen B.W. (1984). Fire climates in the southern and western Cape Province and their potential use in fire control and management. *S. Afr. J. Sci.* **80**, 358–362.
43. Heelemann S., Procheş Ş., Cowling R.M., Rebelo A.G., van Wilgen B.W. and Porembski S. (2007). Fire season effects on the recruitment of non-sprouting serotinous Proteaceae in the eastern (bimodal-rainfall) fynbos biome, South Africa. *Austral Ecol.* **33**, 119–127.
44. Cowling R.M. and Gxaba T. (1990). Effects of a fynbos overstorey shrub on understorey community structure: implications for the maintenance of community-wide species richness. *S. Afr. J. Ecol.* **1**, 1–7.
45. Thuiller W., Slingsby J.A., Privett S.D.J. and Cowling R.M. (2007). Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *Plos ONE* 2(9): doi:10.1371/journal.pone.0000938
46. Bond W.J., Maze K. and Desmet P. (1995). Fire life histories and the seeds of chaos. *Ecoscience* **2**, 252–260.
47. Van Wilgen B.W. (1981). Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. *S. Afr. For. J.* **118**, 42–55.
48. Bond W.J. (1988). Proteas as 'tumbleseeds': wind dispersal through the air and over soil. *S. Afr. J. Bot.* **54**, 455–460.
49. Schurr F.M., Bond W.J., Midgley G.F. and Higgins S.I. (2005). A mechanistic model for secondary seed dispersal by wind and its experimental validation. *J. Ecol.* **93**, 1017–1028.
50. Bond W.J. and Slingsby P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci.* **79**, 231–233.
51. Vlok J.H.J. and Yeaton R.I. (1999). The effect of overstorey proteas on plant species richness in South African mountain fynbos. *Divers. Distrib.* **5**, 213–222.
52. Henderson L. (1998). Southern African Plant Invaders Atlas (SAPIA). *Appl. Plant Sci.* **12**, 31–32.
53. Van Wilgen B.W., Reyers B., Le Maitre D.C., Richardson D.M. and Schonegevel L. (2008). A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *J. Environ. Man.* **89**, 336–349.
54. Holmes P.M., Richardson D.M., van Wilgen B.W. and Gelderblom C. (2000). The recovery of South African fynbos vegetation following alien tree clearing and fire: implications for restoration. *Austral Ecol.* **25**, 631–639.
55. 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. *S. Afr. J. Sci.* **100**, 97–103.
56. Zimmermann H.G., Moran V.C. and Hoffmann J.H. (2004). Biological control of invasive alien plants in South Africa, and the role of the Working for Water programme. *S. Afr. J. Sci.* **100**, 34–40.
57. Moran V.C., Hoffmann J.H., Donnelly D., Zimmermann H.G. and van Wilgen B.W. (2000). Biological control of alien invasive pine trees (*Pinus* species) in South Africa. In *Proceedings of the Xth International Symposium on Biological Control of Weeds,* ed. N.R. Spencer, pp. 941–953. Montana State University, Bozeman.
58. Lennox C.L., Hoffmann J.H., Coutinho T.A. and Roques A. (2009). A threat of exacerbating the spread of pitch canker precludes further consideration of a cone weevil, *Pissodes validirostris,* for biological control of invasive pines in South Africa. *Biol. Control* **50**, 179–184.
59. Stirton C.H. (1978). *Plant Invaders: Beautiful, but Dangerous.* Department of Nature and Environmental Conservation, Cape Town.
60. Macdonald I.A.W., Kruger F.J. and Ferrar A.A. (1986). *The Ecology and Management of Biological Invasions in Southern Africa.* Oxford University Press, Cape Town.
61. Van Wilgen B.W. and Siegfried W.R. (1986). Seed dispersal properties of three pine species as a determinant of invasive potential. *S. Afr. J. Bot.* **52**, 546–548.
62. 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.
63. Rejmánek M. and Richardson D.M. (1996). What attributes make some plant species more invasive? *Ecology* **77**, 1655–1677.
64. Kruger F.J. (1977). Invasive woody plants in Cape fynbos with special reference to the biology and control of *Pinus pinaster.* In *Proceedings of the Second National Weeds Conference of South Africa,* pp. 57–74. Stellenbosch.
65. Versfeld D.B. and van Wilgen B.W. (1986). Impacts of woody aliens on ecosystem properties. In *The Ecology and Control of Biological Invasions in South Africa,* eds I.A.W. Macdonald, F.J. Kruger and A.A. Ferrar, pp. 239–246. Oxford University Press, Cape Town.
66. Van Wilgen B.W. (1991). Water catchment areas in the fynbos: What of the future? *Veld & Flora* **77**, 34–35.
67. 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. *J. Appl. Ecol.* **33**, 161–172.
68. 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.
69. Van Wilgen B.W., Little P.R., Chapman R.A., Görgens A.H.M., Willems T. and Marais C. (1997). The sustainable development of water resources: history, financial costs and benefits of alien plant control programmes. *S. Afr. J. Sci.* **93**, 404–411.
70. Higgins S.I., Turpie J.K., Costanza R., Cowling R.M., Le Maitre D.C., Marais C. and Midgley G.F. (1997). An ecological economic simulation model of mountain fynbos ecosystems: dynamics, valuation and management. *Ecol. Econ.* **22**, 155–169.
71. Hosking S.G. and du Preez M. (1999). A cost benefit analysis of removing alien trees in the Tsitsikamma mountain catchment. *S. Afr. J. Sci.* **95**, 442–448.
72. Turpie J.K. and Heydenrych B.J. (2000). Economic consequences of alien infestation of the Cape Floral Kingdom's Fynbos vegetation. In *The Economics of Biological Invasions,* eds C. Perrings, M. Williamson and S. Dalmazzone, pp. 152–182. Edward Elgar, Cheltenham.
73. De Wit M., Crookes D. and van Wilgen B.W. (2001). Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biol. Invasions* **3**, 167–178.
74. Turpie J. (2004). The role of resource economics in the control of invasive alien plants in South Africa. *S. Afr. J. Sci.* **100**, 87–93.
75. Bekker S.J. (ed.). (2006). CapeNature report to the Provincial Disaster Management Committee regarding fire damage in the Overberg 30 January–6 February 2006. CapeNature, Cape Town.
76. Versfeld D.B., Le Maitre D.C. and Chapman R.A. (1998). *Alien invading plants and water resources in South Africa: a preliminary assessment.* Report TT 99/98, Water Research Commission, Pretoria.
77. Macdonald I.A.W., Clark D.L. and Taylor H.C. (1989). The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941–1947. *S. Afr. J. Bot.* **55**, 56–75.
78. Fenn J.A. (1980). Control of *Hakea* in the western Cape. In *Proceedings of the Third National Weeds Conference of South Africa,* eds S. Neser and A.L.P. Cairns, pp. 167–173. Balkema, Cape Town.
79. Van Wilgen B.W., 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,* eds S.M. Pierce, R.M. Cowling, T. Sandwith and K. McKinnon, pp. 5–20. The World Bank, Washington D.C.
80. Van Wilgen B.W., Le Maitre D.C. and Cowling R.M. (1998). Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water programme. *Trends Ecol. Evol.* **13**, 378.
81. Simberloff D. and Stiling P. (1996). Risks of species introduced for biological control. *Biol. Cons.* **78**, 185–192.
82. Louda S.M. and Stiling P. (2003). The double-edged sword of biological control in conservation and restoration. *Cons. Biol.* **18**, 50–53.
83. McFadyen R.F. (2004). Biological control: managing risks or strangling progress? In *Proceedings of the 14th Australian Weeds Conference,* eds B.M. Sindel and S.B. Johnson, pp. 78–81. Weed Society of New South Wales, Sydney.
84. Gill A.M. (1975) Fire and the Australian flora: a review. *Aust. For.* **38**, 4–25.
85. Gill A.M., Bradstock R.A. and Williams J.E. (2002), Fire regimes and biodiversity: legacy and vision. In *Flammable Australia: The Fire Regimes and Biodiversity of a Continent,* eds R.A. Bradstock, J.E. Williams and A.M. Gill, pp. 429–446. Cambridge University Press, Cambridge.
86. Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Cons. Biol.* **20**, 1610–1619.
87. Richardson D.M. and van Wilgen B.W. (1992). Ecosystem, community and species response to fire in mountain fynbos: conclusions from the Swartboskloof experiment. In *Fire in South African Mountain Fynbos: Species, Community and Ecosystem Response in Swartboskloof,* eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen, pp. 273–284. Springer-Verlag, Heidelberg.