Fire regimes in eastern coastal fynbos:

drivers, ecology and management

by

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Declaration

I, Tineke Kraaij, student number 211211583, hereby declare that the thesis for Doctorate of Philosophy is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

I am now presenting the thesis for examination for the degree of Doctorate of Philosophy.

Tineke Kraaij

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Abstract

Conventional knowledge of fynbos fire ecology is based on the summer-autumn fire regimes of the western Cape Floral Kingdom (CFK) where the climate is Mediterranean. However, the climate in the eastern coastal-CFK is milder and rainfall occurs year-round, with presumed effects on fire regimes. The Garden Route National Park (GRNP) has recently been established in the region, in a landscape where indigenous forests, fire-prone fynbos shrublands and fire-sensitive plantations of invasive alien trees are interspersed. The park faces considerable challenges related to the management of fire, including significant pressure from the adjacent plantation industry to reduce wildfire hazard by burning fynbos at short intervals, and high levels of invasion by alien trees (largely *Pinus* species originating from plantations). This study sought to improve understanding of fire regimes in eastern coastal fynbos shrublands, and to provide guidelines for ecologically sound management of fire in the area. My approach entailed (i) an assessment of the context within which fire management was practiced during the past century; (ii) characterisation of the recent fire history and fire regime (1900–2010); (iii) characterisation of the seasonality of fire weather and lightning; (iv) estimation of minimum fire return intervals (FRIs) from juvenile periods and post-fire recruitment success of overstorey proteoids (non-sprouting, slow-maturing, serotinous Proteaceae); and (v) determination of the ecologically appropriate fire season from post-fire recruitment seasonality of proteoids. I established that historically, plantation protection enjoyed priority over fynbos conservation in the area that is now the GRNP. Fynbos close to plantations has most likely been compromised by frequent and low-intensity burning in the past, as well as by invasion by alien trees. In terms of area burnt (1900–2010), natural (lightning-ignited) fires dominated the fire regime, particularly in the east, whereas prescribed burning was relatively unimportant. Typical fire return intervals (FRIs; 8–26 years; 1980–2010) were comparable to those in other fynbos protected areas and appeared to be shorter in the eastern Tsitsikamma than in the western Outeniqua halves of the study area. Proteaceae juvenile periods (4–9 years) and post-fire recruitment success (following fires in ≥7 year-old vegetation) suggested that for biodiversity conservation purposes, FRIs should be no less than nine years in moist, productive fynbos. Increases in the total area burnt annually (since 1980) were correlated with long-term increases in average fire danger weather, suggesting that fire regime changes may be related to global change. Collectively, findings on the seasonality of actual fires and the seasonality of fire danger weather, lightning, and post-fire proteoid recruitment suggested that fires in eastern coastal fynbos are not limited to any particular season, and for this reason managers do not need to be concerned if fires

occur in any season. The ecological requirements for higher fire intensity may nonetheless be constrained by a need for safety. I articulated these findings into ecological thresholds pertaining to the different elements of the fire regime in eastern coastal fynbos, to guide adaptive management of fire in the Garden Route National Park. I also recommended a fire management strategy for the park to address the aforementioned operational considerations within the constraints posed by ecological thresholds. Finally, I highlighted further research and monitoring needs.

Keywords: Cape Floral Kingdom; climate change; fire-prone shrublands; fire return interval; fire season; Garden Route National Park; post-fire recruitment; prescribed burning; Proteaceae juvenile periods; thresholds of potential concern

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Introduction

Fire has been a key selective force in the evolution of the species- and endemic-rich fynbos shrublands (Myers *et al.* 2000) of the Cape Floral Kingdom (CFK) of South Africa (Naveh 1975; Kruger & Bigalke 1984; Cowling 1987; Keeley *et al.* 2012). Contemporary fire regimes have likely been established during a period of global cooling that followed the mid-Miocene Climatic Optimum (*c.* 15 Ma) (Bytebier *et al*. 2011). Fire is the key management practice for maintaining biodiversity in fynbos shrublands (Kruger & Bigalke 1984; van Wilgen *et al.* 1992), and is also used in the integrated management of invasive alien plants (Roura-Pascual *et al.* 2009; van Wilgen 2009), which currently pose the biggest threat to biodiversity and the delivery of ecosystem services in fynbos systems (van Wilgen *et al.* 2008).

Existing understanding of fynbos fire ecology is largely based on knowledge of the summer-autumn fire regimes of the western, winter-rainfall regions and inland, semi-arid regions of the CFK (Bond 1984; Kruger & Bigalke 1984; van Wilgen *et al.* 1994). In contrast, fire regimes in the southeastern, coastal part of the CFK are poorly understood (van Wilgen 2009). Here, the climate is milder with reduced seasonal extremes in temperature, while rainfall occurs year-round (Schulze 1965). In eastern inland fynbos, overstorey proteoids (non-sprouting, slow-maturing, serotinous Proteaceae) show weak seasonal effects on post-fire recruitment, a consequence of a non-seasonal rainfall and fire regime (Heelemann *et al*. 2008). We expected similar patterns in eastern coastal fynbos, as well as faster plant growth and maturation rates of proteoids, a consequence of the region’s relatively benign climate. These phenomena will have important implications for the management of fire regimes.

The Garden Route National Park (GRNP; *c.* 130 000 ha) has recently been established (Government Gazette 2009) in the eastern coastal part of the CFK, and is situated within a landscape where indigenous forests, fire-prone fynbos shrublands and fire-sensitive plantations of invasive alien trees are interspersed. The park faces considerable ecological and operational challenges pertaining to the management of fire and invasive alien plants. Being a new park, there are still opportunities to influence the development of management policy and practice in the interests of biodiversity conservation.

Managers of fire-prone ecosystems need to understand the historical fire regimes of the areas that they manage, so that they can better understand how the current vegetation was shaped (Morgan *et al.* 2001), and whether or not they need to intervene in cases where contemporary fire regimes may be in conflict with biodiversity conservation requirements (Seydack 1992). To this end, they need to be able to distinguish between acceptable and unacceptable limits to variations in elements of fire regimes (fire frequency, season, intensity and size; Gill & Allan 2008), and whether and how they can influence them where deemed necessary (Biggs & Rogers 2003; van Wilgen *et al.* 2011).

This study sought to improve understanding of fire regimes in eastern coastal fynbos and to provide guidelines for ecologically sound management of fire in the fynbos of the region. The thesis is structured as follows:

Chapter 1 provides the rationale for the study by reviewing historical approaches and current challenges to the management of fire and invasive alien plants in eastern coastal fynbos, and more specifically the GRNP. It essentially provides the background and context for the studies that follow.

Chapter 2 characterises the historical fire regime (in terms of fire season, cause, size, and return interval) in the area during the past century and puts that into perspective with those of other temperate fire-prone shrublands.

Chapter 3 explores seasonality and long-term trends in fire danger weather conditions and lightning incidence in the area to shed light on the season of fires.

Chapter 4 assesses proteoid juvenile periods and recruitment success after fires at different intervals as indicators of ecologically appropriate fire return intervals in eastern coastal fynbos.

Chapter 5 draws on a proteoid seed planting experiment and opportunistic field surveys of post-fire proteoid recruitment to inform the ecologically appropriate season of fire in eastern coastal fynbos.

Chapter 6 synthesises and articulates the findings of the other chapters into ecological thresholds that can be used to guide the management of fire in eastern coastal fynbos. It furthermore makes recommendations for a fire management strategy for the GRNP, and suggests future research and monitoring priorities.

The chapters were all written as independent papers for different journals, necessitating some replication and non-uniform formatting. Despite this independence, each Chapter is a contribution to the central theme of the thesis. The publication status and authors of each Chapter are indicated on its title page.

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CHAPTER 1 – Past approaches and future challenges to the management of fire and invasive alien plants in the new Garden Route National Park

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Abstract

The recently established Garden Route National Park (GRNP) along the Cape south coast of South Africa occurs in a landscape where indigenous forests, fire-prone fynbos shrublands and fire-sensitive plantations of alien invasive trees are interspersed. We used the area as a case study in the challenges facing conservation managers in the achievement of biodiversity goals in a fire-prone environment. We explored the context within which fire management was practiced during the past century by interviewing former catchment managers and reviewing forestry and catchment management policies. Mountain fynbos adjacent to plantations was subjected to burning regimes aimed at the protection of commercial timber resources rather than the preservation of fynbos biodiversity. Prescribed burning of fynbos adjacent to the plantations was typically done in multiple belt systems at rotations of *c.* 4-8 years during spring, summer and autumn, to avoid the winter berg wind season. Such short-rotation and low intensity fires favour resprouting graminoids over slow-maturing reseeders, and likely account for compositional impoverishment observed in fynbos near plantations. Current and future challenges faced by the GRNP include (i) conflicting fire management requirements for plantation safety *vs.* fynbos conservation; (ii) continual invasion of fynbos by fire-propagated alien pines sourced from plantations; (iii) inadequate resources to redress the 'invasion debt' caused by the socioeconomic legacy and past management neglect; and (iv) fragmentation of land use between conservation and forestry threatening the sustainability of the region at large. We provide recommendations for management actions and research priorities to address these challenges.

Keywords: alien invasive plants, fynbos, mountain catchment, *Pinus* species, plantation forestry, protected area

Introduction

Fire has been a key process and evolutionary force shaping plant traits and vegetation communities across the globe for much of its history[1,2]. It has been the most ubiquitous terrestrial disturbance, surpassed more recently only by human transformation of the landscape[3]. Anthropogenic changes in land use have in turn resulted in modifications in the way fire occurs in space and time[1], along with changes in our perceptions of fire and demands placed on land management agencies to protect lives and property[4,5,6].

In the exceptionally diverse[7] and threatened[8] Mediterranean-climate (summer drought, winter rain) biotas of the world[9], fire is the most important ecological disturbance factor and predates humans in these ecosystems[2,10]. Mediterranean floras have evolved specialised post-fire persistence traits, which are sensitive to the specifics of fire regimes, such as seed banking in the soil or canopy, resprouting, and fire-stimulated flowering and germination[9,11]. Fire is instrumental in maintaining diversity in the fynbos of the Cape Floral Kingdom (CFK) of South Africa[12], and may be considered the most important fynbos management practice, being both a key ecological factor and a practical tool for resource manipulation.

The fire ecology of fynbos was well researched from the early 1970s and by the 1990s fairly detailed fire management prescriptions were available[13,14,15]. However, much emphasis was on the western, strictly winter-rainfall part of the CFK[12,16] and the inland arid mountains[17,18,19] whereas the eastern coastal part of the CFK has been neglected. The climate of the latter is less seasonal (rainfall is bi-modal[20,21]) and species' phenology[22] and possibly plant growth and maturation rates differ accordingly, with implications for the management of fire regimes.

Fuel-reduction burning in fynbos (as in southeastern Australia[23]) largely developed from the early 1900s in response to the need to protect commercial timber resources. Early fire legislation has hence been embedded in Forestry Acts[24,25]. Fire management practices aimed at hazard reduction are often in conflict with ecological objectives[6,23]. Simple management compromises intended to reconcile conflicting objectives may ultimately not achieve either hazard reduction or biodiversity conservation[23]. Therefore, management agencies have to set very clear and realistic objectives to determine the most appropriate management practices for each particular area[24,26]. In the fynbos, as elsewhere, invasion by fire-adapted plants can complicate fire management. Invasion of fynbos ecosystems by invasive trees and shrubs, and notably by pines, is one of the largest threats to conservation[15]. These invasive pines originate from commercial plantations that have been established throughout the CFK, and they often exacerbate the potential negative effects of both altered fire regimes and invasive species[1,10,15].

Improved understanding of fire ecology is becoming increasingly important as climates change, protected area networks expand, pressure from alien invasive biota increases, the wildland-urban interface enlarges, and demands to manage fuel loads of natural habitat for asset protection grow[4,15,27,28]. Where new protected areas are established, systems are likely to be poorly researched and management prescriptions may have to be made in the absence of a clear understanding of ecosystem processes and responses. Recent additions to protected areas are often not in pristine condition and are affected by historic management that has implications for management into the future.

The recent establishment of the Garden Route National Park (GRNP; *c.* 130 000 ha[29]) along the Cape south coast of South Africa involved the amalgamation of parcels of land which have in the past been variously managed for water conservation, biodiversity conservation, plantation forestry using alien invasive species, and the harvesting of natural resources, mainly timber from indigenous forests[30]. We use the fynbos areas of the GRNP as a case study for exploring the challenges facing conservation managers in the achievement of biodiversity goals in a fire-prone environment. Our analysis was underpinned by the following issues. Firstly, the GRNP is located within the southeastern coastal part of the CFK where fynbos fire ecology is inadequately understood. Secondly, it is a new park, and a reconstruction and critical review of past fire management approaches is needed. Thirdly, the institutional history and landscape context of the park pose particular difficulties that need to be addressed by the fire management policy, including high levels of invasion by alien trees, and significant pressure from the adjacent plantation industry to reduce wildfire hazard. Being a new park, there is still opportunity to influence the management policy and practice in the interest of biodiversity conservation.

In this paper we present the environmental and institutional context within which historical catchment management practices in the region of the GRNP evolved, and we consider how the adoption of a new mandate, with conservation as its central goal, will require changes to research priorities, management actions and land use practices.

The Garden Route mountain catchments

Biophysical environment

The study area is broadly defined as the southern slopes of the Outeniqua Mountains east of the Touw River, and the southern slopes of the Tsitsikamma Mountains (22.59°E – 24.26°E; hereafter collectively referred to as the Garden Route coastal mountains, GRCMs), with emphasis on those areas recently proclaimed as part of the GRNP[29] (Fig. 1). The GRCMs form part of the Cape Fold

Belt Mountains[31] and run in a west-east direction parallel to the coast[32]. The highest peaks in the eastern Outeniqua and Tsitsikamma Mountains are 1469 m and 1675 m, respectively. Deeply incised remnants of an early Cenozoic peneplain form the coastal foreland south of these mountains[32]. The Table Mountain Group rocks of the Cape Supergroup are the main mountain-forming substrata[31]. Acidic (pH 3.3-5.5) lithosol soils predominate, i.e. moderately deep, dark coloured loamy sands, generally poor in bases, phosphorus and nitrogen[33,34].

Owing to maritime influence, the climate of the GRCMs is relatively temperate. In contrast to the strictly Mediterranean climate in the western part of the CFK, rain falls throughout the year[21,22]. Rainfall peaks in spring and autumn, winter months are the driest, and the proportion of summer rain increases eastwards[35]. Annual rainfall increases eastwards, the mean for the Outeniqua and Tsitsikamma Mountains being 820 and 1078 mm, respectively[34,36]. Rain is mostly cyclonic and orographic with occasional thunderstorms[34]. Lightning occurs throughout the year and at a density of <2 flashes/km^2/year [32]. Temperatures are mild with mean minima and maxima ranging from 7°C and 19°C in June to 15°C and 26°C in January[34,36]. Southeasterly winds prevail in summer and north to northwesterly winds (hot dry berg winds) in autumn and winter, while southwesterly winds occur throughout the year[34,36]. Berg wind conditions in particular increase the fire potential[19] and are associated with higher incidence, severity and size of fires[21].

The coastal slopes of the eastern-Outeniquas contribute run-off to various rivers, some of which support estuarine systems of national and international importance[37] (Fig. 1). The coastal slopes of the Tsitsikammas are drained by short rivers flowing through deep gorges incised through the coastal plain[36]. In 1986, the water draining from the state-managed GRCMs was estimated to be 1046 million m^3 per annum, then valued at R178 billion[30]. Sustained yields of water from these catchments are vital to agriculture and coastal towns in the area[38], a dependency that has been highlighted by recent severe droughts[39].

The vegetation of the area comprises fire-prone and fire-dependant fynbos shrublands, interspersed with lesser areas of fire-free and fire-resistant Afrotemperate forest. The fynbos mostly occurs between the mountain crests and the belt of indigenous forest on the coastal platform at the foot slopes of the mountains[32] (Fig. 1). South Outeniqua Sandstone Fynbos and Tsitsikamma Sandstone Fynbos occur to the west and east of the Keurbooms River, respectively[33]. Both these vegetation types are tall, medium-dense proteoid shrublands, with medium-tall, dense ericoid-leaved shrub understoreys and a prominent restioid component. Ericaceous fynbos dominates at high altitudes, grassy fynbos at lower altitudes, and forest in fire refugia[32,33].

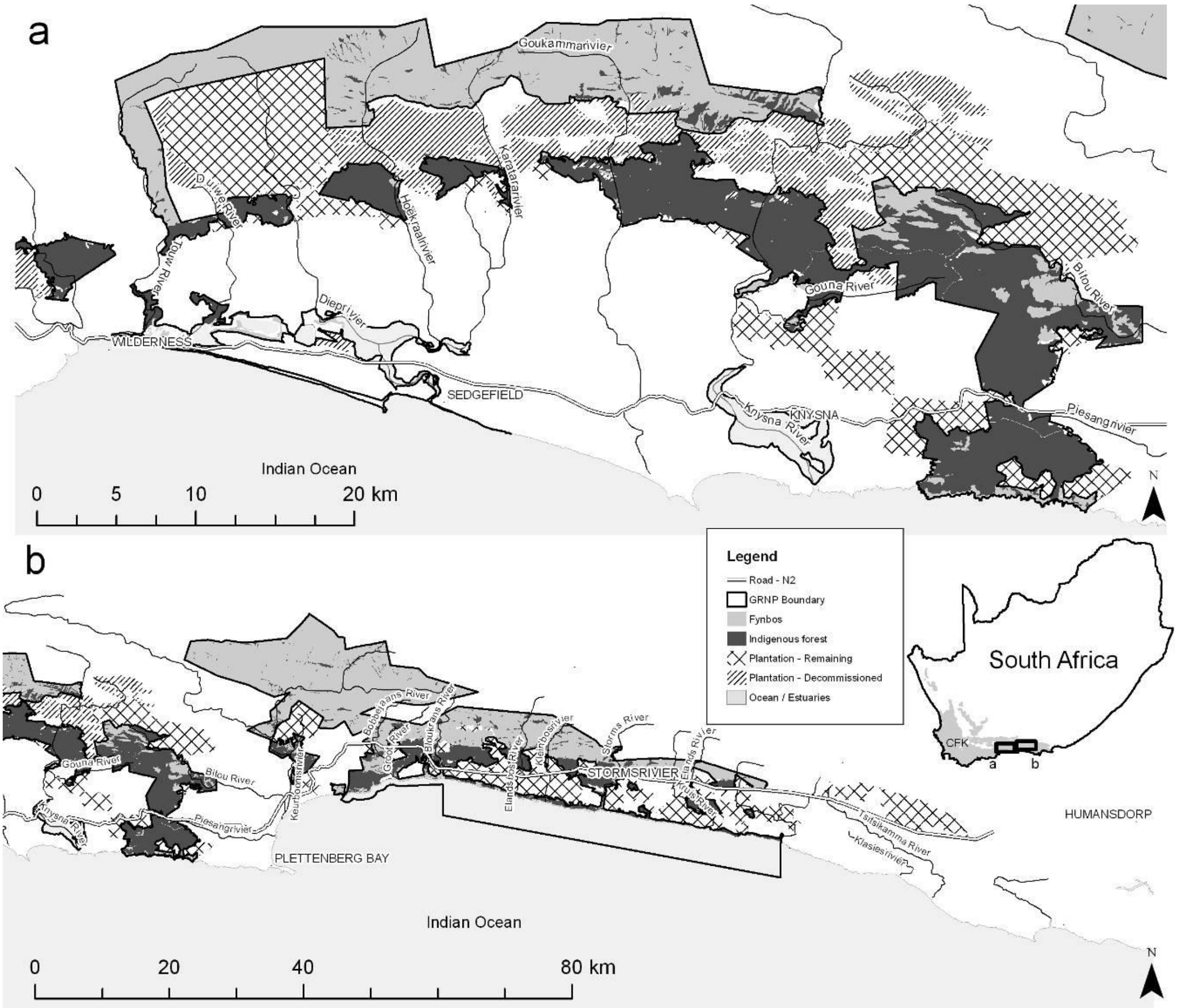

Figure 1: Map of the study area showing the distribution of fynbos, indigenous forest and decommissioning plantations (to be clearfelled and rehabilitated) within the boundaries of the Garden Route National Park (GRNP). The shown distribution of remaining plantations, on state land and managed by MTO Forestry, follows the recommendations for the partial reversal of the plantation decommissioning strategy. The map is split into (a) the Outeniqua region, in forestry terms known as the Southern Cape, and (b) the Tsitsikamma region.

Plantations of alien pine (*Pinus pinaster* Aiton and *P. radiata* D.Don) trees have fragmented and replaced large tracts of fynbos, mostly along the lower and mid-mountain slopes (Fig. 1). The plantations of Bergplaas, Karatara and Buffelsnek in the Outeniquas, and Kromrivier in the Tsitsikammas, reach deeper into the upper catchments. The extant fynbos of the GRCMs thus typically abuts the commercial plantations to the south. Depending on the topography and altitudinal reach of the plantations, the fynbos forms a belt of 2-6 km wide, generally narrower along the Outeniquas than along the Tsitsikammas (Fig. 1). Considerable tracts of unprofitable plantations in the Outeniqua Mountains are in the process of being phased out, scheduled for rehabilitation to fynbos and incorporation into the GRNP during the next decade[40,41]. The landscape setting of the GRNP is thus a mosaic of fynbos and forest among remaining and decommissioned plantations, most of which were formerly owned and managed by the state (extent of these land groupings is indicated in Table 1; Fig. 1). The mix of fynbos and fire-prone pine plantations in the landscape has led to two major management problems: (i) the need to protect the plantations from fire, which kills the adult trees, and (ii) invasions by fire-adapted pines, where fire drives the rapid spread and proliferation of these species[42] (Fig. 2).

Table 1: Extent of Fynbos and Forest Biomes within the Garden Route National Park (GRNP) and extent of former state-owned plantations, now managed by MTO Forestry. Figures are shown for the Outeniqua (east of the Touw River) and Tsitsikamma Mountains respectively (33.8°S, 22.6°E to 34.0°S 24.3°E) and rounded to the nearest thousand hectares.

Vegetation type	Outeniqua (ha)	Tsitsikamma (ha)	Total area (ha)
Fynbos vegetation	17 000	53 000	70 000
Proportion of fynbos vegetation where no active management was done between 1988 and 2006 ('no-man's land')	14 000	21 000	35 000
Indigenous forest	26 000	17 000	43 000
Plantations – remaining	22 000	25 000	47 000
Plantations – decommissioned	17 000	0	17 000

Institutional context

Since the early 1900s, water and soil conservation have been central to the management (and acquisition in places) by the South African state of fynbos mountain catchments, including the approach to fire management in these areas[15,24,30]. However, plantation-based timber production has from early on been recognised as a major land use and catchment management consideration in the GRCMs[30], perhaps more so than in other fynbos catchments. The first state plantations in the area were established in 1883 near the town of Knysna[24,43]. The state has since then, until the early 1990s, actively encouraged and subsidised the industry as a strategic move to provide for the country's demand for timber and to alleviate pressure on the limited and over exploited indigenous forests[43,44]. Considerable expansion occurred in response to timber shortages experienced during the First and Second World Wars. Afforestation was further promoted as a means to relieve poverty among unemployed white people (1918-1938) and Italian prisoners of the Second World War[24,43,44]. 'Off-site planting' resulted from the application of poverty relief labour, whereby some of the areas planted were unsuitable for commercial plantation forestry[44].

The former Cape Province (including the present Western- and Eastern Cape Provinces) was the only province where state plantations covered more area (three times more) than private plantations[45]. The state was thus the main player in the forestry industry in the Cape Province and largely focussed on growing pines[46].

The generally-held notion at the turn of the 19th century was that forests increase rainfall[24]. Afforestation was accordingly seen as a beneficial land use in mountain catchments which otherwise had limited economic potential[24]. However, droughts, public complaints about reductions in stream flow, and alleged desertification of South Africa during the first half of the 20th century prompted the Department of Forestry to undertake hydrological research in mountain catchments[24,47]. This exposed the high water consumption of plantation trees[48], which led to the introduction in 1972 of an afforestation permit system to regulate new afforestation according to impacts on catchment runoff[43,49]. Although it was by then recognised that afforestation competes with the conservation of water supplies and floral diversity, plantation forestry in the GRCMs was justified because 'surplus water [is] presently still flowing into the sea from the humid coastal mountain ranges' [30].

For most of the 20th century, the state-owned mountain catchments of the Outeniquas and Tsitsikammas were managed by the national Department of Forestry (DoF) in its various forms[38,45] – either an independent department, or a branch of the national departments of Environment Affairs or Water Affairs[25,50] (for simplicity, we henceforth refer to DoF). The state managed a combination of fynbos, indigenous forests and exotic timber plantations on state land. During the mid 1970s, DoF adopted a formal policy of 'multiple use', which included timber production (from both indigenous forests and plantations), fire management and alien invasive plant control in the catchments, soil and water conservation, and recreation[24,25,30,51]. The same labour force that planted and tended pine trees also cleared alien invasive plants and conducted prescribed fires. The managers of these forestry estates were compelled to consider all aspects of this 'multiple use'. However, governmental restructuring of DoF during the mid 1980s, separated plantation forestry (a commercial undertaking, earmarked for privatisation), catchment fynbos and indigenous forest management (conservation undertakings), and research[25,49,52,53]. The restructuring divided the land into (i) plantations which were transferred to the South African Forestry Company Limited (SAFCOL), (ii) fynbos areas that had not been afforested to be devolved to provincial nature conservation agencies, (iii) indigenous forests which remained under the jurisdiction of DoF, and (iv) research which went to the Council for Scientific and Industrial Research (CSIR)[49,54].

Following restructuring, large tracts of mountain fynbos within the former Cape Province were transferred to Cape Nature Conservation (which later split into CapeNature in the Western Cape Province and Eastern Cape Parks and Tourism Agency in the Eastern Cape Province), accompanied by reductions in state funding of conservation management functions. However, DoF retained responsibility for large areas of the state-owned catchments in the GRCMs to the north of plantations for the purposes of fire protection[53,55]. Prior to the restructuring, DoF largely achieved the fundamental principles of catchment management, i.e. nature conservation[51] and sustainable water delivery by applying appropriate fire and alien plant control regimes. With the commercialisation of state-owned timber plantations and the establishment of SAFCOL (owned by the Department of Public Enterprises) in 1993, the focus shifted to explicitly growing trees for profit[44,54]. Nationally, privatisation of SAFCOL was largely finalised by 2002, although a buyer could not be found for the Western and Southern Cape (including the study area) plantations, packaged as Mountain To Ocean (MTO) Forestry[56]. MTO Forestry was only sold to Cape Timber Resources in 2004, based on a 70 year land-lease agreement with DoF[54,56]. However, SAFCOL retained a 25% share on behalf of the government in all privatised plantations[41]. The costly burden of catchment management (and in particular fire and alien plant management), which yields no financial return on investment, was not the primary mandate of the plantation companies. Likewise DoF, the landowner, has neglected to assume or delegate management responsibility for those areas originally retained for the purposes of fire protection of the plantations[55]. In the process, large tracts of unafforested fynbos in the GRMCs were left without a custodian and became known as the 'no-man's land' [53]. Management of the GRMCs languished for almost 20 years[44]. Only recently has the management of this 'no-man's land' been assigned to South African National Parks (SANParks) with the incorporation of the formerly DoF-managed forests and fynbos into the new Garden Route National Park[29,41].

In 2000, the South African government decided to phase out plantation forestry in much of the Western Cape Province, including the Outeniqua region, as these plantations were economically and environmentally unsustainable[40,41,54]. Approximately 45 000 hectares of plantations (most of which were in the Outeniqua region) were to be felled over a 20-year period and converted to other land uses[41,54,56,57]. However, this decision was partly reversed in 2006 (Forestry South Africa 2005) with approximately half the area recommissioned for plantation forestry (Table 1; Stehle T 2010, pers. comm., November 25) on account of changing markets and the national demand for timber exceeding the growth of plantations[41]. The decision was based on the presumption that productivity of the plantations in the Outeniqua region could be substantially increased by appropriate silviculture, site-specific soil preparation and continuous fertilisation[58].

History of catchment and fire management

The general approach to fire management in fynbos mountain catchments during the 20th century is presented elsewhere[15,30]. Here we specifically focus on the approach to catchment and fire management in the GRCMs during the past century, as informed by our review of historical policy and management documentation and interviews with past and current land managers (Table 2).

Prescribed burning of mountain fynbos became fully accepted as a management practice during the 1970s to promote water, soil and biodiversity conservation[30]. The general approach to fire management was based on, and continually influenced by, sound ecological principles emerging from a productive fynbos research programme at the time[14,15]. However, and in contrast to policies elsewhere in the fynbos, nature conservation was the primary objective only in parts of state catchments zoned as nature reserves. Fire protection of plantations was the primary objective in vast areas of fynbos in the GRCMs to the north of the plantations (Table 2), where high-hazard, berg wind-driven fires characteristically originated.

For the conservation of fynbos, moderate to high-intensity fires at 10-20 year intervals are optimal[15]. Conversely, for plantation protection purposes, it is desirable to burn adjacent fynbos vegetation under cool, safe conditions as soon as there is sufficient fuel available to sustain a fire, usually at vegetation ages of three to eight years, depending on site characteristics. Various systems have been proposed and/or pursued in the GRCMs in an attempt to reconcile this fundamental conflict of interest[23]. The most common approach has been the so-called double- (or triple-) belt system (Table 2). Accordingly, fynbos to the north of the plantations was divided into two to three parallel belts, each burnt at a fixed rotation, e.g. eight years but four years apart. The vegetation age in one of the belts would consequently always be four years or less, thereby reducing the likelihood of fires spreading from catchment fynbos to the plantations. In some cases, plantation managers aimed to burn the fynbos adjacent to the plantations as soon as it could burn.

Table 2: Chronological account of the approach to fire management in the fynbos of the Garden Route coastal mountains (GRCMs), based on interviews with former catchment managers and a review of catchment management policies of the national Department of Forestry (DoF). 'Mountain belts' (normally >100 m wide) refer to the fynbos north of the plantations and south of the main mountain crests where fire management was generally geared towards protection of the plantations, and where fuel was regularly reduced by prescribed burning in order to reduce the risk and severity of fires. 'Fire breaks' refer to narrower strips (normally <100 m wide) that were burnt, hoed, or brush cut (i.e. virtually devoid of fuel) along the boundaries of the plantations to prevent the spread of fire into the plantations, or to serve as access points and safety zones during fire fighting. The fire protection measures proposed/applied sometimes varied in different areas, accounting for ostensibly conflicting measures listed here. Burning frequency, season and intensity indicated are those deemed appropriate for prescribed burning operations.

Period	General approach	Measures proposed and/or implemented to protect plantations	Fire return periods	Fire season and intensity
1920s	Deemed desirable that catchments be acquired and protected by the State. Contemplated a policy of fire exclusion from Cape mountains (for water preservation), except in the vicinity of afforested areas where burning was to be carried out to reduce fire risk to plantations.	Mountain vegetation adjacent to plantations (often on private land) to be burnt as widely (100-200 m or more) and frequently as possible and grazing permits to be issued freely. Vegetation in exterior fire breaks (50-100 m wide) to be slashed such that it could be burnt at very young age. Gum (*Eucalyptus* spp.) belts (producing little litter) to be planted on ridges as fire breaks. Communal land adjacent to plantations to be ploughed and planted with kikuyu (*Pennisetum clandestinum*) grass to make it fire proof.	Mountain fynbos adjacent to plantations: as frequently as possible.	Forestry approach: summer is safest for prescribed burning. Agriculture approach: winter is best to promote grazing.
1930s to mid-1940s	Exclusion of all fires from catchment fynbos except for prescribed burning of mountain belts to protect plantations. Safety of plantations took precedence over fynbos conservation.	A series of fire breaks along northern boundary of plantations and in places along the mountain crest. Mountain belts (each 300-500 m wide, often on private land) to be burnt (not ploughed) in double-/triple-belt system where and whenever possible. Limited burning of fynbos deeper into catchments, but reported that belt burning often spread upslope to the first crest. Grazing permits issued freely.	Fire breaks and mountain belts: whenever possible.	Mountain belts: spring and early summer. Burn during warmest, driest time of day to obtain clean burn. Fire danger (berg wind) season to be avoided: winter (May-August).

Period	General approach	Measures proposed and/or implemented to protect plantations	Fire return periods	Fire season and intensity
mid-1940s to end-1950s	Fire no longer had to be excluded from fynbos. Adopted the principle of prescribed burning of more than just fire belts on a rotational basis to create a mosaic of veld ages within catchment.	State-managed catchments north of plantations throughout GRCMs to be burnt as soon as they could burn. Double-/triple-belt fire breaks along N boundary of plantations and along mountain crest, and the area in-between divided into one or two (west-east) parallel belts (each *c.* 1-2 km wide). North-south cut-offs subdivided these mountain belts into blocks, with the aim to create a mosaic of veld ages. In some areas short rotation burning of belts along the northern slopes was additionally prescribed (e.g. at Witelsbos). Private land adjacent to plantations to be burnt as often as possible.	Mountain belts: 5-6 yrs, but no less than 3 yrs. Fynbos not immediately adjacent to plantations: 10 yrs.	Spring and early summer (September-December).
1960 to end-1970s	Prescribed burning of mountain belts and where necessary, blocks.	Double mountain belt along southern slopes up to the crest (belts each 300-500 m wide). Fynbos close to plantations on private and state land to be 'tamed' by burning at 7-10 yr rotation. Fire breaks on northern boundaries of plantations were to be ploughed or hoed rather than burnt. Reported that *c.* 500 km of fire breaks/-belts were burnt annually in the catchments of the Southern Cape. All lightning fires and unplanned anthropogenic fires were to be extinguished, whether or not these threatened plantations. Insurance of private plantations against fire damage became the norm[41].	Mountain belts: 5-6 yrs (3 yrs apart). Other fynbos: 7-10 yrs.	Prescribed burning season: (end) October-March. Fire danger season: April-September. Agriculture recommended winter burning to promote grazing value of vegetation.

Period	General approach	Measures proposed and/or implemented to protect plantations	Fire return periods	Fire season and intensity
early-1980s	Fire protection of plantations considered the primary objective in GRCMs. Fynbos conservation the primary objective only in designated nature reserves (i.e. Millwood Nature Reserve in the Outeniquas). Block burning was common practice (mountains regarded as 'tamed').	Well-maintained double-/triple-belt systems (belts each 100-1000 m wide). In places, an additional single- or double-belt system north of crest on private land. Significant areas burnt in block burns. State plantations were not insured against fire damage.	Mountain belts: 6-8 yrs (2-4 yrs apart). Block burning: 8-15 yrs. Increasing motivation for block burn rotations of ≥12 yrs. 12 yr rotation triple-belt system (4 yrs apart) proposed to reconcile fire protection and fynbos conservation objectives.	Block burning: summer, and not from June/July-September/November as this was regarded as detrimental to reseeding plants. Fire break burning: September-November after good rains. Prescribed burning to be done under warm dry conditions but not with dropping air pressure.
mid-1980s to mid-1990s	Plantation and conservation functions split within DoF, the former subsequently operated on a Trading Account. Plantation management was instructed to cut down on fire protection expenses (i.e. external fire breaks/-belts), as this was deemed the responsibility of another division within DoF. Nationally, catchments were transferred to provincial conservation authorities, but GRCMs largely remained with DoF (except for Formosa and Millwood Nature Reserves).	Plantation management wanted prescribed burning of mountain belts (double-belt system with belts each 200 m wide) to continue as before, but neglect commenced in what became the 'no-man's land' and implementation fell behind. A single belt / fire break of 200 m wide was maintained along the northern boundary of some plantations. Block burning ceased during the early 1990s. All lightning fires were to be extinguished. State plantations were not insured against fire damage.	Mountain belts: 8 yrs (4 yrs apart).	Belt burning: October/November-March. Block burning: January-April. Fire danger season: April-October. Extreme danger: June-August.

Period	General approach	Measures proposed and/or implemented to protect plantations	Fire return periods	Fire season and intensity
mid-1990s to early-2000s	Complete separation of catchment and plantation management with the establishment of SAFCOL. Block burning in catchments largely ceased as funding declined. Conservation agencies adopted natural fire zone management in some fynbos areas, while neglect prevailed in the no-man-s land. Alien invasive plant clearing regarded to be a Working for Water function.	Mountain belt system replaced with *c.* 50 m wide fire breaks (tracer belt and brushcut) along northern boundary of plantations. Plantation management (what became SAFCOL) wanted the fynbos north of the plantations to be burnt at 8-10 year rotations as before, but with institutional separation, catchment management no longer had an interest in this expensive undertaking without direct benefits. To cut down on expenses, SAFCOL largely reduced/stopped block and belt burning, as well as post-harvesting burning within plantations to suppress weedy growth of coral fern (*Gleichenia polypodioides*). SAFCOL plantations were insured against fire damage.	Mountain fynbos serving to protect plantations: 8-10 yrs.	Prescribed burning: October-November and February-March.
early-2000s to date	SAFCOL plantations sold to MTO (DoF remained the landowner), and management of a large portion of GRCMs fynbos transferred to SANParks. Conflict of interest between requirements of plantation industry for short rotation burning of fynbos adjacent to plantations, and ecological objectives (longer fire rotations and allowing natural fires) of protected areas. Limited resources available to SANParks to rectify fire and invader plant management after 20 years' neglect.	MTO intended to reinstate fire break and block burning, with 10-30 m wide fire breaks (slashed/hoed/burnt) along northern boundaries of plantations, while larger mountain belts would revert back to fynbos conservation management. MTO and SANParks agreed on jointly implementing prescribed burning in high fire danger zones (divided into double-belt) within Tsitsikammas. History of catchment neglect (particularly the extent of invader plants) makes implementation of prescribed burning under conditions of acceptable fire danger largely unachievable in these zones. Fire management approach in remote parts of SANParks-managed catchment is that of adaptive interference (Seydack 1992), with lightning regarded as the main source of ignition and interventions limited to where/when necessary.	High fire danger zones in Tsitsikammas: 8 yrs (4 yrs apart); not yet established for Outeniquas. Remote catchment fynbos: 10-25 yrs. Fynbos within plantations: 12-15 yrs.	Prescribed burning by plantation managers: October-November and February-March (i.e. no berg winds and less erratic weather conditions). Prescribed burning by protected area managers: November-April, but may be broadened[22] pending local research.

Period	General approach	Measures proposed and/or implemented to protect plantations	Fire return periods	Fire season and intensity
		MTO plantations are not insured against fire damage, only public liability coverage. MTO sued the land owner (DoF) and neighbouring catchment management agencies (SANParks and Eastern Cape Parks Board) for plantation losses suffered during the large 2005 fire in the Tsitsikamma Mountains.		

It is clear that fire management in the GRCMs has, since the establishment of the plantations until the early 1990s, been primarily aimed at the protection of commercial timber resources (Table 2). Although it is unlikely that catchment managers managed to execute prescribed burning every time and everywhere as planned, it seems reasonable to assume that large parts of the GRCMs' fynbos have at times been burnt at shorter fire return intervals, and lower intensities, than those deemed ecologically desirable for fynbos conservation. Both frequent and low intensity fires in fynbos and other Mediterranean-climate shrublands favour resprouters over slow-maturing reseeders[59,60]. This may account for the dominance of graminoid sprouters and paucity of slow-maturing reseeding shrubs of the Proteaceae family in parts of the GRCMs, particularly in areas near plantations (Kraaij T, pers. obs.). With regard to fire season, prescribed burning has mostly been carried out during spring, summer and early autumn (October to April) in order to avoid the winter berg wind season (May to September) associated with conditions of high fire danger and an increased risk of uncontrollable fires (Table 2).

The conflict of interest in terms of fire management (fire return periods in particular) in the GRCMs has been brought into sharp focus by the separation of plantation and catchment management functions within DoF, and later the privatisation of plantations and handover of catchment management to conservation agencies. Catchment management has further been complicated, ecologically and economically, by the extensive infestations of invasive alien plant species (particularly *Pinus* spp.) almost exclusively sourced from adjacent plantations, with hardly any invasive alien plant control carried out in the 'no-man's land' in almost two decades[61] (Fig. 2).

Management challenges

Fire management

Sound ecological management of fires in the study area is constrained by various factors. Repeated institutional disruptions, i.e. transfers of DoF between different state departments and changing land management agencies, resulted in poor record preservation and data continuity. The history of fires in the study area has therefore been inadequately documented. Fynbos fire ecology in the southeastern CFK is poorly understood in terms of appropriate fire season and return interval[15,22]. Moreover, fundamental conflict exists between fire intervals required for the reduction of fire hazard to commercial timber plantations, and those deemed necessary for the conservation of fynbos diversity[6,23].

Negative feedback mechanisms between fire, alien invasive trees and water resources threaten the achievement of the goals of sustained yields of water[48] from the GRCMs, which are important catchment areas[53]. Fire behaviour and ease of access for the purposes of prescribed burns or fire fighting are negatively affected by the invasion of fynbos by alien shrubs and trees. The invaders increase fuel loads and therefore, fire intensity, particularly under extreme conditions[62]. Extreme fire intensities increase the risk to infrastructure and assets (such as plantations) and fire fighters, and detrimentally affect post-fire recovery of fynbos, soil and water conservation[63,64,65]. Alien pines are spread and proliferated by fire[42], which in turn exacerbates their detrimental impacts. Areas in close proximity to plantations, where fire safety measures in the GRCMs ought to be focussed, are often the worst invaded, thereby rendering prescribed burning and fire fighting operations impossible. Pines had invaded 54% of the catchment of the Keurbooms River in 1999 to some degree, causing an estimated 22% reduction in river flow[66]. It was further estimated that in the absence of management intervention, the invasions could potentially occupy 77% of the catchment by 2025, with a projected flow reduction of 95% [66].

Historical legacy

Past neglect of fire and alien plant management in large parts of the GRCMs has left current conservation agencies financially incapable of correcting the situation given normal operational funding, and thus unable to fulfil their primary mandate of conserving biodiversity. Previous joint government ownership and management of plantations and surrounding catchment fynbos fostered the expectation that contemporary fynbos managers should provide protection from fire to adjacent commercial plantations – at a considerable cost to the former. This political and institutional legacy yielded a plantation industry which is commercially and environmentally unsustainable[44,56] in the absence of subsidisation in the form of fire safety management and alien plant control on adjacent land. Even with government subsidisation (prior to the 1990s), and without taking on the costly burden of catchment management (during the period of neglect of the 'no-man's land'), SAFCOL plantations in the Western Cape Province operated at a financial loss[44]. This is why a buyer could initially not be found at the time of privatisation[56] and why the decision to phase out plantation forestry in the area was taken[40,41,44,54].

Sustainable management at landscape scale

Sustainable management of the current conservation-plantation matrix will not be achievable in the study area if the continual invasion of the surrounding landscape by self-sown timber species is not controlled[53]. The current environmental and social certification system (the Forestry Stewardship Council, FSC), adhered to by the plantation industry[67] inadequately appraises environmental accountability (i.e. spread of invasive trees and their impact on water resources) beyond the borders of the plantation management unit. Indeed, in 2004, environmental NGOs requested that a moratorium be placed on further certification of plantations worldwide, which led to a review of standards for FSC certification of plantations[41,68]. The development of new standards and the implementation of trial audits have not resolved this issue, which remains contentious among FSC stakeholder groups. Whether plantation forestry can be undertaken sustainably in South Africa and whether it should be certified remains an open question[67]. Biological control, which may be seen as the only viable option for the control of vast infestations of invasive pines in remote catchments, continues to be opposed by the plantation industry[42,69,70]. Legislation pertaining to the control of alien invasive plants is not enforced, while a discrepancy between the capacities to enforce legislation pertaining to fire risk management *vs.* invasive plant control[70] intensifies the conflict between the conservation and plantation sectors. This is evident from substantial legal claims instituted against conservation authorities for fire damage to plantations in recent years (Table 2). Finally, the sustainability of both sectors is additionally compromised by government's decision to partially reverse the plantation decommissioning programme[58]. The outcome will be a more fragmented landscape where neither plantations nor protected areas can be suitably consolidated or coherently managed in terms of fire, invasive plants or general operations[44] (Stehle T 2010, pers. comm., November 25).

Way forward

Research priorities

The challenges associated with managing the new national park are substantial, and knowledge and solutions are not always available, indicating the need for further research. Firstly, understanding of the historical fire regime in the area and how it has changed during the past century[71] has to be improved through the creation and analysis of a database of historical fire records[72]. Ongoing accurate mapping of future fires is furthermore necessary to serve as a basis for the design of natural experiments and fire management decisions[28]. Secondly, the ecological requirements of eastern coastal CFK fynbos in terms of fire season and minimum fire return intervals need to be determined. To this end, post-fire recruitment success and youth periods of slow-maturing reseeding species (e.g. the Proteaceae[16,18]) should be studied. Similarly, the youth periods of invasive pine species need to be established under local conditions. In combination, these should inform fire management guidelines aimed at facilitating fynbos conservation and invasive pine control. It should furthermore inform thresholds[73] within which fire managers can attempt to resolve the conflicting demands of fire hazard reduction and biodiversity conservation. Thirdly, a legal review should be conducted to consider the practicalities of implementing fire legislation in the face of conflicting land management objectives (fire risk *vs.* biodiversity conservation). The respective responsibilities applicable to the conservation and commercial forestry sectors in terms of fire and invader plant legislation need to be clarified. This should facilitate cross-cutting compliance and cooperation without the need for costly legal action. Lastly, resource economics research should further explore alternative funding for alien plant clearing initiatives in watersheds. Approaches based on payment for ecosystem services[38] should be expanded, targeting major water users, such as agricultural industries, municipalities and the tourism industry. Cost-benefit analyses need to compare the environmental and socioeconomic advantages of invasive plant clearing *vs.* desalinisation of sea water as different means to secure water supply to water-stressed coastal towns[39] (Preston G 2010, pers. comm., October 1).

Management interventions to be considered

Fire management

Land owners and managers in the area need to realise that fynbos and plantations cannot be fire-proofed[71]. It has been shown for fire-prone shrublands and forests across the globe that large fires are not dependent on a build-up of fuel, and therefore frequent burning to reduce fuel loads will not necessarily reduce the risk of runaway wildfires[27,74,75,76]. The combination of fire danger restrictions and financial constraints furthermore makes large-scale prescribed burning of catchment vegetation unattainable[27]. The most effective strategy for facilitating fire safety where necessary is to focus effort on (limited) strategic locations. A legal review should furthermore clarify the respective responsibilities of the conservation and forestry sectors under current fire legislation. Official agreements between neighbouring land managing agencies should clearly stipulate fire management protocols, and should be formalised within regional Fire Protection Agencies.

Invasive plant control

The timber industry should recognise its legal responsibility to control the spread of invasive alien trees from their plantations in terms of the Conservation of Agricultural Resources Act[42]. The South African government has proposed the introduction of a seed pollution levy on the forestry sector in 2005 under the National Environmental Management Act: Biodiversity Act, which has been vehemently opposed by the industry on account of its potential economic impact and it being perceived as discriminatory[77]. Plantation forestry in the Cape has in the past externalised its environmental costs, and continues to do so by not taking sufficient responsibility for invasive plant clearing beyond plantation borders and by leaving the task to the neighbouring conservation agencies[44]. As the intention of government is now clearly to separate the functions of commercial forestry and conservation, the former has an obligation to the latter to offset these previously-externalised costs, as government has been cautioned to 'not end up subsidising a single business' [44]. Nonetheless, a 'polluter pays' policy remains to be implemented, possibly through the imposition of a levy on timber products[42]. Likewise, the FSC and other certification bodies should consider adopting stricter criteria for the mitigation of the negative effects of invasive trees beyond the borders of forestry estates[42,67]. The best approach to management of invasive alien plants would be to integrate various control methods[35]. Options include (i) manual clearing, (ii) manipulation of disturbance regimes, i.e. fire, (iii) future planting of less invasive species and/or sterile varieties, and (iv) allowing the release of host-specific, seed-attacking biological control organisms for invasive *Pinus* species[42]. Biological control for pines has been considered[78], but, in a highly conservative move, has been abandoned for fears that it could potentially be detrimental to the forest industry[69].

Landscape rationalisation

The invasive pine problem in the GRCMs is an example of 'invasion debt'[79] where the current pattern of invasion primarily reflects the historical socioeconomic and political legacy. Neglect of the 'no-man's land' during the past 20 years further aggravated the invasive plant problem. Government appropriately stated in its White Paper on sustainable forest development in South Africa[52] that 'the costs and benefits of this [the plantation] industry in terms of water resources and the environment in general need to be properly evaluated' and furthermore that 'Government believes that a responsible attitude in forestry would have plantation forests removed from areas where demonstrable environmental damage has been done'. This implies three distinct undertakings by the state: (i) Application of sound economic and environmental standards to the commercial forestry industry (DoF is ultimately responsible to oversee and regulate the industry[25,52]); (ii) Appropriate allocation of resources for the rehabilitation of decommissioned plantations and neighbouring areas damaged by invader plants historically sourced from plantations[38]; and (iii) A review of the decision to reverse the plantation decommissioning strategy[44,58]. A balanced analysis of the full public costs and benefits of the plantations, and their economic and ecological impacts and future risks, have to be considered at landscape scale[54,80].

Land use fragmentation needs rationalisation in the interest of both the plantation and conservation sectors. This was the original intention of DoF with their plantation decommissioning strategy. In the latter, DoF emphasised the link between plantation withdrawal and the transfer of other conservation land to SANParks, and required that these processes be well coordinated[57].

Figure 2: A landscape mosaic characteristic of the Tsitsikamma region, with dairy pastures in the foreground, a pine plantation in the middle ground, and mountain fynbos invaded by pine trees in the background. The lucrative diary industry and coastal towns in the region are dependent on water emanating from the pine covered catchments.

Conclusion

Owing to successive institutional disruptions in the study area, the collation of fire management related policies, practices and data has been challenging. Our account constitutes a first qualitative regional history of fire management in the CFK published in the primary literature. Such published accounts will become invaluable where there is a reliance on tacit knowledge, and particularly where institutional memory is rapidly fading. Fire management in the fynbos catchments of the new Garden Route National Park presents considerable challenges that cannot be overcome without addressing the invasive alien plant problem in the area. In the short and medium term, substantial resources will be required to correct the situation left by decades of management neglect. Longer term sustainability of the region necessitates rationalisation of the currently highly fragmented land use with their conflicting requirements.

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CHAPTER 2 – Historical fire regimes in a poorly-understood, fire-prone ecosystem: eastern coastal fynbos

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Abstract

We characterised the historical fire regime (1900–2010) in eastern coastal fynbos shrublands, which occur in a poorly-studied part of the Cape Floral Kingdom (CFK). Natural (lightning-ignited) fires dominated the fire regime. Fire seasonality decreased from west (Outeniqua region) to east (Tsitsikamma region) within the study area, and between the study area and further west in the CFK. This is consistent with a west-east climatic gradient in the CFK, where rainfall is concentrated in winter in the west, and evenly distributed across months in the east. Median fire return intervals (FRIs) (1980–2010) were broadly comparable to other fynbos areas but estimates varied widely depending on whether or not the data were censored (16-26 years and 8-13 years, with and without censoring, respectively). FRIs appeared to be shorter in the Tsitsikamma, where rainfall and plant growth rates are higher, than in the Outeniqua. The total area burnt annually has increased significantly since 1980, correlated with an increase in weather conducive to fires, suggesting that fire regimes may be responding to climate change. Frequent recurrence of very large fires and the virtual absence of vegetation in older post-fire age classes are potential causes for concern for achieving fynbos conservation objectives.

Keywords: fire cause, fire frequency, fire season, fire size, Garden Route National Park, shrublands, South Africa.

Introduction

Fire is an important process in many ecosystems worldwide (Naveh 1975; Bond and van Wilgen 1996; Bond *et al.* 2005), where it shapes the structure and composition of the vegetation (Keeley 1986; van Wilgen *et al.* 1992; Morrison *et al.* 1995). The occurrence of fires over an extended period in a given area is referred to as a fire regime (Gill 1975), described in terms of the frequency, season, intensity and size of fires (Morgan *et al.* 2001; Gill and Allan 2008). Managers of fire-prone ecosystems need to understand the historical fire regimes of the areas that they manage, so that they can better understand how the current vegetation was shaped (Morgan *et al.* 2001; Schuler and McClain 2003), and whether or not they need to intervene in cases where contemporary fire regimes may be in conflict with biodiversity conservation requirements (Seydack 1992).

Fire is a dominant disturbance in the fynbos shrublands of the Cape Floral Kingdom (CFK) of South Africa. The CFK is an internationally renowned hotspot of biodiversity (Myers *et al.* 2000), where sound fire management is fundamental to the attainment of conservation objectives (Kruger and Bigalke 1984). Fynbos (literally meaning fine-leaved bush) is an evergreen, sclerophyllous shrubland on sandy, infertile soils associated with the winter and aseasonal rainfall regions of southwestern South Africa (Cowling *et al.* 1997). This vegetation type is fire-prone and fire-adapted, with the frequency, season, and intensity of fires being important determinants of vegetation structure and composition (Kruger and Bigalke 1984; van Wilgen *et al.* 1992; Vlok and Yeaton 1999).

Within the CFK, a climatic gradient exists in which the seasonality in rainfall, solar radiation, temperature, and evaporation decreases from west to east (Deacon *et al.* 1992). The Mediterranean climate (cool, wet winters and warm, dry summers) of the west contrasts with the all-year rainfall and relatively temperate conditions of the east (Schulze 1965; van Wilgen 1984; Southey 2009), with presumed effects on the fire regimes of the respective areas. Despite the climatological differences, existing guidelines for the management of fire in fynbos are largely based on research carried out in the west (Kruger and Bigalke 1984; van Wilgen and Richardson 1985; van Wilgen and Viviers 1985; van Wilgen *et al.* 1994), and little is known about the fire ecology of the eastern coastal region (van Wilgen 2009). Fires in western and inland parts of the CFK normally occur at intervals of 8–40 years (van Wilgen *et al.* 1992) although fuel loads are seldom limiting beyond the initial 2–4 years post-fire (Brown *et al.* 1991; Fernandes and Botelho 2003; Moritz *et al.* 2004; van Wilgen *et al.* 2010). Recruitment of fynbos in these areas is best after fires in summer and autumn (van Wilgen and Viviers 1985; Midgley 1989). In the east, however, recruitment success is less dependent on fire season than post-fire rainfall amounts (Heelemann *et al.* 2008); here, in addition to rainfall, conditions conducive to fires show little seasonality (Chapter 3). Similarly, plant growth rates may be higher in response to an increasing amount of warm-season rainfall towards the east, with effects on fuel accumulation rates and thus fire frequency.

Comprehensive fire histories in the CFK (Seydack *et al.* 2007; Forsyth and van Wilgen 2008; van Wilgen *et al.* 2010) and other temperate shrublands (Keeley *et al.* 1999; Montenegro *et al.*

2004; Syphard *et al.* 2009; Moreira *et al.* 2011) provide mounting evidence for long-term changes in fire regimes (notably increases in fire frequency), possibly related to climate change (Piñol *et al.* 1998; Mouillot *et al.* 2002; Keeley and Zedler 2009; Wilson *et al.* 2010). In the eastern coastal CFK, weather conditions conducive to the occurrence and spread of fires have increased since 1940 (Chapter 3) but it is not known whether the fire regime has changed accordingly. The historic approach towards fire management in the east differed from that in the western parts of the CFK. In the west, the focus was on burning for conservation, whereas in the east, extensive fuel-reduction burning was attempted in fynbos to protect plantations of exotic pines (Chapter 1).

The recent establishment of the Garden Route National Park (GRNP; Government Gazette 2009) in the eastern coastal CFK shifted the focus of management from the protection of pine plantations to the conservation of natural fynbos vegetation, and called for the formulation of new fire policies and practices, which in turn requires better understanding of historical fire regimes. In this paper, we explore the historical fire regimes in this area in terms of the seasonality, cause, size and frequency of fires. More specifically, we assess whether the west-east climatic gradient within the CFK is reflected in a west-east trend of decreasing fire seasonality and increasing fire frequency. For these purposes, we distinguish between a western and eastern region within the study area as well as comparing the historical fire regimes of the study area with well-documented fire histories of other areas further west in the CFK. Finally, we ask whether the frequency of fires in the study area has increased during its recorded history, and we examine the relationship between fire occurrence and fire climate.

Methods

Study area

The study area (33.80°S 22.59°E – 34.01°S 24.26°E) occurs within the eastern coastal CFK and comprises the coastal slopes of the Outeniqua Mountains (east of the Touw River) and the coastal slopes of the Tsitsikamma Mountains – hereafter respectively referred to as the Outeniqua and Tsitsikamma regions (the western and eastern portions of the study area, respectively) (Fig. 1). Owing to maritime influence, the climate of the study area is relatively temperate (Schulze 1965). Rainfall occurs throughout the year, with winter months being the driest. Mean annual rainfall increases eastwards, from 820 to 1 078 mm in the Outeniqua and Tsitsikamma Mountains, respectively (Bond 1981; Southwood 1984). The proportion of summer rain also increases eastwards (Schulze 1965; Tyson and Preston-Whyte 2000). Weather conditions suitable for fires dominate in the dry summer months in the west of the CFK, but become progressively less seasonal towards the east (Chapter 3). Hot and desiccating katabatic winds that flow from the interior (known locally as bergwinds) (Seydack *et al.* 2007) occur most frequently during autumn and winter in the study area, when they increase the likelihood of fires (Southey 2009; Sharples *et al.* 2010). Lightning occurs throughout the year at an average of 30 days per annum and at a mean density of <1 flashes km^{-2} annum^{-1} (Chapter 3).

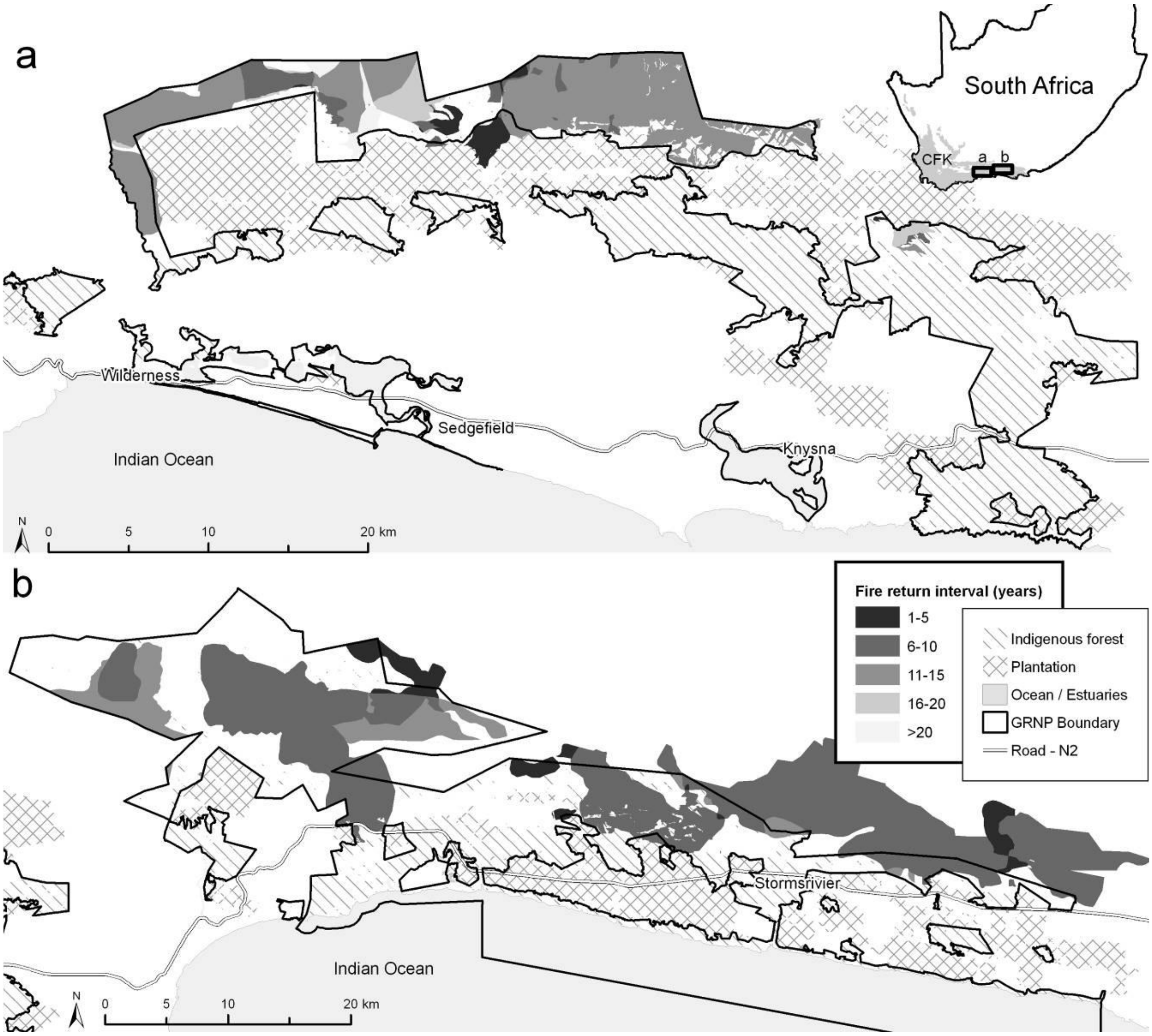

Figure 1: The insert shows the location of the **a**. Outeniqua and **b**. Tsitsikamma regions of the study area in relation to the Cape Floral Kingdom (CFK) and South Africa. Shading denotes mean fire return interval per unique fire history polygon during 1980–2010. Boundaries of the Garden Route National Park (GRNP) are shown; and indigenous forest and plantations in areas for which there are no fire return intervals on record.

The fire-prone vegetation within the study area includes approximately 110 000 ha of fynbos shrublands (Mucina and Rutherford 2006) and 47 000 ha of commercial pine plantations. Fire-resistant indigenous forests occur largely on the coastal plateau to the south of this area, as well as in the mountains in fire refugia (Geldenhuys 1994). Our assessment of the historical fire regime focused on the fynbos of the study area occurring on state land, most of which was incorporated into the GRNP in 2009. Chapter 1 provides a comprehensive account of the study area in terms of its management history and challenges pertaining to fire management.

Fire history database

We compiled a database of all fires recorded in the study area since the beginning of the 20th century by land managers of the national Department of Forestry and subsequent authorities responsible for the management of state land (Chapter 1). A limitation, particularly pre-1980, was the inadequacy and selectivity of wildfire and prescribed burn reporting: wild fires were generally only reported when they would have threatened timber or other assets, while successful prescribed burns were often not reported in a similar traceable format (van Wilgen 1981; Marshall 1983). We distinguished between records with and without sufficient spatial information on fire boundaries to allow capturing in GIS, hereafter referred to as spatial and non-spatial records, respectively. Two discrete databases were compiled, i.e. a GIS database of spatial records, and a qualitative database of spatial and non-spatial records combined (Fig. 2). The qualitative database (1900–2010) was used to explore fire season, size and cause, whereas the spatial database was used to explore FRIs (1980–2010) and vegetation post-fire age distribution.

Fire cause, season and size

We determined the relationship between the number of fires and the area burnt on record (1900–2010) per decade, using Spearman rank correlation analysis. There were far fewer fire records in earlier years, and these accounted for a much smaller area burnt when compared to later years, suggesting that earlier records (particularly pre 1980) were incomplete (*cf.* Seydack *et al.* 2007; Chapter 1). We compared the importance of different causes of fires, classified as natural (ignited by lightning), prescribed (burning for fuel reduction or catchment management purposes, including for grazing), accidental (including incendiary, warming/cooking fires, power lines, and escaped prescribed fires), and unknown. Given the inadequacy and selectivity of fire reporting in terms of cause (see above), we interpreted results with circumspection.

We furthermore assessed the seasonality and size distribution of fires, assuming that the fires on record were a random sample of all fires in terms of these factors, as nothing suggested that fires have been reported differentially among seasons or fire size classes. We classified fires into size classes as very small (<10 ha), small (10–100 ha), medium (100–1 000 ha), large (1 000–10 000 ha), or very large (≥10 000 ha). Seasonality of fire was explored in terms of the austral seasons, defined

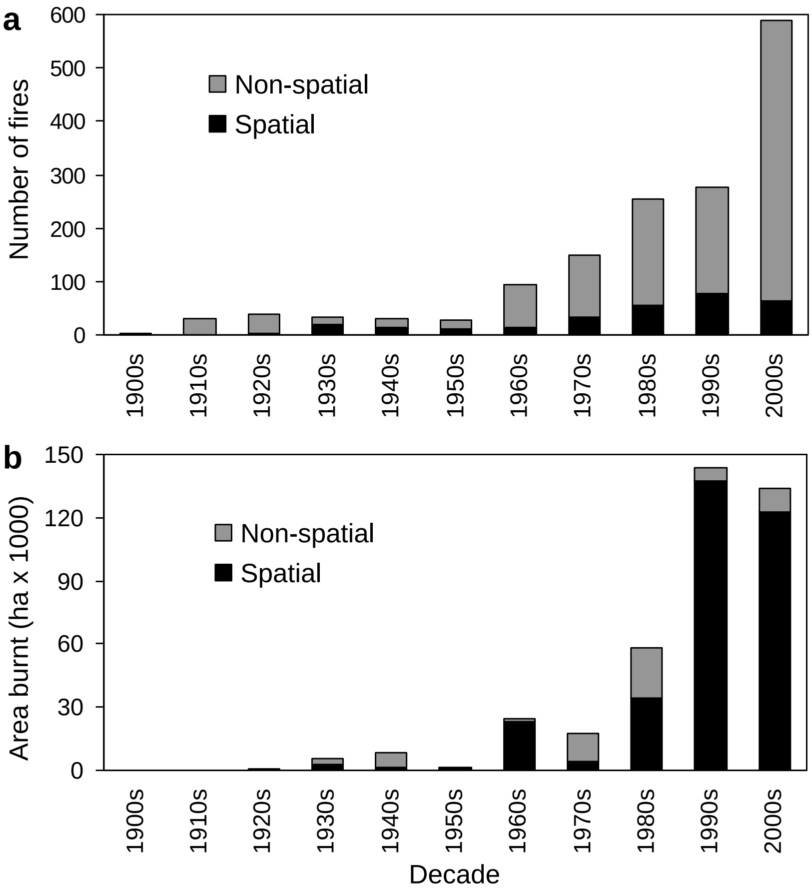

Figure 2: Distribution across decades of fire records assimilated for the study period, expressed in terms of **a**. the number of fires, and **b**. the area burnt. The qualitative database comprised of spatial records (which also constituted the GIS spatial database) and non-spatial records (for which fire size, but not fire boundaries, were known).

as summer (December–February), autumn (March–May), winter (June–August), and spring (September–November). For the analyses of fire season and cause, we assessed the Outeniqua and Tsitsikamma regions separately for comparison. We used Spearman rank correlation analysis to examine the relationship between time (decades) and proportion of area burned by firstly, fires of different causes, and secondly, fires of different size classes. To explore potential long-term changes, we assessed trends in the annual area burnt (since 1980, as earlier records were considered incomplete), as well as its relationship with the annual mean of daily fire weather conditions, using least-squares regression. Fire weather conditions were calculated (Chapter 3) in terms of the McArthur fire danger index, FDI (Noble *et al.* 1980). To moderate extreme inter-annual variability in burnt area, we used 3-year moving means of annual area burnt and annual mean FDI and log-transformed these variables to conform to the assumption of normality. Finally, we compared the seasonal distribution of area burnt between the Outeniqua and Tsitsikamma regions, using contingency tables with chi-squared test statistic. Statistical analyses were done in StatGraphics Centurion XV.

Fire return intervals

We confined our analysis of FRIs to the fynbos of the GRNP (extent indicated in Table 1) and to the period 1980–2010, as earlier spatial records were considered incomplete (*cf.* Forsyth and van Wilgen 2008; van Wilgen *et al.* 2010; Wilson *et al.* 2010). To assess FRIs, we delimited areas (polygons) of unique fire history by intersecting all spatial fire records (Forsyth and van Wilgen 2008; van Wilgen *et al.* 2010) in GIS (using ArcGIS 9.2). We only considered polygons ≥1.0 ha, as omission of the smallest fires is a negligible source of uncertainty in fire frequency analysis (Moritz *et al.* 2009).

Table 1: Extent of the study area and Outeniqua and Tsitsikamma regions, respectively; the percentages of these areas over which spatial records of fires and fire return intervals (FRIs) were recorded during 1980–2010; and the degree to which the data on FRIs were complete.

	Study area	Outeniqua	Tsitsikamma
Total extent (ha)	110 020	22 590	87 429
% of area burnt at least once	92.6	85.2	94.6
% of area with at least one complete FRI	53.1	64.0	50.3
% of FRIs censored*	62.5	59.3	69.6

*proportion of complete FRIs expressed as a % of complete plus open-ended FRIs

Each polygon of unique fire history was characterised by zero or more fires, and polygons with two or more fires had one or more complete FRIs recorded. The fire interval prior to the first fire on record, and subsequent to the last fire on record resulted in FRIs of unknown duration, unless the first or last fire was in 1980 or 2010 respectively. Such open-ended FRIs can be accommodated in analyses through censoring (Polakow and Dunne 1999; Moritz *et al.* 2009) and are referred to as 'censored', while complete FRIs are referred to as 'uncensored'. We estimated FRIs in three ways in order to allow comparison with other studies using various methods: (1) by treating each polygon as a single observation point (regardless of size) and restricting the analysis to uncensored intervals; (2) by treating each polygon as a single observation point and accounting for censored and uncensored intervals; and (3) by repeating the first two analyses but weighting the contribution of individual polygons by area. We used maximum likelihood survival analysis by fitting a two-parameter Weibull function to the FRI distributions (Johnson and Gutsell 1994; Moritz 2003), weighed according to burnt area (polygon size) (Fernandes *et al.* 2012). The Weibull hazard of burning $\lambda(t) = ct^{c-1}/b^{c}$ gives the instantaneous probability of a fire occurring in a specific time interval: the scale parameter b is the typical FRI that will not be exceeded 63.2% of the time; the shape parameter *c* describes the change in burn probability since the last fire (*t*) and is useful to measure how fire recurrence is affected by fuel age; hazard is constant in time (i.e. age-independent) when c=1, increases linearly with time when c>1, and increases exponentially when c>2 (Fernandes *et al.* 2012). We also calculated the median Weibull fire-free interval, which is a central tendency measure of asymmetrical fire interval distributions (Grissino-Mayer 1999). Models were fitted to the study area and the Outeniqua and Tsitsikamma regions, respectively, using SAS 9.3.

The fire record (1980–2010) was furthermore examined in each unique polygon for the frequency of occurrence of short (<7 year) FRIs. Such intervals approximate the vegetation age below which fires result in poor or no recruitment of slow-maturing obligate reseeding plants (Chapter 4). The proportional distribution of current (2011) post-fire vegetation age classes was also calculated for the study area and Outeniqua and Tsitsikamma regions, respectively.

Results

Fire history database

A total of 1 538 fires (719 in Outeniqua and 809 in Tsitsikamma) burnt 399 683 ha during 1900–2010. The area burnt and the number of fires increased in later years, suggesting that record-keeping improved over time, particularly from 1980 onwards (Fig. 2). The area burnt per decade was significantly correlated with the number of fires on record per decade (correlation coefficient $r_{S'}$=0.88, P<0.01, n=11). However, there were outliers, e.g. during the 1990s and 2000s when relatively few fires burnt disproportionately large areas compared to the 1980s.

Fire cause, season and size

Natural fires accounted for almost 60% of the total area burnt in the study area, while fires of accidental, unknown and prescribed cause (in decreasing order of importance) were much less important in terms of areas burnt (Table 2). However, fires of natural or prescribed cause were less numerous than those of accidental or unknown cause. In terms of area burnt, natural fires dominated the fire regime in the Tsitsikamma, while prescribed fires were unimportant (Table 2). The area burnt was more evenly distributed among fire causes in the Outeniqua, with accidental fires contributing most to area burnt.

The proportion of the area burnt by natural fires per decade increased from 1900 to 2010 ($r_{S'}$=0.97, P<0.01, n=11), while the proportion of the area burnt by accidental fires per decade decreased over the same period ($r_{S'}$=-0.73, P<0.05, n=11); there was no change in the area burnt by fires of unknown origin (prescribed fires were not assessed, see Methods) (Fig. 3). The proportional increase in area burnt by natural fires was particularly apparent in the Tsitsikamma since the 1990s.

Table 2: Proportional distribution of fires (1900–2010) of different causes, expressed in terms of the area burnt and the number of fires. Results are shown for the study area and Outeniqua and Tsitsikamma regions, respectively.

Cause	Study area		Outeniqua		Tsitsikamma	
	Area burnt (%)	No. of fires (%)	Area burnt (%)	No. of fires (%)	Area burnt (%)	No. of fires (%)
	n=1439	*n* =1538	*n*=673	*n*=719	*n*=766	*n*=819
Natural	59.3	16.4	25.7	19.1	82.8	14.2
Prescribed	5.5	4.7	12.7	7.4	0.4	3.9
Accidental	20.0	53.1	34.7	45.9	9.8	59.5
Unknown	15.2	24.9	26.9	27.7	7.0	22.5

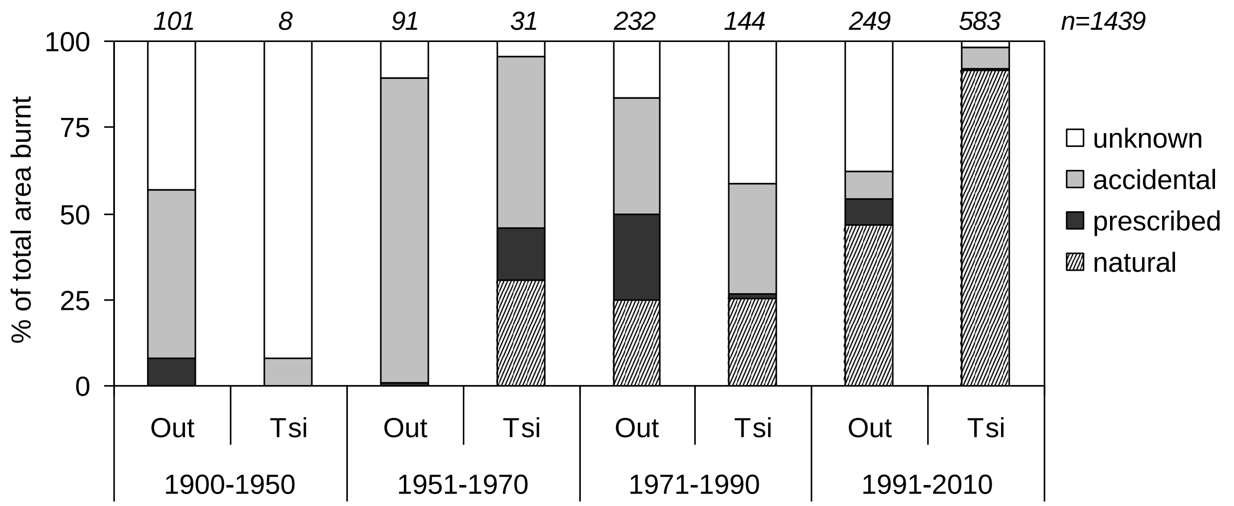

Figure 3: Proportional distribution of fires of different causes within the Outeniqua (Out) and Tsitsikamma (Tsi) regions between 1900 and 2010 (to prevent cluttering, periods longer than decades are shown). Numbers of fires recorded in the respective periods and regions are indicated in italics above the bars.

Overall, the distribution of fires (of all causes) was more seasonal in the Outeniqua (Coefficient of Variation, CV, in proportional area burnt among austral seasons = 50%) than in the Tsitsikamma (CV=39%) (Fig. 4). The proportional distribution of natural fires among seasons differed significantly between the regions in terms of area burnt (χ^2=52.1, df=3, *P*<0.001). Natural fires burnt the largest areas during summer and spring in the Outeniqua, while the distribution of natural fires was more even among seasons in the Tsitsikamma, with the smallest areas burnt in summer (Fig. 4).

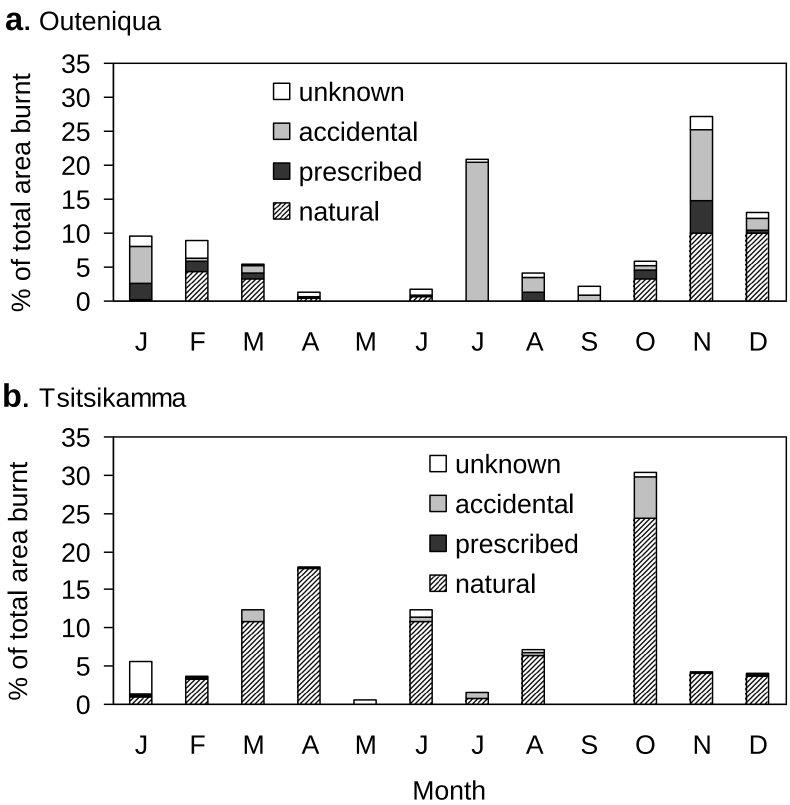

Figure 4: Percentage of the total area burnt per month from 1900 to 2010 in fires of different causes in the **a**. Outeniqua and **b**. Tsitsikamma regions.

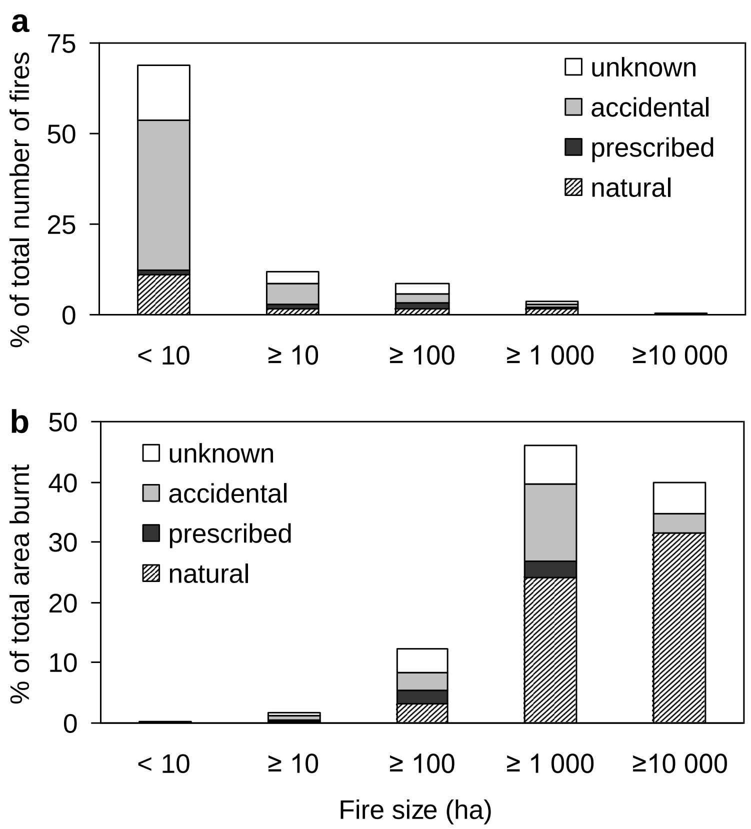

Figure 5: Size distribution of fires in the study area from 1900 to 2010 by fires of different causes expressed as a percentage of **a**. the total number of fires, and **b**. the total area burnt.

Fire sizes ranged from <1 to 41 902 ha. Most (74%) reported fires were very small, and collectively these accounted for less than 1% of the total area burnt (Fig. 5). Large and very large fires were infrequent but accounted for 86% of the total area burnt. All the recorded very large fires in the Outeniqua occurred in spring, whereas very large fires in the Tsitsikamma occurred in all seasons with a peak in autumn (Fig. 6). The proportional area burnt by very large fires increased with time ($r_{S'}$=0.77, P<0.05, n=11). Of the eight largest fires on record, seven occurred since 1990, and five were of natural cause. The total area burnt annually increased significantly since 1980 ($F_{1,29}$=4.6, P<0.05, R^2=0.14), and was significantly positively related to mean annual FDI ($F_{1,29}$=12.5, P<0.01, R^2=0.30).

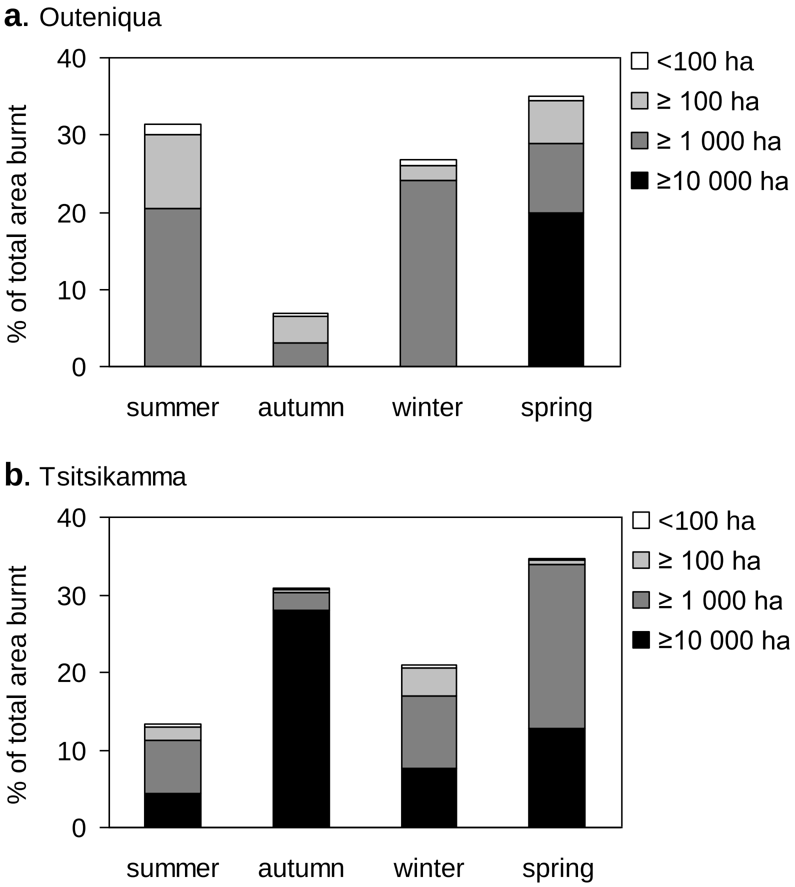

Figure 6: Percentage of the total area burnt from 1900 to 2010 per season in fires of different size classes in the **a**. Outeniqua and **b**. Tsitsikamma regions.

Fire return intervals

Fires were (spatially) recorded over most of the study area during 1980–2010, but complete FRIs (areas with at least two overlapping fires) were recorded across only *c.* half of the study area (Table 1). The percentage of FRIs that required censoring (the number of open-ended FRIs expressed as a percentage of complete plus open-ended FRIs, Table 1) was higher in the

Tsitsikamma than in the Outeniqua. Estimates of median FRI varied widely (range 6.6–26.2 years) depending on the method of estimation (Table 3). Estimates of median FRI were greater if data were censored, whereas weighting by area had a lesser and varying effect. Estimates of FRI (and the Weibull scale parameter *b*) based on uncensored data only were significantly lower for the Tsitsikamma (median 8.3 years) than for the Outeniqua (13.2 years), while the trend was reversed for estimates based on censoring (Table 3; Fig. 1). During the period 1980–2010, 10% of the study area burnt at least once at post-fire ages of <7 years.

Table 3: Median fire return interval (FRI) and Weibull parameters *b* and *c* (with 95% confidence limits) for FRI distribution analysis (1980–2010) incorporating and not incorporating censoring and area weighting (see text). Results are shown for the whole study area and for the Outeniqua and Tsitsikamma regions separately.

Modelling approach / Area / Region	Median FRI (years)	Scale parameter *b* Mean	(95% Cl)	Shape parameter *c* Mean	(95% Cl)	No. of intervals (uncensored, censored)
Excluding censored data; No area weighting:						
Study area	9.9	12.2	(11.4-13.0)	1.8	(1.6-1.9)	(308, 0)
Outeniqua	11.3	13.7	(12.7-14.7)	1.9	(1.7-2.1)	(231, 0)
Tsitsikamma	6.6	8.0	(7.1-8.9)	2.0	(1.7-2.4)	(77, 0)
Excluding censored data; Area weighting:						
Study area	9.6	11.3	(11.2-11.3)	2.3	(2.2-2.3)	(308, 0)
Outeniqua	13.2	15.3	(15.2-15.4)	2.5	(2.5-2.5)	(231, 0)
Tsitsikamma	8.3	9.3	(9.3-9.3)	3.2	(3.2-3.2)	(77, 0)
Including censored data; No area weighting:						
Study area	17.7	22.2	(20.6-23.9)	1.6	(1.5-1.8)	(308, 513)
Outeniqua	16.9	20.6	(19.2-22.2)	1.8	(1.7-2.0)	(231, 337)
Tsitsikamma	22.5	30.8	(24.2-39.3)	1.2	(1.0-1.4)	(77, 176)
Including censored data; Area weighting:						
Study area	22.1	27.5	(27.3-27.6)	1.7	(1.7-1.7)	(308, 513)
Outeniqua	16.4	19.0	(18.9-19.1)	2.5	(2.4-2.5)	(231, 337)
Tsitsikamma	26.2	33.9	(33.6-34.2)	1.4	(1.4-1.4)	(77, 176)

The Weibull shape parameter *c* ranged from 1.2–3.2 and was consistently reduced by censoring and increased by area weighting (Table 3). Censoring thus decreased the estimated dependency of burn probability on fuel age, whereas area weighting increased the estimated dependency on fuel age. Survival functions (Fig. 7) based on uncensored and area weighted data only, predict that half of the study area is likely to burn at <10 years of age, while <3% of the area is likely to survive beyond 20 years of age. The slope of the curve for the Tsitsikamma is steeper than that of the Outeniqua, suggesting shorter FRIs in the former region.

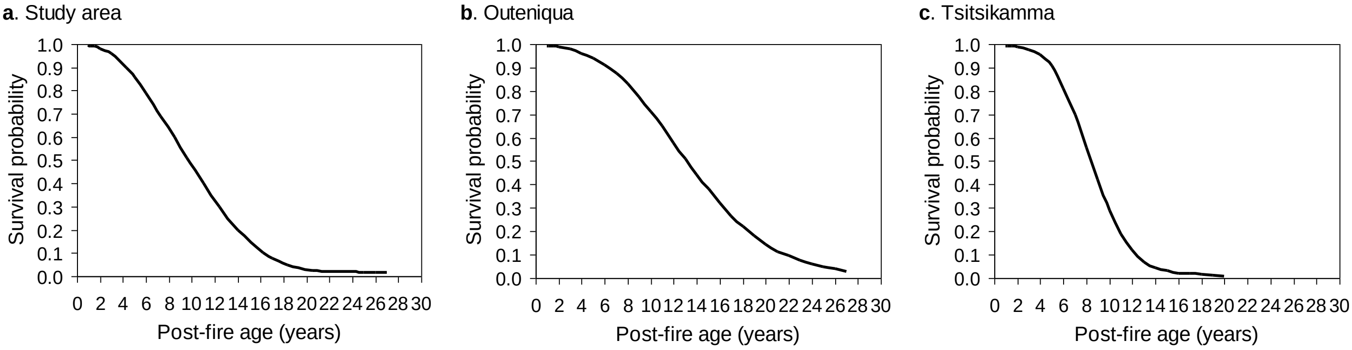

Figure 7: Survival functions (the proportion of the area surviving without a successive fire) for the **a**. Outeniqua, **b**. Tsitsikamma, and **c**. study area based on uncensored and area weighted fire return interval data (1980–2010) as modelled by the two-parameter Weibull distribution (see Table 3).

The current (2011) distribution of post-fire vegetation age classes is skewed towards the younger age classes, with 61% of the study area at 1-6 years of age, 12% at 7-12 years of age and 27% at >12 years of age. Less than 2% of the study area (and virtually none in the Tsitsikamma) is older than 20 years. The fynbos is younger on average in the Tsitsikamma (mean post-fire age 7.4 years) than in the Outeniqua (11.3 years).

Discussion

Fire cause

Trends in fire records from 1900–2010 indicated that natural fires dominated the fire regime in the Tsitsikamma in terms of area burnt, whereas fires of human origin accounted for almost half of the area burnt in the Outeniqua (Table 2). Prescribed burning had little influence on the overall fire regime in the study area. It accounted for <5% of the total area burnt since 1980, a period for which records are regarded as reasonably comprehensive (Fig. 2), and for only 11% during 1970–1989, when prescribed burning of fynbos is known to have been practised more widely than at any other time (Seydack *et al.* 2007; van Wilgen 2009; Esler *et al.* 2010; Chapter 1). Although our result needs to be interpreted with caution (given inadequacies in the reporting of fire cause), it is supported by similar findings in other fynbos protected areas (Brown *et al.* 1991; Seydack *et al.* 2007; Forsyth and van Wilgen 2008; van Wilgen *et al.* 2010). Prescribed burning has historically been constrained by various factors, including economical, ecological, physical, and political (van Wilgen 2009; van Wilgen *et al.* 2012; Chapter 1), and wide-scale implementation is likely to remain unfeasible.

The relative importance of fire causes changed from 1900 to 2010 – natural fires increased in areal importance while accidental fires of human origin decreased (Fig. 3), which is consistent with historical trends of fires in the Swartberg further inland (Seydack *et al.* 2007). The significance of natural fires in the study area (59% of the area burnt; Table 2), particularly since the 1990s (Fig. 3), is comparable to or exceed that recorded in the remote Swartberg, Kammanassie and Cedarberg Mountains (54%, 50% and 43%, respectively; Forsyth and van Wilgen 2007) and far exceeds that found in more accessible fynbos areas (1–17%, mean 10%, *n*=5; Forsyth and van Wilgen 2007).

Fire season

The distribution of natural fires was more seasonal (concentrated around summer) in the Outeniqua than in the Tsitsikamma (Fig. 4). This is consistent with a west-east climatic gradient across the CFK at large, from strictly-winter to all-year rainfall (Tyson and Preston-Whyte 2000) and an associated trend in fire seasonality from summer-autumn dominated to all-year round (van Wilgen *et al.* 2010). However, a detailed climatic assessment (Chapter 3) has not revealed a west-east gradient in terms of the seasonality of either weather conditions conducive to burning or lightning occurrence within the study area. In the Outeniqua, natural fires burnt the largest areas between November and March (Fig. 4a), similar to the findings of Marshall (1983) for the entire Outeniqua mountain catchment. The inclusion of fires of human origin produced peaks in the area burnt in winter and (to a lesser extent) summer, as found by Marshall (1983) and Le Roux (1969) for the Outeniqua for 1910–1965. In the Tsitsikamma, natural fires occurred throughout the year with peaks in spring and autumn, while summer fires were comparatively unimportant in terms of area burnt (Fig. 4b). Fires of human origin burnt a negligible area but numerous small fires occurred throughout the year. Brink (1990) likewise recorded little seasonality of fires on forestry estates in the Tsitsikamma during 1987–1990.

Bergwind conditions increase fire potential (van Wilgen 1984) and are thought to result in higher incidence, severity and size of fires (Le Roux 1969; Southey 2009). Mountain catchment managers deem the bergwind season in the study area to be from May to September (Le Roux 1969) and generally discourage burning during this time (Chapter 1). Although high fire danger conditions peak during May to July/August, large fires may also occur under moderate fire danger conditions (Chapter 3). Extensive areas accordingly burnt in the Tsitsikamma during mid-spring (October) and autumn (March–April) (Fig. 4b) signifying that high fire danger periods are not restricted to the bergwind season and may occur year round.

Fire size

The observed relationship between number of fires and area burnt (Fig. 5), with few, very large fires dominating the fire regime, is characteristic of many vegetation types globally (Keeley *et al.* 1999; Forsyth and van Wilgen 2008; Gill and Allan 2008; van Wilgen *et al.* 2010; Moreira *et al.* 2011). However, the incidence of very large natural fires seems to have increased in the study area since the 1990s (Fig. 3). It may be argued that poor record-keeping in earlier years (pre 1980) led to the absence of large fires from the fire record. However, large fires are unlikely to have gone unnoticed, as seen from the large fires in the Outeniqua during the 1960s and 1940s, which were widely documented in unpublished reports. An increase over time in large fires has also been observed in the Swartberg, but has been attributed to a change in fire management policy (Seydack *et al.* 2007). An increase in the frequency of very large fires may be a cause for concern, as they would reduce FRIs over extended areas. FRIs that are shorter than plant juvenile periods may lead to local extinctions (Bond *et al.* 1984; Bell 2001), whereas skewed vegetation age class distributions may complicate fire risk management and invasive alien plant clearing initiatives (Haidinger and Keeley 1993; Esler *et al.* 2010) by spreading workloads unevenly in time.

Fire return intervals

Mediterranean shrubland communities (perhaps with the exception of those in Chile) are generally resilient to FRIs of 20-50 years (Keeley 1986; Le Maitre and Midgley 1992). In the study area, estimates of median FRIs (since 1980) are variable (8-26 years), but are broadly comparable to estimates of median FRI in other fynbos protected areas (15-55 years based on uncensored, weighted data; Seydack *et al.* 2007; 10-21 years based on censored, unweighted data, van Wilgen *et al.* 2010). Restricting the analyses to known FRIs produced lower estimates of median FRI, as found by Moritz *et al.* (2009) and Fernandes *et al.* (2012). The high level of censoring required in our study (and particularly in the Tsitsikamma; Table 1) approximates a level (75%) thought to produce unrealistic models (Fernandes *et al.* 2012). The high level of censoring, and the magnitude of its effect on estimates of median FRI, suggest that these medians are likely to be overestimates of FRI. On the other hand, estimates of median FRI based solely on uncensored data are likely to be underestimates, in that fire free intervals are disregarded. Typical FRIs are thus likely to be intermediate between estimates based on censoring and no censoring. The variability in our results (and limitations or differences in the analysis or presentation of results in other studies) makes comparison with FRIs of other fynbos protected areas problematic. Discrepancies between results from censored and uncensored data emphasise the importance of comprehensive and long-term records for accurate characterisation of historical FRIs, and the need to ensure that similar methods of estimation have been used when comparing FRIs across studies.

Median FRI, based on uncensored data, was shorter in the Tsitsikamma than in the Outeniqua, but the trend reversed with consideration of censored data (Table 3). For our within-study comparison of FRIs, and from a management perspective, we deem the estimates based on uncensored data to be a more realistic reflection of regional differences in recent times (supported by Fernandes *et al.* 2012). Although not conclusive, our results provide some evidence for a west-east gradient of increasing fire frequency with increasing rainfall and increasing plant growth rates (Le Maitre and Midgley 1992) within the eastern CFK. Shorter FRIs may well be the norm in the Tsitsikamma and may be acceptable from an ecological point of view (*cf.* Chapter 4). Seydack *et al.* (2007) similarly found an inverse relationship between FRI in fynbos shrublands and rainfall (~plant productivity) along an altitudinal gradient in the Swartberg Mountains. However, at CFK-scale, FRIs are broadly comparable between the east and west, suggesting that variation is related to local or regional moisture regimes (Kruger and Bigalke 1984) rather than a west-east gradient within the CFK at large (*cf.* Chapter 4).

Ten percent of the study area burnt at least once at post-fire ages of <7 years since 1980, with the Tsitsikamma having experienced these short FRIs more extensively than the Outeniqua (Fig. 1). In these areas, post-fire recruitment of slow-maturing reseeding shrubs may have been compromised. Recent ecological studies in the area found that post-fire recruitment success of this functional type was near zero following a FRI of five years and always above replacement levels following FRIs of seven years or more (Chapter 4). This suggests that minimum fire return intervals to ensure survival of this functional type would be similar to those from other parts of the CFK (van Wilgen *et al.* 2011). Further research on maturation rates of slow-maturing reseeding plant species (Lamont *et al.* 1991) and success of vegetation recovery after fires at different intervals (Morrison *et al.* 1995) would be required to confirm these preliminary findings. Further research on the frequency of repeated short-interval burns in the landscape would also be informative. Short FRIs also have implications for the management of alien invasive plant species, particularly those that are fire-adapted (such as the *Pinus* species grown in adjacent plantations; Chapter 1) where fire drives their rapid spread and proliferation in fynbos (Richardson 1998). The recent occurrence of very large fires at short intervals and the virtual non-existence of older vegetation age classes are undesirable, as it may cause a shortage of seed of slow-maturing obligate seeders (Chapter 4) and inadequate habitat diversity for fauna (Martin and Mortimer

1991) in the landscape, in addition to leaving managers unable to deal with demands for clearing of invasive alien plants.

Fuel age dependency

Our estimates of the Weibull shape parameter *c*, a measure of fuel age dependency, varied with the modelling approach. Restricting the analysis to known FRIs (uncensored data) suggested an increased dependency of fire return probability on fuel age, consistent with the findings of others (Moritz *et al.* 2009; Fernandes *et al.* 2012). Our models with censoring and without area weighting produced estimates of *c* similar to those obtained for other fynbos areas (van Wilgen *et al.* 2010). We suspect that van Wilgen *et al*. (2010) underestimated fuel age dependency by only having modelled FRI distributions without weighting by area. Nevertheless, the levels of fuel age dependency existent in fynbos do not imply that young vegetation is fire-proof, as seen from our survival functions (Fig. 7). Fuel reduction treatments designed to maintain young vegetation post-fire age classes therefore would not necessarily provide reliable barriers to fire spread, although strategic placement of areas with reduced fuel may benefit fire suppression activities by providing safer areas for fire-fighting (Moritz 2003; Keeley and Zedler 2009).

Long-term changes in fire regimes

We recorded an increase in the incidence of large (mostly lightning-ignited) fires since 1990. The total area burnt per annum has also increased significantly since 1980 correlated with a significant increase over time in weather conditions conducive to the spread of fires (Chapter 3). This suggests that the increase in the extent of fires in recent decades is not an artefact of incomplete data, but a real trend, possibly related to climate change effects. Globally, and in the CFK, many areas have similarly experienced recent increases in fire frequency (Keeley *et al.* 1999; Montenegro *et al.* 2004; Syphard *et al.* 2007; Forsyth and van Wilgen 2008; Moreira *et al.* 2011), which have been associated with increases in the frequency of weather conditions favourable for fires (Piñol *et al.* 1998; Mouillot *et al.* 2002; Keeley and Zedler 2009; Wilson *et al.* 2010), or increases in human densities and related ignition sources (Keeley *et al.* 1999; Radeloff *et al.* 2005). Although we demonstrated a correlation between trends in fire occurrence and fire climate, the potential influences of (direct) anthropogenic effects (e.g. human-caused ignitions, fire suppression effort) also need to be discerned (Moreira *et al.* 2011) through long-term monitoring, which can also be used to discriminate between the effects of medium-term climatic cycles and long-term change.

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CHAPTER 3 – Lightning and fire weather in eastern coastal fynbos shrublands: seasonality and long-term trends

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Abstract

Daily weather data (since 1939) from four localities in the southeastern, coastal part of the Cape Floral Kingdom ('southeastern-CFK') were used to calculate daily fire danger indices (FDIs). Cloud-to-ground lightning strike distributions (2006–2010) were explored for geographical and temporal trends. Low or moderate fire danger conditions were the norm year-round, and even large fires occurred under these conditions. Lightning occurred throughout the landscape at fairly low densities (mean=0.4 strikes $km^{-2}a^{-1}$) and in all seasons, increasing somewhat during summer. Lightning presence increased with increasing rainfall, relative humidity, temperature and wind speed. Lightning seasonality in the southeastern-CFK did not differ from that in the southwestern-CFK. Our results provide evidence of a largely aseasonal fire regime in eastern coastal fynbos shrublands: FDIs peaked in winter (due to low rainfall and hot, dry katabatic winds) but were not associated with a winter fire regime; lightning and the co-occurrence of lightning and elevated FDIs were aseasonal and were correlated with the incidence of lightning-ignited fires throughout the year. The implication for management is that season of burn is largely unimportant. Mean annual FDI increased significantly over the study period, a trend which is likely to manifest in increased frequency and severity of fire, some of which has already been observed.

Keywords: climate change, Garden Route National Park, Mediterranean-climate ecosystems, Outeniqua, rainfall, relative humidity, South Africa, temperature, Tsitsikamma, wind speed

Introduction

Fires ignited by lightning are the dominant natural disturbance in the species- and endemic-rich fynbos shrublands (Myers *et al.* 2000) of the Cape Floral Kingdom (CFK), South Africa (Kruger and Bigalke 1984; Seydack *et al.* 2007). However, fire regimes in the southeastern, coastal part of the CFK (hereafter 'southeastern-CFK') are poorly understood (Heelemann *et al.* 2008; van Wilgen 2009) with existing fynbos fire management protocols largely based on knowledge of the summer-autumn fire regimes of the western and inland regions (Kruger and Bigalke 1984; van Wilgen *et al.* 1994; Cowling *et al.* 2005).

The Mediterranean climate (cool, wet winters and warm, dry summers) of the southwestern-CFK contrasts with the all-year rainfall and relatively temperate conditions of the southeastern-CFK (Schulze 1965; van Wilgen 1984; Southey 2009), with presumed effects on the seasonality of fires in the respective regions (van Wilgen 1981). Moreover, information on lightning in fynbos is limited to rudimentary assessments of lightning density at national- or biome-scale (Edwards 1984; Manry and Knight 1986; Archibald *et al.* 2009; Gijben 2012). Little is known about geographic and temporal variation in lightning distribution in the CFK and how this may relate to the incidence of lightning-ignited fires (Keeley *et al*. 2012).

In Chapter 2 we established that, in the southeastern-CFK, lightning fires (accounting for 59% of the area burnt since 1900) occurred throughout the year, but are more seasonal (concentrated around summer) in the west than in the east of this region. Foresters regard the fire danger season in the southeastern-CFK to be during autumn-winter, when hot, desiccating, katabatic *foehn* winds (Sharples *et al*. 2010), known locally as “bergwinds”, prevail (Le Roux 1969; Geldenhuys 1994). Information on the seasonality of lightning and weather conditions conducive to fire is needed to provide further insight into the natural fire season of the area.

Fire regimes are not static, and will change if the climate changes (Morgan *et al.* 2001). Fire occurrence in the CFK is strongly affected by climatic variability at local and global scales, and fire frequency is likely to increase under predicted changes in temperatures and rainfall (Wilson *et al.* 2010). Large fires have increased in recent years in the southeastern-CFK (Chapter 2) and to decide on appropriate management responses, the respective influences of climate change and other anthropogenic factors need to be understood (Moreira *et al.* 2011).

This study aimed to characterise the natural fire season in the southeastern-CFK, by exploring:

1. spatial and seasonal trends in weather variables influencing the likelihood of fires, and whether these have changed in the long-term;
2. geographic and temporal variation in lightning incidence; and
3. the relationship between weather conditions, lightning, and historical fires.

Methods

Study area

The study area (4 383 km^2) occurs within the southeastern-CFK and comprises the coastal slopes of the Outeniqua Mountains (east of the Touw River) and Tsitsikamma Mountains, hereafter termed the Outeniqua and Tsitsikamma regions, respectively (Fig. 1). A large portion of the study area occurs within the recently established Garden Route National Park (Chapter 1). At a wider scale, we compared the southeastern-CFK (6 078 km^2) to part of the southwestern-CFK (5 857 km^2) (Fig. 1). Accounts of the climate, vegetation and fire management history of the study area are provided elsewhere (Chapter 1, 2).

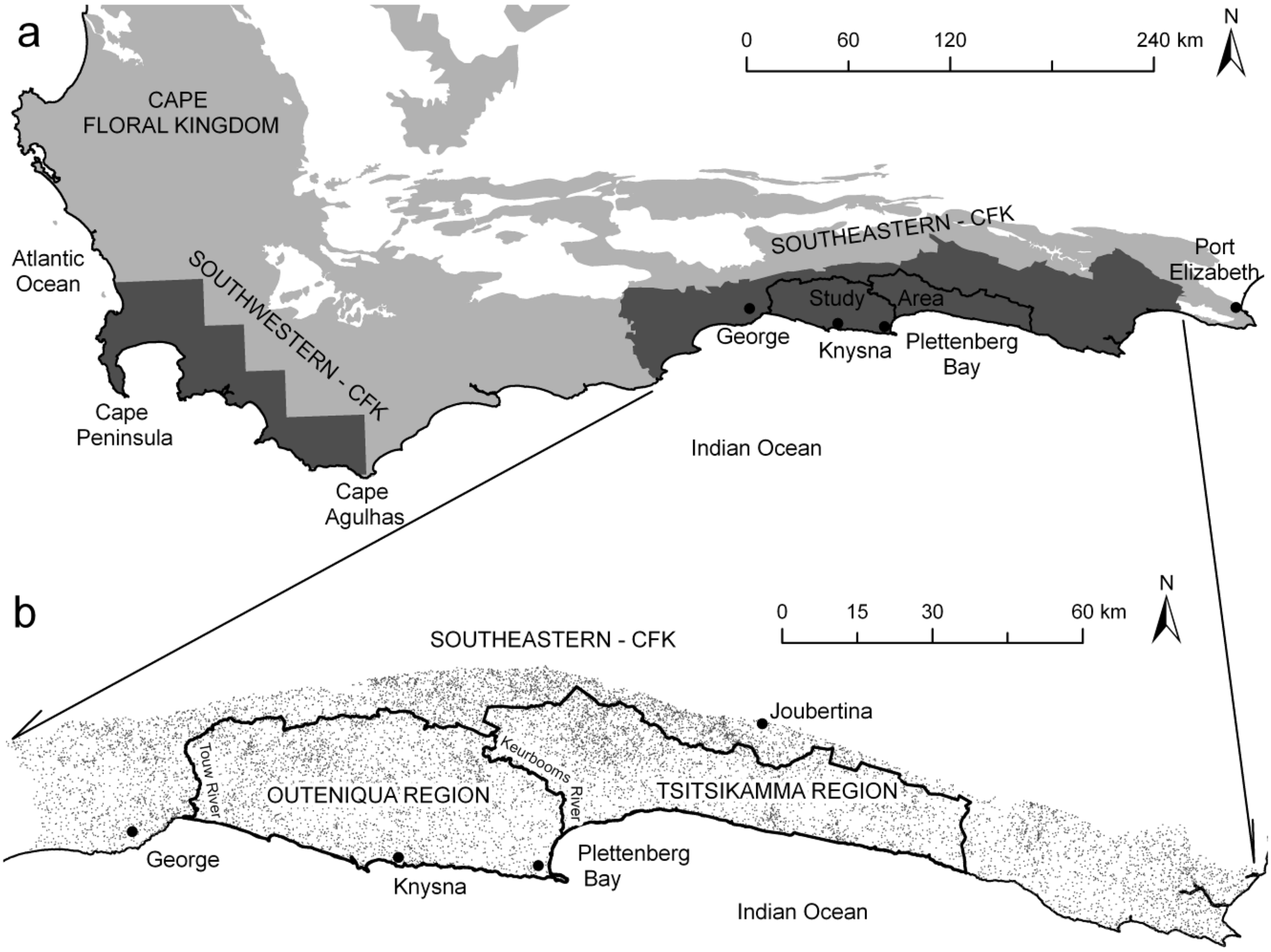

Figure 1: **a**. Location of the study area in relation to the entire east-west extent of the Cape Floral Kingdom (CFK; shaded in light grey) and the southwestern- and southeastern-CFK, respectively (in dark grey). Point localities of the weather stations at George, Knysna, Plettenberg Bay and Port Elizabeth are indicated.
b. Lightning strike distribution (2006–2010) over the southeastern-CFK, also showing the location of the study area divided into the Outeniqua and Tsitsikamma regions.

Fire weather

We assessed daily weather data (South African Weather Service) for the following stations (along a west-east gradient) and periods: George 1943–1964, 1978–2010; Knysna 1997–2010; Plettenberg Bay 1993–2010; Port Elizabeth 1939–2010 (Fig. 1). We used the McArthur Forest Fire Danger model (Noble *et al.* 1980) to calculate daily fire danger indices (FDIs) from daily (measured at 1400 hours, local time) maximum temperature, minimum relative humidity, rainfall and wind speed. Fire danger ratings were classed as low (FDI 0-5), moderate (5-12), high (12-25) and very high (25-50) (Noble *et al.* 1980). The McArthur fire danger model incorporates the Keetch-Byram drought index, which may also be used as a stand-alone index to measure the effect of seasonal drought on fire potential, the value of the index being an estimate of the amount of precipitation needed to bring the soil back to saturation (Noble *et al.* 1980). We looked for spatial (along a west-east climatic gradient) and seasonal trends in the incidence of fire danger ratings. Long-term trends in annual means of weather variables and FDI were explored using least squares regression.

Lightning

We assessed cloud-to-ground lightning strike data (South African Weather Service) for 2006–2010 (earlier records do not exist, Gijben 2012) for the southeastern- and southwestern-CFK, respectively. We computed the number of lightning strikes, and the number of days with at least one lightning strike per month (Krawchuk *et al.* 2006) and compared the seasonality in these measures between the Outeniqua and Tsitsikamma regions, and between the southeastern- and southwestern-CFK. We explored the effects of vegetation type (Vlok *et al.* 2008; Holness *et al*. 2010), altitude (extracted from a 10 m-resolution digital elevation model), longitude and latitude on spatial patterns (across a grid of 2 x 2 km cells) in lightning density using general linear model (GLM). To characterise temporal variability in lightning, and weather conditions associated with lightning, we assessed the effects of year, month, weather variables, and FDI, on the probability of lightning presence, using GLM (binomial distribution, logit function) with daily presence or absence of lightning as response variable.

Relationships between fire danger indices, lightning and fires

We assessed the prevalence and seasonality of lightning co-occurring with the respective fire danger ratings within the southeastern CFK. We related fire size (1940–2010, Chapter 2) to FDI on the day of ignition, using Spearman rank correlation. We explored the relationship between the number of fires (of all causes) or area burnt per month and (i) mean FDI or (ii) number of days with

FDI >5 per month during 1940–2010. We furthermore explored the relationship between the number of lightning-ignited fires or their area burnt and (i) lightning incidence or (ii) number of days with lightning co-occurring with FDI>5 during 2006–2010. We also compared FDI associated with fires in the respective seasons and of different causes (Chapter 2), using ANOVA and Fisher's least significant difference procedure. Lastly, we performed a qualitative assessment of weather associated with extreme fire events. Statistical analyses were done in StatGraphics Centurion XV.

Results and Discussion

Fire weather

The study area is not characterised by frequent conditions of high fire danger, as 87% of days had low fire danger ratings, 10% moderate, <3% high, and <0.2% very high ratings. The maximum FDI in recorded history in the study area was 41.5 at Port Elizabeth. Mean monthly FDI and the mean number of days per month with high or very high ratings peaked in winter (May–August) at all four stations (Fig. 2), associated with low rainfall and the occurrence of bergwinds. There was no clear west-east gradient within the study area in terms of the (i) severity of fire danger conditions, (ii) specific season of highest fire danger, or (iii) degree of seasonality in fire weather (Fig. 2). However, at CFK-scale, the peak in FDI in winter in the southeastern-CFK is opposite to the summer peaks in other areas further west (with a pronounced summer dry season) or inland (where summer months are hotter) in the CFK (van Wilgen 1984; Southey 2009).

We found consistent increases in the long term in mean FDI and number of days with moderate or higher ratings across the study area (Table 1). At George and Port Elizabeth, mean annual FDI increased at 0.4% p.a. since the 1940s, and at Knysna and Plettenberg Bay at 3% p.a. since the mid-1990s. Contrary to the predictions based on changes in temperature and precipitation, Hoffman *et al.* (2011) showed that although temperatures have mostly increased at 20 stations throughout the CFK (1974–2005), rainfall has not declined, and evaporation and wind run have decreased. Because the last-mentioned trends are likely to reduce fire frequency and intensity, there is a need to consider factors besides temperature and rainfall on the effect of climate change on fire regimes (Hoffman *et al.* 2011). We found consistent and significant decreases in minimum relative humidity (Table 1), whereas this measure decreased in only half the stations considered by Hoffman *et al.* (2011; unpublished data). In our study, changes in other weather parameters were more variable. Temperature increased significantly at George and Port Elizabeth at rates (0.01–0.02 °C per annum) comparable to that measured elsewhere in the CFK (Hoffman *et al.* 2011) and the Mediterranean Basin (Piñol *et al.* 1998). Wind speed at mid-day

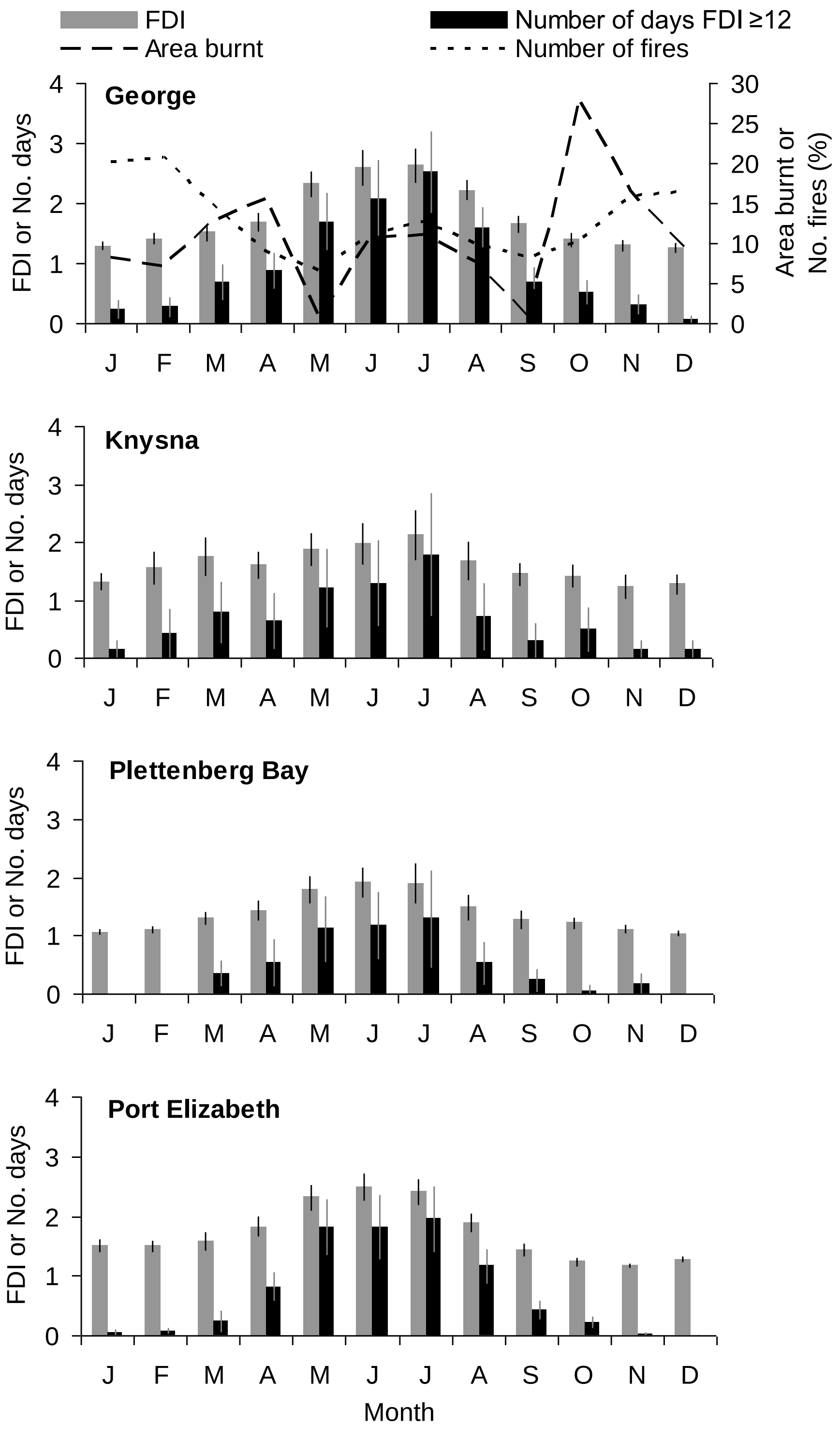

Figure 2: Annual cycles of the mean monthly fire danger index (FDI) and the mean number of days per month with high or very high (FDI≥12) fire danger ratings. Data are shown for four weather stations along the west-east gradient of the study area. Bars are 95% confidence intervals of the mean, where n_{George}=53, n_{Knysna}=14, $n_{\text{Plettenberg Bay}}$=17, $n_{\text{Port Elizabeth}}$=72. The top graph additionally shows the monthly distribution (%) of area burnt and number of fires of all causes for the period 1940–2010 over the entire study area.

mostly increased, contrary to the decrease in wind run reported by Hoffman *et al.* (2011). Our results provide evidence of a long-term increase in fire danger conditions, similar to trends reported or predicted for Mediterranean-climate ecosystems (Piñol *et al.* 1998; Pausas and Vallejo 1999; Williams *et al.* 2001; Keeley and Zedler 2009). These trends are likely to manifest in increased fire frequencies or severity, the former of which has already been observed in the study area (Chapter 2).

Table 1: Long-term trends in weather parameters at 1400 hours (local time), number of days since the last rainfall, McArthur fire danger index (FDI), and number of days with FDI being moderate to very high (>5) at four weather stations along a west-east gradient associated with the study area. Mean annual values, the percentage change per annum (p.a.), and the slope and R^2-value of the linear regression line for changes with time are shown. Significant trends (P<0.05) are indicated in bold.

		Weather station			
		George	Knysna	Plettenberg Bay	Port Elizabeth
	n (years)	53	14	17	72
Rain (mm)	Annual mean	726	872	697	619
	% change p.a.	-0.1	-0.2	-2.2	-0.2
	slope	-0.86	-2.16	**-15.63**	-1.04
	R^2	0.01	0.00	0.23	0.02
Temperature (°C)	Annual mean	19.9	21.4	19.3	21.0
	% change p.a.	0.1	-0.1	0.0	0.1
	slope	**0.02**	-0.03	0.01	**0.01**
	R^2	0.42	0.02	0.01	0.34
Relative humidity (%)	Annual mean	62.5	62.7	67.6	62.0
	% change p.a.	-0.1	-0.9	-1.0	-0.1
	slope	**-0.08**	**-0.57**	**-0.70**	**-0.06**
	R^2	0.33	0.46	0.57	0.24
Wind speed (m/s)	Annual mean	4.3	2.9	4.1	6.5
	% change p.a.	0.3	0.2	-1.0	0.5
	slope	**0.01**	0.01	**-0.04**	**0.03**
	R^2	0.22	0.01	0.55	0.29
Days since rain	Annual mean	2.3	2.7	3.2	3.0
	% change p.a.	0.3	0.0	0.1	0.3
	slope	**0.01**	0.00	0.00	0.01
	R^2	0.12	0.00	0.00	0.04
FDI	Annual mean	3.0	2.9	2.2	3.2
	% change p.a.	0.4	2.8	3.0	0.4
	slope	**0.01**	**0.08**	**0.07**	**0.01**
	R^2	0.22	0.29	0.48	0.24
No. days with FDI >5	Annual mean	48.8	40.6	25.4	48.3
	% change p.a.	0.7	7.6	5.4	0.9
	slope	**0.36**	**3.07**	**1.36**	**0.42**
	R^2	0.19	0.34	0.38	0.23

Lightning

Lightning as a source of ignition in the study area appears to occur throughout the landscape, albeit at low density (0.39±0.14 strikes $km^{-2}a^{-1}$, mean ± 95% confidence intervals; range 0.17–0.59) relative to many other areas of southern Africa (Archibald *et al.* 2009). The study area experienced an average of 30 days with lightning per annum. Lightning density did not differ significantly between the Outeniqua (0.37±0.17 $km^{-2}a^{-1}$) and Tsitsikamma (0.42±0.15 $km^{-2}a^{-1}$) regions. Lightning density was significantly higher in the southeastern-CFK (0.42±0.09 $km^{-2}a^{-1}$) than in the southwestern-CFK (0.16±0.03 strikes $km^{-2}a^{-1}$), the latter being comparable to that measured in chaparral (0.1 $km^{-2}a^{-1}$) and coastal sage scrub (0.04 $km^{-2}a^{-1}$) in Baja California (Minnich *et al.* 1993).

Lightning density was significantly related to vegetation type, altitude and latitude but not longitude, although the contribution of these variables to explaining total variation was low (R^2=0.06). Lightning density was higher in fynbos than in indigenous forest, pine plantations or disturbed habitats, but this effect was largely accounted for by the location of most fynbos in high-altitude, inland (lower latitude) sites. Other studies accordingly found positive relationships between lightning density and altitude and distance from the coast (Keeley and Zedler 1978; Krawchuk *et al.* 2006). Lightning density thus appears to be related to the position of habitat types in the landscape (Minnich *et al.* 1993; Hodanish *et al.* 1997) rather than their inherent properties (e.g. vegetation structure, substrate type). However, the magnitude of the effects of altitude and latitude was small (as found by Krawchuk *et al.* 2006), and spatial variation in lightning density remained largely unpredictable.

There were no apparent or consistent seasonal trends among the different measures of lightning incidence considered (Fig. 3a). There was little difference in the seasonality of lightning between the Outeniqua and Tsitsikamma regions. We expected the lightning regime of the southwestern CFK to reflect the summer-autumn seasonality displayed by natural fires in this region (van Wilgen *et al.* 2010). However, lightning incidence was equally aseasonal in the southwestern- and southeastern-CFK (Fig. 3b). In both areas there appeared to be a weak trend of higher incidence of lightning during the warmer months (October–February) compared to the cooler months (May–September) (Fig. 3), possibly related to increased thunderstorm activity in summer, as observed elsewhere (Granström 1993; Vazquez and Moreno 1998; Wotton and Martell 2005).

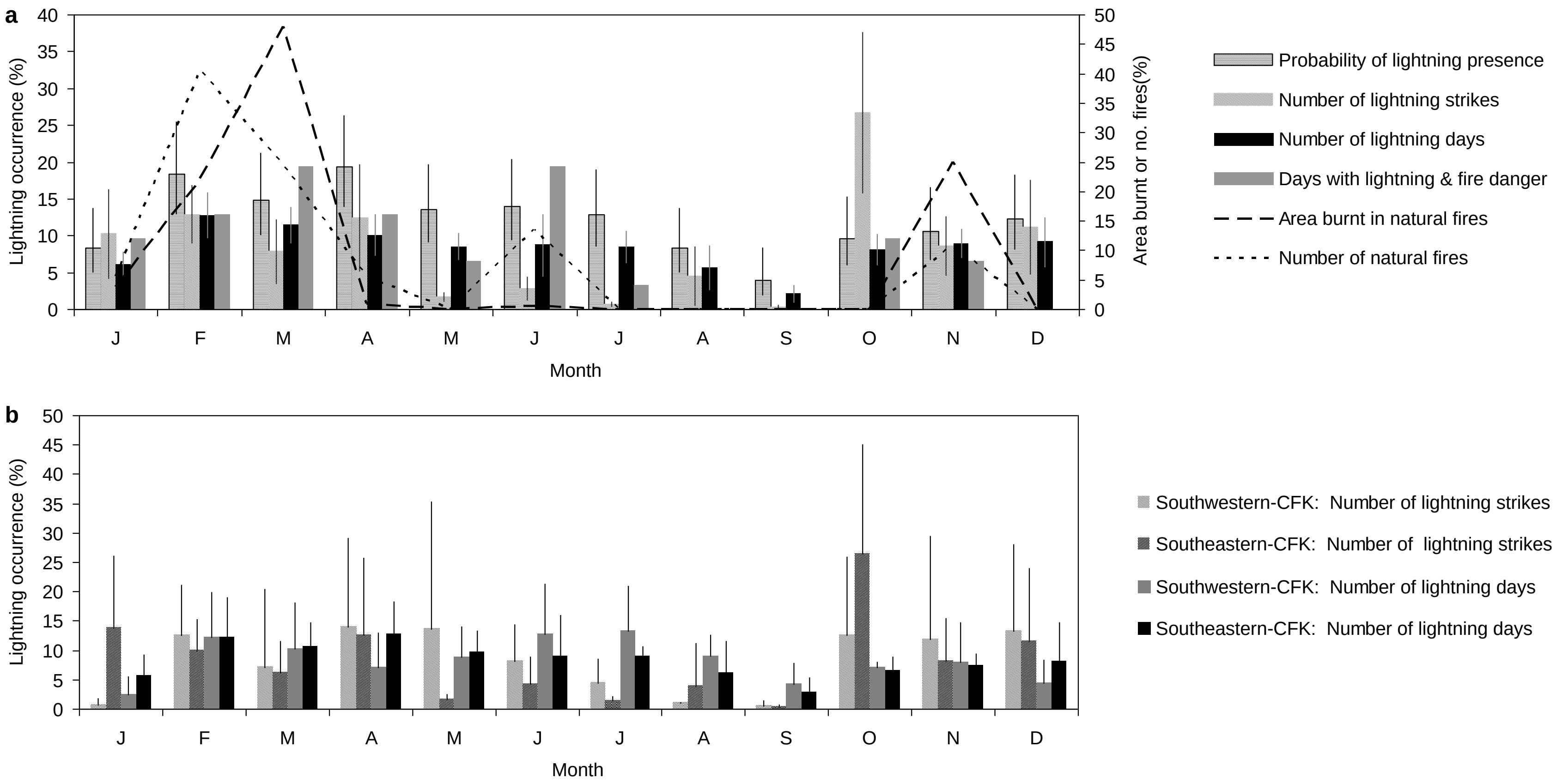

Figure 3: **a**. Seasonality of lightning occurrence in the Garden Route coastal mountains during 2006–2010, expressed as four different measures: (i) the percentage probability of lightning occurrence per month as predicted by a binomial general linear model; and the percentage monthly distribution in (ii) the mean number of lightning strikes per month; (iii) the mean number of lightning days per month; and (iv) the number of days with lightning co-occurring with moderate or higher fire danger ratings on or the day after lightning occurrence. Means ± 95% confidence intervals across years are shown for measures (ii)–(iv). The percentage monthly distribution in area burnt and number of lightning-ignited fires are furthermore shown for the period 2006–2010.

b. Seasonality of lightning in the southwestern- and southeastern-Cape Floral Kingdom (SW-CFK and SE-CFK, respectively) during 2006–2010, expressed as the percentage monthly distribution in the mean number of lightning strikes per month and the mean number of lightning days per month. Means ± 95% confidence intervals across years are shown.

Relationships between fire danger indices, lightning and fires

Lightning occurrence was significantly related to rainy, humid weather (~low FDI), as well as with warm, windy conditions (~high FDI), and thus not with FDI *per se*. Fire danger ratings on or immediately following days with lightning (n=153) were mostly low (84% of cases) or moderate (13%), and rarely higher (3%). Fire incidence on, or immediately after, lightning days was higher when moderate to high fire danger ratings prevailed (*c.* 50%) than it was with low ratings (12–16%) (*cf.* Wotton and Martell 2005).

The size of fires was positively correlated with FDI on the date of ignition ($r_{S'}$=0.06, P<0.05, n=1180) suggesting that fires are more extensive during periods of elevated fire danger. FDIs associated with fires in spring and summer were lower than those in autumn, and those in autumn lower than in winter ($F_{3,1240}$=45.4, P<0.001). FDIs did not differ significantly among fires of different causes. Weather conditions prior to and during the course of the largest fires on record (1940–2010) were variable rather than consistently extreme. The maximum FDI recorded during the course of any fire >1000 ha in extent, was 26.3. Provided that there is fuel, large fires can thus occur under conditions of moderate fire danger. Although the study area occasionally experiences very large fires (≤41 902 ha, Chapter 2), extreme warm-season weather conditions associated with destructive fires in winter-rainfall regions such as the Cape Peninsula (Forsyth and van Wilgen 2008), California (Keeley and Zedler 2009), Australia (Williams *et al.* 2001), and the Mediterranean Basin (Piñol *et al.* 1998; Pausas and Vallejo 1999), are not characteristic of the study area, and neither are these confined to a narrow fire season.

We attempted to establish relationships between the seasonality of FDIs, lightning and fires, because lightning-ignited fires would be most likely and most extensive when lightning co-occurs with high fire danger conditions (Krawchuk *et al.* 2006; Wotton and Martell 2005). The seasonality in numbers of fires or area burnt was not correlated with the seasonality in mean or elevated FDIs (Fig. 2; Table 2). Seasonality in the number of lightning-ignited fires and their area burnt was correlated with seasonality in the number of lightning days (but not the number of strikes) as well as the co-occurrence of lightning and elevated FDI ($r_{S'}$=0.64, P<0.05, n=12) during 2006–2010 (Fig. 3a). Seasonality in lightning fires in the long-term (1940–2010) was, however, not correlated with the seasonality in lightning days in the short-term (2006–2010), suggesting that the fire season is variable in time, and not necessarily fixed to the same calendar months every year. The correlation in the short-term between the seasonality of lightning days and lightning-ignited fires suggests a level of ignition limitation, contrary to the findings of Archibald *et al.* (2009)

although these authors considered fires of all causes in relation to lightning as the only source of ignition.

Table 2: Spearman rank correlations ($r_{S'}$) between (i) the size of individual fires and fire danger index (FDI) during fires; (ii) the seasonality (monthly distribution) in the number of fires or area burnt and that of mean FDI or number of days with FDI>5; (iii) the seasonality of lightning-ignited fires and that of lightning days or strikes or the co-occurrence of lightning and FDI >5. Significant correlations (*P*<0.05) are indicated in bold.

Variable 1	Variable 2	$r_{S'}$	*P*	*n*	Data considered
Fire size	FDI on ignition date	**0.06**	0.03	1180	All fires individually (1940–2010)
Number of fires	FDI	-0.07	0.84	12	Data pooled per month; Fires of all causes (1940–2010)
	Number of days with FDI >5	-0.24	0.43		
	FDI	-0.01	0.92	84	Data pooled per month per decade; Fires of all causes (1940–2010)
	Number of days with FDI >5	-0.11	0.30		
Area burnt	FDI	-0.28	0.35	12	Data pooled per month; Fires of all causes (1940–2010)
	Number of days with FDI >5	-0.30	0.31		
	FDI	0.09	0.41	84	Data pooled per month per decade; Fires of all causes (1940–2010)
	Number of days with FDI >5	-0.02	0.86		
Number of fires	Number of lightning strikes	0.31	0.31	12	Lightning-ignited fires (2006–2010)
	Number of lightning days	**0.69**	0.02		
	Number of lightning days	0.46	0.13		Lightning-ignited fires (1940–2010)
Area burnt	Number of lightning strikes	0.33	0.28		Lightning-ignited fires (2006–2010)
	Number of lightning days	**0.62**	0.04		
	Number of lightning days	0.41	0.18		Lightning-ignited fires (1940–2010)
Number of fires	Number of days with lightning and FDI >5	**0.80**	0.01	12	Lightning-ignited fires (2006–2010)
		0.22	0.46		Lightning-ignited fires (1940–2010)
Area burnt	Number of days with lightning and FDI >5	**0.69**	0.02		Lightning-ignited fires (2006–2010)

Overall, our results provide evidence for a largely aseasonal fire regime in southeastern-CFK fynbos: FDIs peaked in winter but was not associated with a winter fire regime; lightning and the co-occurrence of lightning and elevated FDIs were aseasonal and correlated with year-round incidence of lightning-ignited fires (Chapter 2). A lack of seasonality in fires is to be expected in an area where rainfall and lightning are aseasonal, where low or moderate fire danger conditions are the norm, and where warm, dry, windy conditions may occur periodically at any time of year (caused by solar heating in summer and bergwinds in winter). The aseasonal fire climate has profound implications for evolution of the biota, fynbos community structure, and fynbos management. The implications for management are that season of burn is largely unimportant although fire intensity should not be disregarded (Vlok and Yeaton 2000), and that fire hazard is not restricted to a particular time of year.

This study is the first seasonal and multi-year analysis of lightning activity in the CFK based on the continuous operation of a lightning network (*cf.* Hodanish *et al.* 1997; Gijben 2012). It is furthermore a first attempt in the CFK to relate fires on record to actual lightning and weather data. This integrated assessment of fire seasonality is an improvement on previous independent analyses of the seasonality of reported fires or the seasonality of fire weather.

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CHAPTER 4 – Proteaceae juvenile periods and post-fire recruitment as indicators of minimum fire return interval in eastern coastal fynbos

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Abstract

Question: Fire management practices aimed at biodiversity conservation are often in conflict with hazard reduction requirements. Particularly in protected areas where such conflict of interest exists, the question is asked: what are the ecological thresholds within which fire should be managed?

Location: Montane proteoid fynbos shrublands in the eastern coastal part of the Cape Floral Kingdom; the coastal slopes of the Tsitsikamma and Outeniqua Mountains, South Africa.

Methods: Estimates of optimal fire frequencies are often based on the relationship between plant age and the rate of seed accumulation of the slowest-maturing species. We established juvenile periods and recruitment success (measured as the ratio of post-fire recruits to the pre-burn population) after fires at different intervals, of serotinous, reseeding shrubs in the Proteaceae family. From this we estimated minimum fire return intervals (FRIs) that would allow for their persistence in eastern coastal fynbos shrublands.

Results: Juvenile periods ranged from 4–9 years, which are comparable to ecologically similar proteoids elsewhere in fynbos and southeastern and southwestern Australian shrublands. There was large variability among sites and within species in the degree of flowering at given plant ages, some of which seemed related to the moisture regime. There were no consistent differences among species in their rate of maturation. Post-fire recruitment success was near zero following a fire in 5 year-old vegetation, always above replacement levels following fires in ≥7 year-old vegetation, and at a maximum in old (38 years) fynbos. There was considerable variation in post-fire recruitment success for any particular FRI, species or site. The lack of a significant relationship between recruitment success and pre-fire vegetation age, suggests that once a critical post-fire age is attained, factors other than seed abundance affect recruitment success.

Conclusions: From an ecological perspective, our findings imply a minimum FRI of nine years for eastern coastal fynbos. This is not intended to prescribe rigid management of fire according to a fixed rotation and does not negate the need to consider site- or species-specific requirements.

Instead it provides a lower threshold for a range of acceptable FRIs below which a significant decline of species populations is predicted.

Keywords: Cape Floral Kingdom; fire frequency; fire rotation; *Leucadendron*; maturation rate; *Protea*; shrublands; threshold of potential concern; youth phase

Nomenclature: Rebelo (2001)

Introduction

Ecosystem integrity can be compromised by disturbance regimes which are outside of the historical range of variability to which the ecosystem's component species are adapted (DellaSala et al. 2004). Fire is such a disturbance regime, and empirical evidence indicates that variation in fire return intervals (FRIs) can affect species abundance and floristic composition in Mediterranean-type ecosystems and other temperate shrublands (van Wilgen 1981; Haidinger & Keeley 1993; Morrison et al. 1995; Lloret et al. 2003).

Life history attributes that render species vulnerable to certain disturbance regimes, especially variations in the interval between fires, are well recognised (Noble & Slatyer 1980; van Wilgen et al. 1992; Bond & van Wilgen 1996; Bradstock & Kenny 2003). Obligate reseeders are particularly prone to population decline under increased fire frequency when the interval between fires is shorter than the time taken to accumulate a seed bank adequate for post-fire regeneration (Morrison et al. 1995; Knox & Morrison 2005). Obligate reseeders with canopy-stored (serotinous; Lamont et al. 1991a) seed banks are most susceptible to short FRIs because their whole seed bank is released post-fire (Noble & Slatyer 1980; Bradstock & Kenny 2003). Estimates of ecologically appropriate FRIs for a site are thus often based, at the lower end of the range, on the age of maturation and rate of seed accumulation of the slowest-maturing obligate reseeder species, and at the higher end, on the lifespan of the shortest-lived reseeder species that does not accumulate soil seed banks (Bond 1980; Enright et al. 1996; Gill & McCarthy 1998). At both ends, the most sensitive plant guild is the slow-maturing, short-lived, serotinous, reseeding shrubs (Noble & Slatyer's (1980) CI species), in South African and Australian temperate shrublands typically of the Proteaceae family (hereafter termed 'proteoids') (Cowling 1984; Kruger 1984; Le Maitre & Midgley 1992; Enright et al. 1996, 1998; Gill & McCarthy 1998; Bradstock & Kenny 2003).

FRIs equal to twice the primary juvenile period (time elapsed between germination and flowering) were shown to be necessary to allow for adequate seed production in western

Australian jarrah forest (Bell 2001). Similar methods of determining appropriate minimum fire intervals have also been suggested for eastern Australian shrublands (Gill & McCarthy 1998) and fynbos shrublands of the Cape Floral Kingdom (CFK) (Kruger & Lamb 1978). A rule of thumb used in the fynbos is that half of the individuals in a population of the slowest-maturing proteoid species should have flowered in at least three successive seasons before the area may be burnt (Kruger & Lamb 1978; Kruger 1982).

There is a need to incorporate ecological thresholds for FRIs into fire management systems (Bradstock & Kenny 2003; van Wilgen et al. 2011), particularly in protected areas where the primary goal is biodiversity conservation. Fire management practices aimed at ecological objectives are, however, often in conflict with hazard reduction requirements (Morrison et al. 1996; Driscoll et al. 2010; van Wilgen et al. 2012). Simple management compromises intended to reconcile conflicting objectives may ultimately not achieve either hazard reduction or biodiversity conservation (Morrison et al. 1996). In the Garden Route Coastal Mountains (GRCMs), conflict of interest in terms of desired FRIs is a matter that remains to be addressed (Chapter 1). Firstly, the landscape comprises fynbos, of which large tracts occur within the newly established Garden Route National Park (GRNP), interspersed with plantations of fire-sensitive alien pine trees. As a result, there is significant pressure from the plantation industry to reduce wildfire hazard by burning fynbos, in places, at short intervals (Chapter 1). Secondly, the GRCMs occur within the eastern coastal part of the CFK where fynbos fire ecology in general, and thresholds for FRIs in particular, are inadequately understood (van Wilgen 2009). Thirdly, high levels of invasion of fynbos by alien trees (most of which originate from the timber plantations) require integration of alien plant control considerations with fire management measures (Richardson 1998). As the GRNP has only recently been established, it is important to influence the development of management policy and practice in the interests of biodiversity conservation (Chapter 1).

In this study we established juvenile periods and recruitment success (Noble & Slatyer 1980) in proteoids after fires at different intervals, and used this information to estimate minimum FRIs (van Wilgen et al. 2011) that would allow for their persistence in eastern coastal fynbos.

Methods

Study area and species

We focussed on the GRCMs (33.80°S 22.59°E – 34.01°S 24.26°E) that occur along the Cape south coast of South Africa. The area includes the southern slopes of the Outeniqua (east of the Touw River) and Tsitsikamma Mountains. Within the study area, we distinguished between the

Outeniqua and Tsitsikamma regions, to the west and east of the Keurbooms River, respectively (Fig. 1). The climate of the GRCMs is relatively temperate, owing to maritime influence. In contrast to the strictly Mediterranean climate in the western part of the CFK, rain falls more evenly throughout the year (Schulze 1965). Rainfall peaks in spring and autumn in the GRCMs, and winter months are the driest. The proportion of summer rain increases eastwards (Schulze 1965; Tyson & Preston-Whyte 2000). Mean annual rainfall increases eastwards, from 820 mm in the Outeniqua to 1079 mm in the Tsitsikamma Mountains (Bond 1981; Southwood 1984). Hot and desiccating winds that flow from the interior (known locally as bergwinds) occur most frequently during autumn and winter, when they increase the likelihood of fires (Geldenhuys 1994; Southey 2009). The weather conditions suitable for fires dominate in the dry summer months in the west of the CFK, but become progressively less seasonal towards the east (Chapter 3).

The fire-prone vegetation within the study area includes approximately 100 000 ha of mountain fynbos shrublands (Rebelo et al. 2006) and 47 000 ha of commercial pine plantations (Chapter 1). Fire-resistant indigenous forests occur largely on the coastal plateau along the foothills of the mountains, as well as in fire refugia such as gorges, scree slopes, and berg-wind shadows in the mountains (Geldenhuys 1994). Large parts of the GRCMs are remote and natural fires accounted for 60 % of the area burnt during the past century (Chapter 2). Fynbos comprises fire-dependent (Kruger & Bigalke 1984) evergreen shrublands with evergreen graminoid understoreys (Rebelo et al. 2006) that burn at median intervals of 10–21 years elsewhere in the CFK (van Wilgen et al. 2010) and at 8–26 years locally (Chapter 2). Overstorey proteoids common to the fynbos of the region are *Protea neriifolia*, *P. mundii* and *Leucadendron eucalyptifolium*, while *L. uliginosum* and *P. eximia* occur less commonly. In the eastern part of the CFK, there is a shift from winter-spring flowering to summer-autumn flowering compared to the west (Pierce & Cowling 1984; Johnson 1993; Heelemann et al. 2008) both across and within lineages.

Study design

Data collection was non-manipulative, relying on the sampling of areas in the field with known recent histories of fire occurrence. We undertook three types of surveys (Fig. 1) of proteoids:

(1) One-off surveys to determine juvenile periods of populations where the date of the last fire, and thus plant age (i.e. time since last fire) was known (range 4–11 years). We randomly selected 50–250 individuals per species per site by means of the wandering quarter method (Catana 1963). For each individual, we recorded the number of times (seasons) it has flowered. We located six survey sites within the Tsitsikamma region (Fig. 1), two of which were sampled

twice, two years apart. Most sites had more than one species of interest and some sites offered different habitat types related to aspect and slope. In total, 29 site-species replicates were sampled and 2 789 plants.

(2) Recurrent surveys of post-fire growth and flowering of permanently-marked plants at sequential plant ages at two sites. The first site was on a dry west-facing slope at Keurbooms Nature Reserve (200 m a.s.l.) after a prescribed fire (223 ha) in April 1996, where 100 seedlings of *P. neriifolia* were marked along ten transects (spaced 2 m apart) in 2006. Plant height from ground level and the number of flowerheads of the current season were recorded annually until 2011. The second site was on a moist south-facing slope at De Vasselot Nature Reserve (280 m a.s.l.) after a lightning fire (29 855 ha) in November 2005, where 100 seedlings each of *P. mundii* and *L. eucalyptifolium* were marked along six transects (spaced 10 m apart) in 2008. Plant height from ground level and the number of flowerheads of the current season were recorded at approximately annual intervals until 2011. The two sites are situated 15 km apart and both are *c.* 5 km from the coast.

(3) Surveys of recruitment success within four years post-fire (mean ± standard deviation (SD) = 1.8 ± 0.5 years), where populations occurred in areas where the pre-fire vegetation age was known (range 5–38 years). We counted within belt transects (2 m x 30 m) the number of proteoid seedlings (post-fire recruits) in relation to the number of burnt parents, using the non-destructive method of Bond et al. (1984) as modified by Husted et al. (2007). We located 12 survey sites throughout the study area (Fig. 1), which provided 22 site-species replicates. The mean (± SD) number of transects done per site-species replicate was 5.0 ± 2.8.

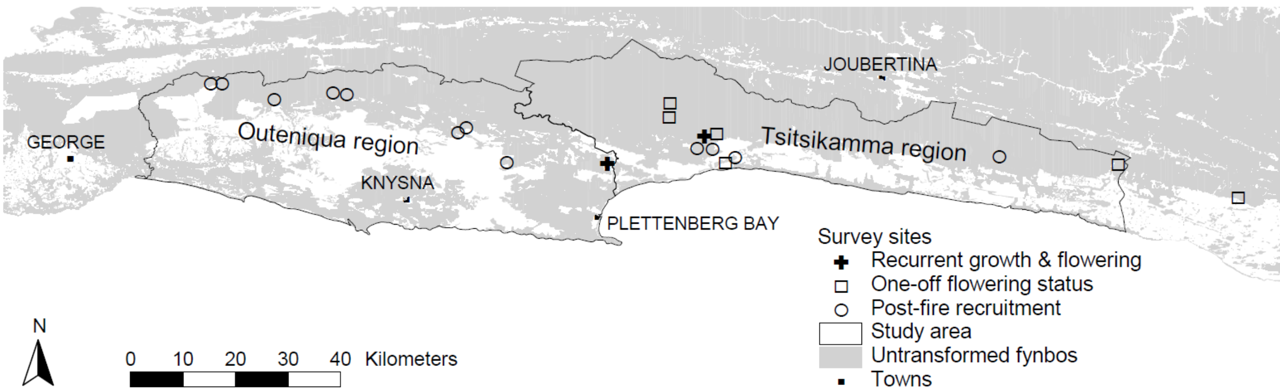

Figure 1: Locations of sites where three different types of surveys were done of proteoids, i.e. recurrent surveys of growth and flowering status, one-off surveys of flowering status, and post-fire recruitment success. The study area is divided into the Outeniqua and Tsitsikamma regions, to the west and east of the Keurbooms River, respectively.

Data analysis

Analyses of the three types of survey data outlined above were done as follows:

(1) We calculated for each site-species replicate, the proportion of the population that had flowered at least once, twice and three times or more at the time of surveying (at known plant ages).

(2) We calculated, for each plant age sampled and for the species and sites separately, the mean height of survivors, the proportion of the original marked population flowering, the proportion of the population surviving, and the mean number of flowerheads per flowering plant. We explored the relationship between plant height and the number of flowerheads per flowering plant at the time of the last survey (2011) for each of the respective species by means of least-squares regression.

(3) We calculated the seedling-parent ratio for each site-species replicate and applied a square root-transformation to conform to the assumption of normal distribution (Kolmogorov-Smirnov, P=0.91). We assessed the relationship between seedling-parent ratio and pre-fire vegetation age for all species combined using least-squares regression. Season of burn, age of the vegetation at the time of surveying, and pre-fire parent density (Bond 1984; Bond et al. 1984; Le Maitre 1988 a&b; Heelemann et al. 2008) may additionally affect recruitment success. However, in our sample, the seedling-parent ratio did not differ significantly between cool-season (June–November; 10.2 ± 5.7, mean ± SD, n=6) and warm-season (December–May; 9.4 ± 9.5, n=13) fires (*cf.* Heelemann et al. 2008), neither was it influenced by the (post-fire) age of the vegetation at the time of surveying ($F_{1,20}$=0.72, P=0.41, R^2=0.03), nor by parent density ($F_{1,20}$=0.03, P=0.87, R^2=0.01). We therefore did not account for these factors in our analysis of the effects of pre-fire vegetation age on recruitment success.

Results

Juvenile period

Juvenile periods of proteoids ranged from four to nine years (Table 1). There was considerable variation in the degree of flowering at any given plant age among sites and within species (Fig. 2). There were no consistent differences among the three most common study species in their rate of maturation. Across sites and species, less than 40 % of individuals had flowered once by the age of four years, while more than half had flowered once by the age of five years. At 11 years of age, 90–100 % of individuals had flowered at least once, more than half had flowered at least twice, while 28–83 % had flowered at least three times.

Table 1: Primary juvenile periods (years) of reseeding proteoids in the Tsitsikamma region, the Outeniqua Nature Reserve (immediately west of this study's Outeniqua region) and the western part of the Cape Floral Kingdom (CFK). The post-fire age (years) at which 50 % of the individuals in proteoid populations flowered once and three times (respectively) are also shown.

	Eastern-CFK		Western-CFK
	Tsitsikamma[a]	Outeniqua[b]	
Juvenile periods			
Protea neriifolia	4 – 9	4 – 6	4 – 5[c]
P. mundii	4		7[d]
P. repens		≥ 4	3[d]
P. lorifolia		5	
P. eximia	4		3[d]
50 % of population flowered once			
P. neriifolia	5 – 6	8 – 11	8[c]
P. mundii	6		
P. repens		10	
P. lorifolia		7	
50 % of population flowered 3x			
P. neriifolia	11	8 – 14	12[c]
P. mundii	11		
P. repens		14 – 15	
P. lorifolia		> 13	

Source: [a]Current study; [b]CapeNature (unpubl.); [c]Le Maitre (1992); [d]Kruger & Bigalke (1984)

Mortality of permanently-marked plants was low, with 93 % of *L. eucalyptifolium* and 98 % of *P. mundii* surviving four years post-marking and six years post-fire, and 95 % of *P. neriifolia* surviving six years post-marking and 15 years post-fire. The number of flowerheads per flowering plant was positively related to plant height in *L. eucalyptifolium* ($F_{1,30}$=12.7, P=0.001, R^2=0.30) and *P. mundii* ($F_{1,24}$=7.6, P=0.01, R^2=0.24), but not in *P. neriifolia* ($F_{1,28}$=2.9, P=0.10, R^2=0.09) at the time of the last survey (2011). The number of flowerheads per flowering plant did not vary widely within or among years (apart from *L. eucalyptifolium* where limited data restricted inference) and did not appear to increase with time during the periods surveyed (Fig. 3). The post-fire age at which populations attained a particular height or degree of flowering differed substantially between the two sites, but not between *P. mundii* and *L. eucalyptifolium* on the moist southern slope. A few individuals of *P. mundii* but none of *L. eucalyptifolium* started flowering at four years of age, while *c.* 30 % of the populations flowered by six years of age. At the drier site, few *P. neriifolia* flowered by 9–10 years of age, while only *c.* 30 % of the population flowered by 13–15 years of age.

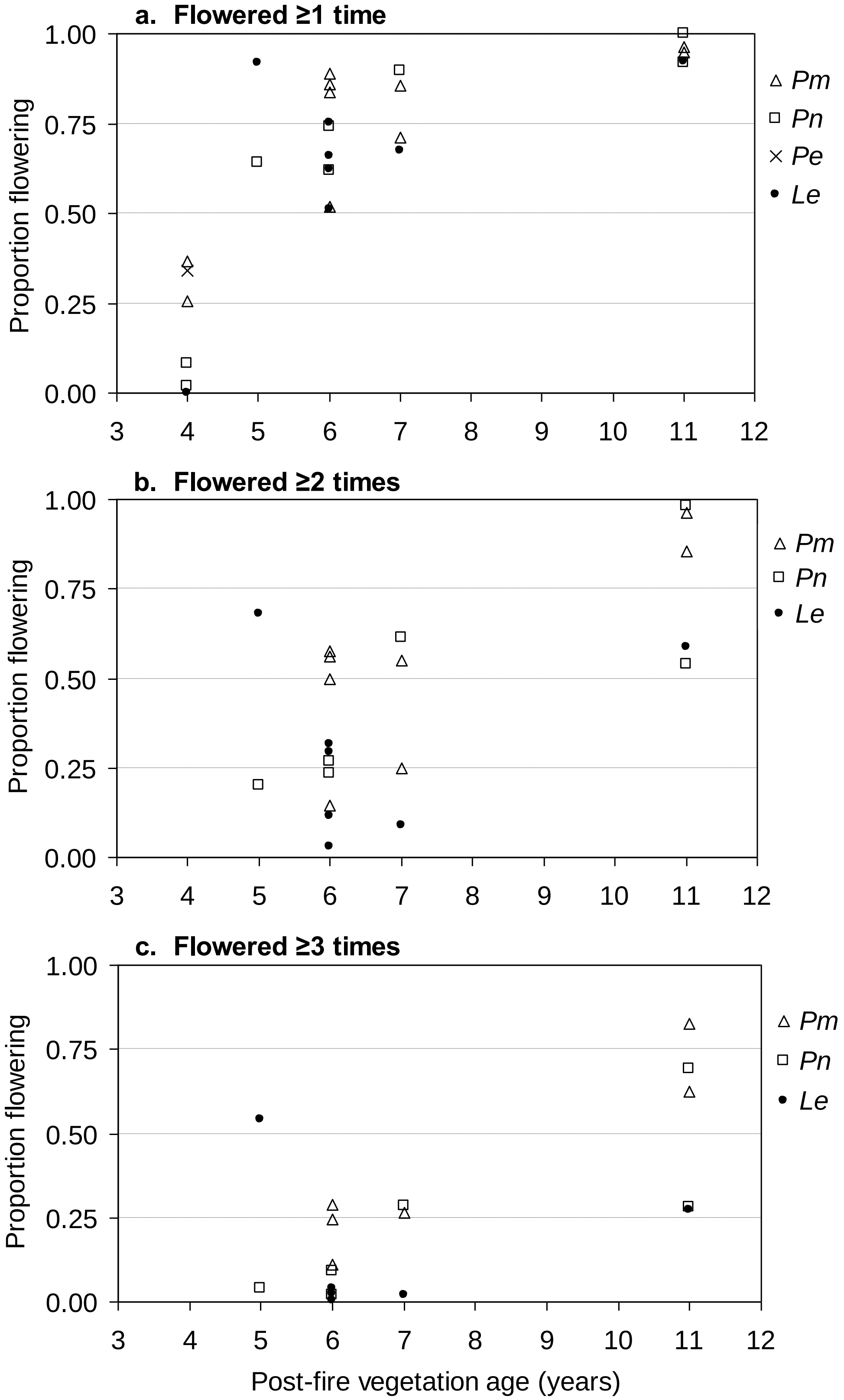

Figure 2: Proportions of populations of *Leucadendron eucalyptifolium* (*Le*), *Protea mundii* (*Pm*), *Protea neriifolia* (*Pn*) and *Protea eximia* (*Pe*) that have flowered at least (**a**) once, (**b**) twice, and (**c**) three times at different post-fire vegetation ages.

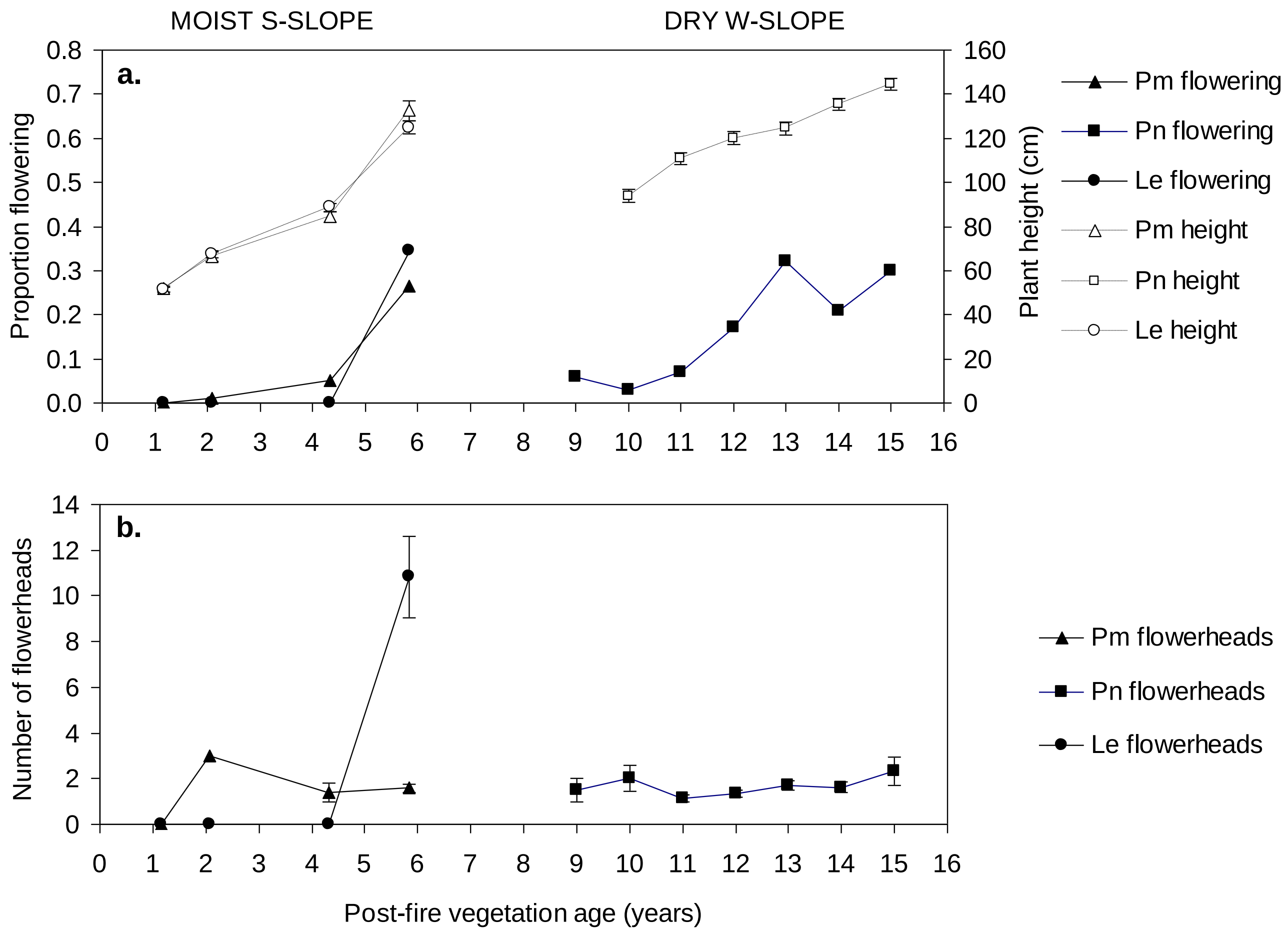

Figure 3: (**a**) The proportion of the population flowering, the above-ground plant height (mean ± standard error) and (**b**) the number of current-season flowerheads per flowering plant (mean ± standard error) at sequential post-fire vegetation ages of *Protea mundii* (*Pm*), *Protea neriifolia* (*Pn*) and *Leucadendron eucalyptifolium* (*Le*). *Pm* and *Le* were measured at 1–6 years post-fire on a relatively moist, south-facing slope, and *Pn* at 9–15 years post-fire on a relatively dry, west-facing slope.

Post-fire recruitment

Seedling-parent ratios (of all species collectively) were not significantly correlated with pre-fire vegetation ages ($F_{1,20}$=2.87, P=0.11, R^2=0.13) and ranged from 0 to 35.7 (Fig. 4). Post-fire recruits of *P. neriifolia* were absent from the site that burnt at five years of age, while recruitment was below replacement levels in *L. eucalyptifolium* and *P. mundii* (seedling-parent ratios of 0.05 and 0.11, respectively). Juvenile period surveys done at this particular site one year prior to the fire showed that less than 2 % of the individuals of *P. neriifolia* and *L. eucalyptifolium* flowered once, while 25 % of the individuals of *P. mundii* flowered once at the post-fire vegetation age of four years. Overall, seedling-parent ratios varied widely (coefficient of variation 105 %) within and among species as well as within pre-fire vegetation age classes (Fig. 4).

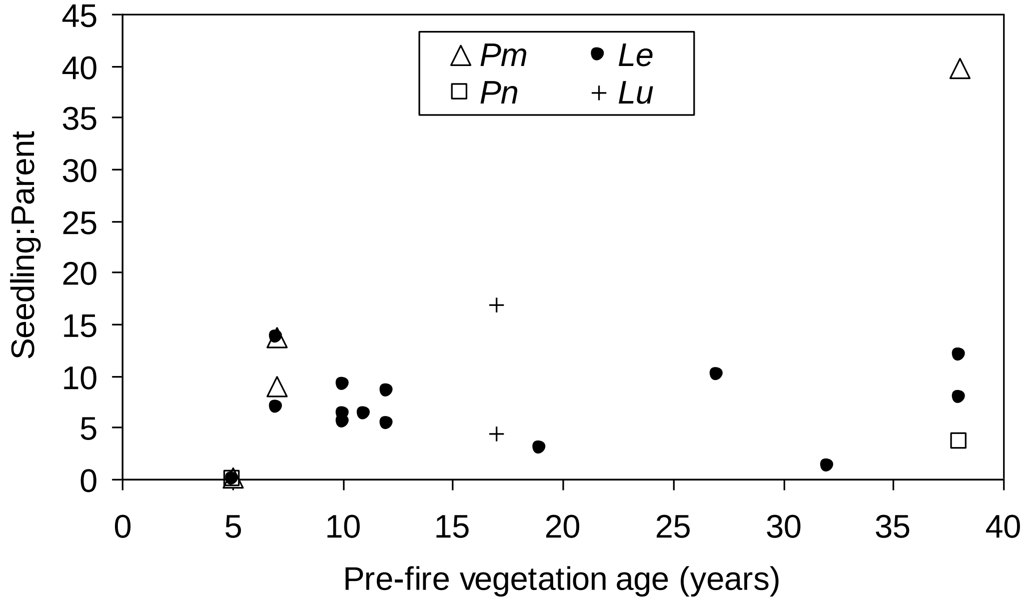

Figure 4: Post-fire recruitment in relation to the age at which the vegetation burnt. Recruitment is expressed as the ratio of the number of seedlings to burnt parents, and shown for four proteoid species, i.e. *Leucadendron eucalyptifolium* (*Le*), *L. uliginosum* (*Lu*), *Protea mundii* (*Pm*) and *P. neriifolia* (*Pn*).

Discussion

Juvenile period

Juvenile periods of proteoids ranged from four to nine years in our study, which are comparable to those at Outeniqua Nature Reserve, immediately west of the study area, those reported for the western part of the CFK (Table 1; CapeNature unpubl.; Kruger & Bigalke 1984; Le Maitre 1992), and those of proteoids in southeastern and southwestern Australia (Cowling et al. 1987; Richardson et al. 1990; Lamont et al. 1991b; Enright et al. 1996, 1998; Gill & McCarthy 1998; Bell 2001; Bradstock & Kenny 2003). However, there is usually a lag between the age at which the first plants flower and the majority flower (Kruger & Bigalke 1984). Early inflorescences furthermore do not necessarily produce fertile cones (Enright et al. 1996). In western Australian scrub heath, a detailed study of the canopy seed bank dynamics of *Banksia hookeriana* showed that even though the species started flowering at 3–4 years of age (similar to our findings), FRIs optimising the likelihood of successful recruitment were estimated at 15–18 years (Enright et al. 1996).

In North American temperate serotinous pine forests, under regimes of frequent disturbance, maturation ages optimising plant fitness were estimated to be 0.4 times the average disturbance interval (Clarke 1991). Median FRIs recorded in the study area since 1980 varied considerably (8.3–26.2 years) depending on the method of estimation (Chapter 2), and predict optimal juvenile periods of 3.3–10.5 years, which are in line with what we observed.

There was large variability in the degree of flowering of populations at given plant ages among sites and within species. In *B. hookeriana* (in western Australia), within and between year variability in cone production increased with plant age (Enright et al. 1996). In our study, the number of flowerheads produced per flowering plant did not vary widely within or among years in *Protea* species although it was more variable in the single year that *L. eucalyptifolium* flowering was recorded. Results from the two sites where we undertook recurrent surveys suggest that flowering status is more closely related to plant height than to plant age (*cf.* Le Maitre & Midgley 1991). The substantial difference between the two sites in the plants' age to maturation is unlikely to be due to species differences, given the lack of a species effect observed at the moist site as well as in our one-off surveys of flowering status. Site differences thus appear to play a key role in plant growth and maturation rates. The most noticeable abiotic difference between the two sites was aspect, with plants on the relatively dry, western slope being slower to grow and mature than those on the relatively moist, southern slope. Evidence for the effects of aspect (dry, northern or western slopes *vs*. moist, southern or eastern slopes) on flowering status as measured in one-off surveys was, however, ambiguous.

Post-fire recruitment

Recruitment was always above replacement levels following fires that burnt in vegetation of ≥7 years post-fire age. The lack of a relationship between recruitment success and pre-fire vegetation age, suggests that once a critical post-fire age (and by implication, seed bank size) is attained, factors other than seed abundance affect recruitment success. These factors may include season of fire, slope and aspect in relation to moisture regimes, pre-fire parent density and interspecific competition (Bond et al. 1984, 1995; Le Maitre 1988 a&b; Mustart & Cowling 1993; Laurie & Cowling 1994; Heelemann et al. 2008, 2010).

There was considerable variation in recruitment success for any given FRI, species or site (*cf.* Bond et al. 1984, 1995; Midgley 1989; Laurie & Cowling 1994). Average to very good (including the highest of all records) recruitment occurred at the site with the longest FRI (38 years). This finding is at variance with that of Bond (1980) in the Swartberg Mountains (*c.* 100 km inland from our study area) where senescence (40–45 years of age) negatively affected post-fire recruitment of fynbos. We concur with van Wilgen et al. (2011) that the occurrence of very old vegetation is not a key concern in the ecological management of fire in montane proteoid fynbos, both because it is very limited in extent (Bond 1980; Chapter 2), and because recruitment does not appear to be negatively affected by relatively long inter-fire periods.

Minimum fire return interval

Our results on post-fire recruitment success of proteoids suggest that FRIs of less than six years would result in the local extirpation of this guild from eastern coastal fynbos, whereas recruitment above replacement levels consistently should occur after fires at ≥7-year intervals. Application of Kruger & Lamb's (1978) rule of thumb (that 50 % of the individuals in a population should have flowered for at least three seasons) to observed proteoid flowering status (50 % of plants flowered once by 5–6 years of age, Fig. 2a), and assuming that plants flower every year after first flowering and that seeds take seven months to ripen (van Staden 1978), implies a minimum FRI of nine years for Tsitsikamma proteoid fynbos. We do not have data on the flowering status of populations at a post-fire age of nine years in order to support this estimate, but most, though not all, species surveyed had reached the required level of flowering at 11 years post-fire (Fig. 2c; Table 1). Using twice the primary juvenile period (in our case, twice >4 years; Figs. 2a & 3) as a guide for minimum FRIs (Bell 2001), suggests a lower threshold in excess of eight years. Substantial variation, both in flowering status and post-fire recruitment, as well as disparity among estimates of minimum FRI based on these measures, emphasise the need to empirically verify rules of thumb that are currently used as fire management guidelines. Verification may be done by relating pre-fire flowering status of proteoid populations to their post-fire recruitment response at corresponding sites (as done for the site which burnt at five years of age).

All sites from which we collected data to estimate juvenile periods were located in the Tsitsikamma region. Juvenile periods (and by implication, minimum FRIs) are likely to be considerably longer in dry habitats where plant growth rates are lower (Le Maitre & Midgley 1992). This is substantiated by the difference observed in growth rates and flowering status between the sites on a relatively dry, western and moist, southern slope, respectively. At a regional scale, rainfall is lower in the Outeniqua than in the Tsitsikamma region, and at Outeniqua Nature Reserve (immediately west of the study area) the time needed for 50% of individuals to flower once and three times, respectively, was longer than that in the Tsitsikamma region (Table 1). Median FRIs, recorded since 1980, have accordingly been shorter in the Tsitsikamma than in the Outeniqua region (Chapter 2). Overall, maturation rates of proteoids are comparable between the eastern- and western-CFK (Table 1) suggesting that variation is related to local moisture regimes (Kruger & Bigalke 1984) rather than a general east-west gradient within the CFK. Seydack et al. (2007) accordingly found an inverse relationship between FRI in fynbos shrublands and rainfall (related to plant productivity) along an altitudinal gradient in the Swartberg Mountains.

Range-restricted species or habitat specialists may have very specific FRI requirements (Kruger & Bigalke 1984). For instance, *P. grandiceps* (Near Threatened; Raimondo et al. 2009), a slow-growing, high-altitude species from the study area and elsewhere in the CFK, is slow to mature (>10 years; J.H.J. Vlok, pers. comm., 2012, local botanist) and favours rocky outcrops and steep slopes where it is relatively safe from frequent fires (Rebelo 2001). Some subpopulations of this species have been exterminated as a result of too frequent fires (J.H.J. Vlok, pers. comm., 2012, local botanist). A survey done on the Kammanassie Mountains (30 km inland of our Outeniqua region) showed that only 10 out of 200 plants flowered for the first time at nine years post-fire (CapeNature unpubl.).

Bradstock & Kenny (2003) discuss the limitations of using juvenile periods and life spans of the most sensitive plant guilds to inform boundaries for FRIs, and *inter alia* state that consistent favouring of one guild may in the long term lead to a loss of biodiversity. However, retention (and even dominance) of proteoids was shown to be key to the conservation of diversity in fynbos overall (Vlok & Yeaton 1999). Experience furthermore suggests that rigid control over fire regimes is largely unattainable (Keeley et al. 1999; Moritz 2003; van Wilgen et al. 2010), with wildfires providing sufficient variation to preclude consistent favouring of a particular plant guild.

In the same way that plant characteristics can be used to establish thresholds for FRIs, the post-fire development of habitat and fuel attributes (Haslem et al. 2011), and the life cycles and behaviour of selected animal species may be used (Gill & McCarthy 1998). In the Mediterranean shrublands of southwestern Australia, population modelling based on the demography and behaviour of rare, poorly-dispersing, ground-dwelling bird species suggested optimum FRIs in excess of plant maturation rates (Brooker & Brooker 1994; Gill & McCarthy 1998). South African fynbos does not have many endemic bird species, but some may be adversely affected by short FRIs. Both the Cape Sugarbird (*Promerops cafer*) and Protea Seedeater (*Crithagra leucopterus*) require mature proteoid fynbos for feeding and breeding, and it may take ≥10 years post-fire for fynbos to attract breeding birds (Milewski 1978; Martin & Mortimer 1991). The existence of adequate areas of mature fynbos in the landscape is thus a requisite for these birds' persistence. While the focus of this paper has been on establishing minimum FRIs based on plant attributes, it would also be important to ensure that at least a proportion of the vegetation is in the age classes of 10–20 years to conserve these faunal elements. This implies that the minimum age for burning would have to be greater than ten years for a proportion of the area.

Management implications

The suggested minimum FRI of nine years in relatively moist and productive Tsitsikamma fynbos is not intended to prescribe rigid management of fire according to a fixed burning rotation. Neither does it negate the need to consider site- or species-specific requirements. Instead it provides a lower threshold for a range of acceptable FRIs beyond which a significant decline of species populations is predicted (Bradstock & Kenny 2003; van Wilgen et al. 2011). Where two or more species of slow-maturing reseeders coexist, the FRI for maximising survival or abundance may be different (Gill & McCarthy 1998). Variation in fire regimes is therefore necessary to maintain plant diversity in the landscape (Cowling 1987; Gill & McCarthy 1998; Thuiller et al. 2007). In light of climate change and the associated increases in fire frequency that have been recorded locally (Forsyth & van Wilgen 2008; Wilson et al. 2010; Chapter 2, 3) and in temperate shrublands globally (Piñol et al. 1998; Williams et al. 2001; Keeley & Zedler 2009), managers attempting to maintain fire regimes within ecological thresholds ought to follow a precautionary approach, particularly at the lower end of the FRI range. In addition to allowing for variation in the fire regime, they should aim for mean FRIs towards the middle of the ecologically acceptable range, rather than at the lower end, as the increasing occurrence of unplanned fires is likely to reduce mean FRIs overall.

Both frequent and low intensity fires in fynbos and other temperate shrublands favour resprouters over slow-maturing, serotinous or myrmechocorous reseeders, leading to a loss in diversity overall (Haidinger & Keeley 1993; Vlok & Yeaton 1999, 2000). In large parts of the GRCMs, graminoid sprouters dominate, while proteoids are sparse or absent (Heelemann et al. 2010), notably in areas near plantations of alien pine trees (TK, pers. obs.). This likely resulted from frequent and low intensity burning in the past, aimed at protecting timber plantations from fire (Chapter 1). Facilitation of FRIs that would ensure the long-term persistence of proteoids in the GRNP is therefore a priority for fynbos conservation management, particularly where this guild has persisted in the landscape. Short interval fires, which alter vegetation structure (from woody to herbaceous; Kruger 1984; Lloret et al. 2003) and thus fuel dynamics, may set up negative feedback loops whereby short FRIs persist in the landscape (Haidinger & Keeley 1993; Milton 2004).

Fynbos vegetation in the GRCMs is currently severely threatened by widespread invasion by pine trees (*Pinus pinaster* and *P. radiata*) grown in plantations that are scattered throughout the landscape (Cowling et al. 2009; Chapter 1). Like the proteoids, pine trees are serotinous and fire-adapted, and repeated fires drive their rapid spread and proliferation (Richardson 1998). Prolonging the FRI (i.e. reducing the fire frequency) would thus generally be in the interest of invasive plant control by curbing the rate of spread of pines. On the other hand, in areas where the proteoids have already been lost due to past management practices, application of a single FRI that is shorter than the juvenile period of these pines (*c.* 5–6 years; Richardson et al. 1990) may in some instances provide an inexpensive means of substantially reducing dense infestations of young pine recruits.

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CHAPTER 5 – Vegetation responses to season of fire in an aseasonal, fire-prone environment and implications for management

To be re-submitted as a research paper:
Kraaij T, Cowling RM, van Wilgen BW, Rikhotso DR, Difford M. Vegetation responses to season of fire in an aseasonal, fire-prone environment and implications for management.

Abstract

1. Season of fire has marked effects on floristic composition in fire-prone Mediterranean-climate shrublands. In these winter-rainfall systems, summer-autumn fires lead to optimal recruitment of overstorey, reseeding, serotinous shrubs (often Proteaceae; hereafter 'proteoids') which are key to the conservation of floral diversity overall. We explored the effects of fire season on early establishment of proteoids in eastern coastal fynbos shrublands, a part of the Cape Floral Kingdom (South Africa) where rainfall occurs year-round and where fire danger weather and fire occurrence are largely aseasonal.

2. We planted proteoid seeds into exclosures, designed to prevent predation by small mammals and birds, in cleared fynbos in each of four seasons and monitored their germination and mortality for a year post-planting. We also surveyed recruitment success (the ratio of post-fire recruits to pre-fire parents) of proteoids after fires in different seasons.

3. Germination occurred during the cooler months and mostly within two months of planting, except for summer-plantings, which exhibited an additional 2–3 month delay. Germination appeared less rainfall-dependent than in winter-rainfall fynbos, suggesting that summer drought-avoiding dormancy is contracted and less influential on differences in recruitment success among fire seasons.

4. Recruitment success (survival after one year) in our seed planting experiment peaked following winter- and autumn-planting, while post-fire recruitment success in our field surveys peaked after autumn and spring fires. This discrepancy, coupled with large variation in recruitment success that was observed both within and among species and sites in both datasets, collectively suggests that seasonal patterns in post-fire recruitment are weak.

5. Other factors that affected recruitment success were species, pre-fire parent density and the post-fire age of the vegetation at the time of assessment, whereas rainfall (for six months post-fire) and fire return interval (>7 years) were unimportant.

6. *Synthesis and applications:* The weak and inconsistent response of proteoid recruitment to fire season implies that season of burn is essentially unimportant in eastern coastal fynbos. The lack of

a seasonal constraint on burning has encouraging management implications. It affords more flexibility for fire management than in shrublands associated with winter rainfall, although the need for adequate fire intensity remains.

Keywords: Cape Floral Kingdom, fire season, germination, *Leucadendron*, mortality, post-fire recruitment, prescribed burning, *Protea*, seed planting experiment, South Africa

Introduction

Fires ignited by lightning are the dominant natural disturbance in the species- and endemic-rich fynbos shrublands (Myers *et al*. 2000) of the Cape Floral Kingdom (CFK), South Africa (Kruger & Bigalke 1984; Seydack, Bekker & Marshall 2007). Empirical evidence indicates that season of fire can affect species abundance and floristic composition in fire-prone Mediterranean-climate shrublands (Bond 1984; Enright & Lamont 1989; Midgley 1989). Knowing how species respond to fire regimes (including fire season) is essential for ecologically sustainable management (Driscoll *et al.* 2010).

In the CFK, existing fynbos fire management protocols are largely based on knowledge of the summer-autumn fire regimes in the west (Kruger & Bigalke 1984; van Wilgen, Richardson & Seydack 1994). In the west, the climate is Mediterranean, with cool, wet winters and warm, dry summers (van Wilgen 1984) and post-fire plant recruitment is accordingly seasonally constrained (van Wilgen & Viviers 1985; Midgley 1989). In contrast, rainfall in the southeastern (coastal) part of the CFK occurs year-round (Schulze 1965), fire danger weather conditions (Chapter 3) and fire occurrence (Chapter 2) are largely aseasonal, and comparatively little is known about the effects of fire season on post-fire plant recovery (van Wilgen 2009).

Obligate reseeding shrubs with canopy-stored (serotinous) seed banks (almost exclusively members of the Proteaceae; hence, hereafter, ‘proteoids’) are highly susceptible to population decline under fire regimes that do not provide favourable post-fire recruitment conditions (Bell 2001; Lamont *et al.* 1991; Enright *et al*. 1998). This is owing to their whole seed bank being released post-fire (Lamont, Connell & Bergl 1991) and the seeds being short-lived after release, mostly germinating during the first favourable period (Cowling & Lamont 1987). Extreme variation in post-fire recruitment is characteristic of proteoids (van Wilgen & Viviers 1985; Cowling & Gxaba 1990), but in the Mediterranean-climate shrublands of the CFK and Australia, proteoid recruitment is generally higher after fires in summer-autumn than in winter-spring (van Wilgen & Viviers 1985; Cowling & Lamont 1987; Bradstock & O’Connell 1988; Enright & Lamont 1989; Midgley 1989).

Variation in recruitment success has been explained on the basis of: the size of pre-fire seed banks which vary with plant age (Le Maitre 1990; Lamont, Connell & Bergl 1991; Chapter 4), plant phenology (Jordaan 1949), pre-fire density (Bond, Vlok & Viviers 1984; Le Maitre 1988; Cowling & Gxaba 1990), pre-dispersal seed predation (Esler & Cowling 1990), post-dispersal seed predation and decay (and thus duration of seed exposure between release and germination; Bond 1984), climatic conditions favourable to germination, and the extent of post-germination mortality due to fungal pathogens, vertebrate and invertebrate herbivory, drought-stress and density-dependent thinning (Cowling & Lamont 1987; Enright & Lamont 1989; Midgley 1989; Botha & Le Maitre 1992).

Few studies have examined the effects of fire season on plant populations in fire-prone shrublands with a non-seasonal rainfall regime, where both fire season and intensity are variable (Bradstock, Williams & Gill 2002; van Wilgen 2009). In eastern inland fynbos, Heelemann *et al.* (2008) established that plant phenology and thus, seed availability, do not impose seasonal constraints on proteoid recruitment (*cf.* Le Maitre 1988), but that recruitment peaked after fires in autumn and spring, presumably coinciding with the bimodal peaks in rainfall.

We aimed to determine whether post-fire recruitment seasonality in the coastal (climatically more equable) part of the eastern CFK mirrors that of Heelemann *et al.* (2008) or whether recruitment success is unrelated to fire season, as hypothesised by van Wilgen and Viviers (1985). In addition to field surveys of recruitment success after fires in different seasons, our approach entailed a seed planting experiment aimed at identifying the mechanisms that underpin post-fire recruitment seasonality. Finally, we explore the management implications of our findings to inform ecological fire management protocols in fynbos shrublands associated with a non-seasonal rainfall regime.

Materials and methods

Study area

We focussed on the southeastern-CFK, and in particular, the coastal slopes of the Outeniqua Mountains (east of the Touw River) and Tsitsikamma Mountains (Fig. 1). A large portion of the area occurs within the recently established Garden Route National Park (Chapter 1).

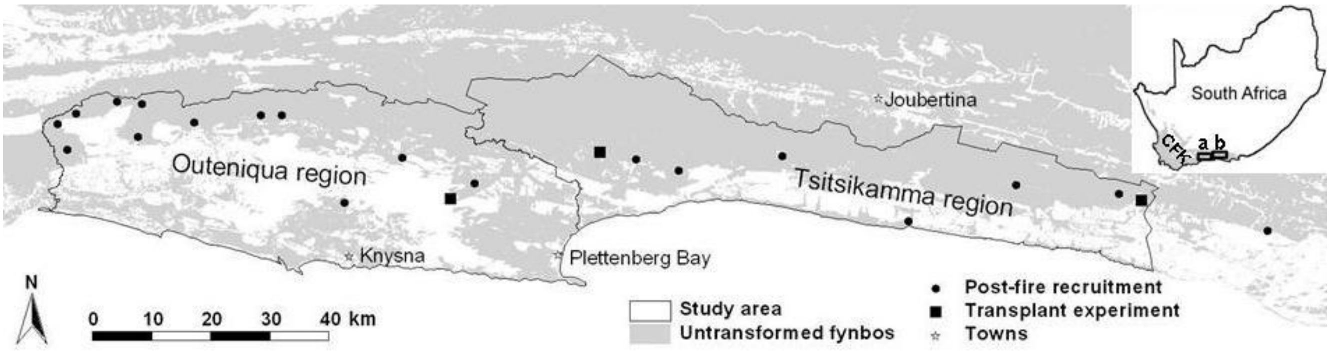

Figure 1: Locations of the sites where post-fire recruitment surveys and a seed planting experiment were conducted. The study area is divided into the Outeniqua and Tsitsikamma regions (**a** and **b** in insert, respectively), the Keurbooms River being the divide between these mountain ranges. The insert shows the location of the study area in relation to the Cape Floral Kingdom (CFK, grey-shaded) and South Africa.

Owing to maritime influence, the climate of the area is relatively equable (Schulze 1965). Rainfall occurs throughout the year, with winter months being the driest. Mean annual rainfall increases eastwards, from 820 to 1 078 mm in the Outeniqua and Tsitsikamma Mountains, respectively (Bond 1981; Southwood 1984). The proportion of summer rain also increases eastwards (Schulze 1965). While in the western-CFK, weather conditions suitable for fires dominate in the dry summer months (van Wilgen 1984), they are less seasonal in the southeastern-CFK (Chapter 3).

The fire-prone and fire-dependent vegetation of the study area largely comprises South Outeniqua Sandstone Fynbos and Tsitsikamma Sandstone Fynbos, in the Outeniqua and Tsitsikamma Mountains, respectively (Rebelo *et al*. 2006). These are tall, medium-dense proteoid shrublands, with an ericoid-leaved shrub understorey (dominated by Ericaceae) and a prominent restioid (Restionaceae) component. Overstorey proteoids common to both these vegetation types are *Leucadendron eucalyptifolium* (*Le*), *L. uliginosum* (*Lu*), *Protea eximia* (*Pe*), *P. mundii* (*Pm*) and *P. neriifolia* (*Pn*) (nomenclature follows Rebelo 2001). Flowering times are: *Le*, July–October; *Lu*, November–December; *Pe*, July–December (mainly August-October); *Pm*, January–September (mainly February–April); and *Pn*, February–November; (Rebelo 2001). However, there is a shift from winter-spring flowering to summer-autumn flowering both across and within lineages in the eastern-CFK (Cowling 1987), where *Pn* flowers in summer and *Le* in spring (Heelemann *et al.* 2008).

Seed planting experiment

We conducted a seed planting experiment to assess proteoid recruitment across planting (fire~) seasons and along a west-east gradient in the study area (Fig. 1). The respective sites were (i) 'West' (33.98094°S, 23.20743°E, elevation 312 m), (ii) 'Central' (33.90880°S, 23.43462°E, 553 m), and (iii) 'East' (33.96483°S, 24.26432°E, 488 m). All sites occurred at post-fire vegetation ages of >10 years, on gentle north-facing slopes. The experiment entailed three factors in a completely crossed design: (i) planting season – summer, autumn, spring and winter; (ii) site – West, Central and East; and (iii) species – *Le*, *Pm* and *Pn*, the most common overstorey proteoids in the area.

At each site, the vegetation in an area of 15 m x 15 m was slashed at ground level and removed to simulate the effect of fire. The cleared area was furthermore treated with a domestic disinfectant to simulate the sterilising effect of fire on pathogens, notably the fungi *Colletotrichum gloeosporoides* and *Phytophthora cinnamomi* (Botha & Le Maitre 1992). The cleared area had a 3 m buffer around the perimeter (to reduce edge- and shading effects) and the experimental site in the centre, comprising twelve plots (of 2.0 m × 2.5 m each), three per season (allocated randomly to plots).

Flower heads or seed cones of the study species were harvested from local populations one month prior to each of the four planting events. Cones were harvested from the current or previous season's crops and oven-dried at 40°C until seeds were released (Mustart & Cowling 1993). Apparently viable (plump and unscarred) seeds were hand-sorted (Mustart & Cowling 1991); about 90 % of such sorted seeds will germinate in controlled conditions (Le Maitre 1990). The seeds were planted on four occasions: in July 2010 (winter), October 2010 (spring), January 2011 (summer) and April 2011 (autumn). One month prior to the planting of seed, regrowth of vegetation was cleared and disinfectant reapplied to the respective season's plots. Seeds were lightly pushed into the ground (approx. 5 mm deep), simulating the habit of *Protea* seeds to anchor and orientate optimally in the soil by means of specialised hairs (Rebelo 2001). Seeds and seedlings were protected from small mammal and bird predation (Bond 1984; Le Maitre 1988) by exclosures made from bird mesh (13 mm gauge size) pegged to the ground. Each plot contained three exclosures (each approx. 1.5 m x 0.4 m and 0.15 m high, closed at the top) and each exclosure contained 34 seeds of each species (102 seeds per species per plot), planted in rows such that seeds within and between rows were 50 mm apart (Midgley, Hoekstra & Bartholomew 1989; Mustart & Cowling 1993). Germination and seedling survival were monitored during the first week of each month for one year after planting. A standard rain gauge was mounted 1.2 m above the ground at each site and rainfall measured monthly.

For analyses, exclosure data were combined per species per plot (*n*=108). We explored the effects of season, site and species on germination, mortality and survival at one year post-planting (expressed as proportions of planted seed), respectively, using logistic regression models, and assessed the significance of effects using Wald tests (Harrell 2001; Agresti 2002).

Post-fire recruitment surveys

In areas with known recent histories of fire occurrence, we surveyed (during 2007–2012) recruitment success of overstorey proteoids (*Le*, *Lu*, *Pe*, *Pm*, *Pn*) within four years post-fire (1.9 ± 0.7 years, mean ± standard deviation). We counted the number of proteoid seedlings (post-fire recruits) in relation to the number of burnt parents (pre-fire population) (Bond, Vlok & Viviers 1984) within belt transects (2 m x 30 m). We located 19 survey sites throughout the study area (Fig. 1), providing 46 site-species replicates, and surveyed 3.9 ± 2.4 transects per survey site. Fire return interval (~pre-fire vegetation age) ranged from 7–38 years, i.e. intervals where recruitment is unlikely to be constrained by seed shortages associated with juvenile proteoids (Chapter 4). We obtained rainfall figures (measured at Knysna) for a period of six months after each fire surveyed.

For each site-species replicate we calculated the seedling-parent ratio as a measure of recruitment success. We were primarily interested in the effects of fire season (*n*=46) on recruitment success, but considered other variables known to affect recruitment (Bond 1984; Bond, Vlok & Viviers 1984; Heelemann *et al.* 2008), namely fire return interval (pre-fire vegetation age) (*n*=21), post-fire age of the vegetation (at the time when recruitment was assessed) (*n*=46), parent density (*n*=33), post-fire rainfall (*n*=46) and species (*n*=46).

We used a linear plus rule-based ensemble procedure 'RuleFit' with ten-fold cross-validation (Friedman & Popescu 2008) to determine the importance of predictor variables in affecting seedling-parent ratio. Predictor importance is expressed relative to the most important predictor and reported on a percentage scale. Predictor effects are shown using partial dependence plots; these show the marginal effect of a predictor on the response variable, after integrating out the effect of the other variables in the model (Friedman & Popescu 2008). We subsequently used a generalised linear model (GLM) fitted by quasi-likelihood and the so-called square link (McCullagh & Nelder 1989; Hilbe 2010), to test for the significance of the effect of fire season on seedling-parent ratio. Statistical analyses were done in R version 2.15.0 (2012).

Results

Seed planting experiment

Rainfall patterns during the course of the experiment were similar to long-term trends and thus representative of the conditions that characterise the region, except for the second winter being relatively wet (Fig. 2). Overall, 38% of planted seeds (*Le* 20%, *Pm* 45%, *Pn* 50%), germinated, and 16% of these germinants (*Le* 30%, *Pm* 14%, *Pn* 10%), i.e. 6% of planted seeds, died within one year post-planting (Fig. 2). Germination was limited to the cooler months (March/April–November) and largely occurred within two months post-planting excepting a further 2–3 month delay in germination of summer-plantings (Fig. 3). Additionally, a small proportion of winter- and spring-plantings germinated during their second cold season post-planting (Figs 2&3). Mortality did not differ among planting seasons and rather appeared to peak after heavy rainfall events. Trends in germination and survival (at one year post-planting) were similar; we henceforth only present the latter as a composite measure of recruitment success (accounting for germination and mortality).

Survival differed significantly among planting seasons, sites and species, with *Le* survival being poorer than that of *Pm* and *Pn*. Survival pooled across sites and species was highest in winter-plantings, decreasing through autumn- and summer- to spring-plantings (Figs 2&4). Significant interactions occurred among the experimental factors (Table 1; Fig. 4), i.e. seasonality in survival was not consistent among species within sites, nor among sites within species. The western and central sites were more similar to each other than to the eastern site.

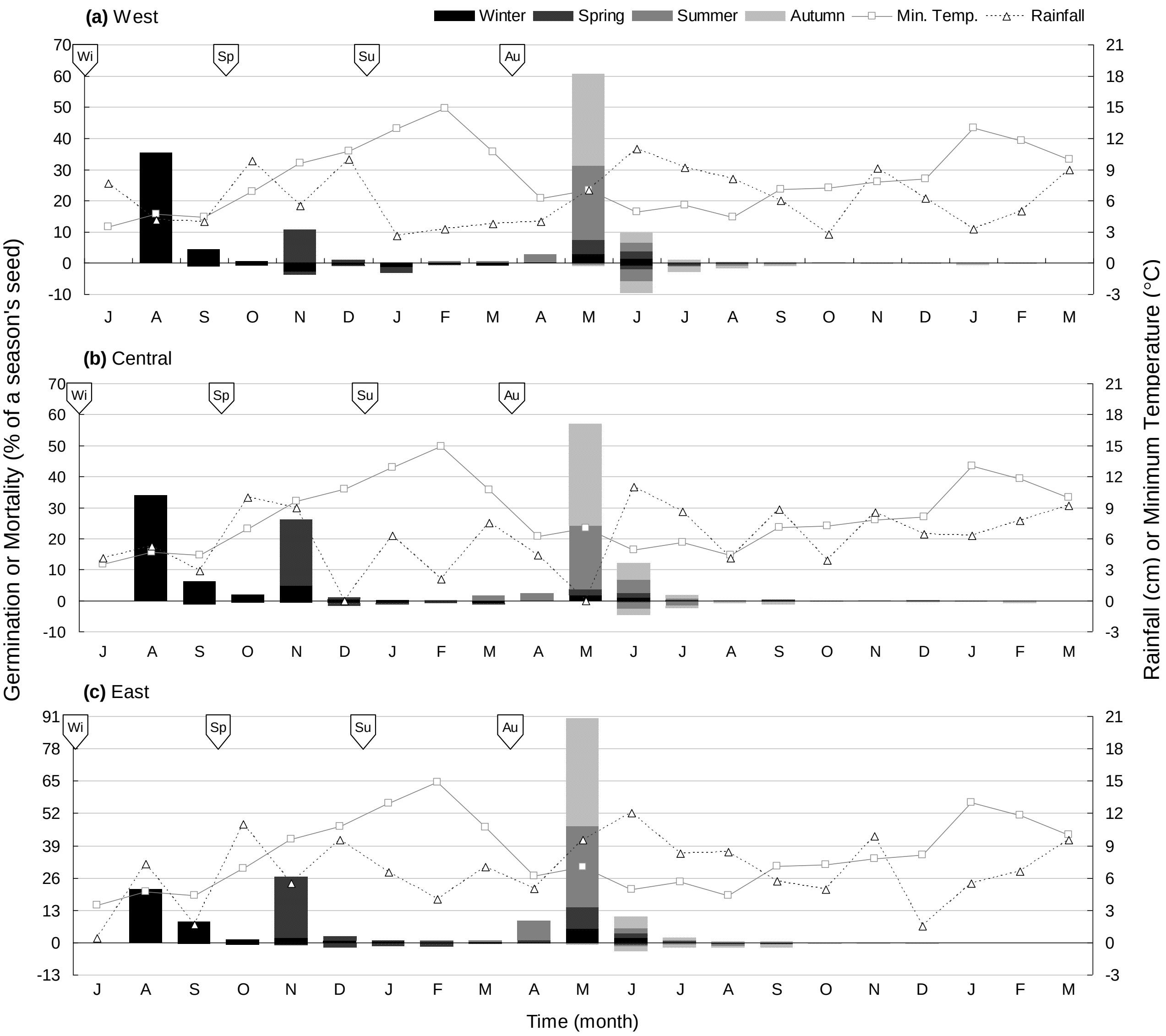

Figure 2: The number of new germinants (positive y-axis) and mortalities (negative y-axis) recorded during each month (as observed during the first week of the following month), expressed as a percentage of seeds planted per season at three sites **(a-c)** along a west-east gradient. Block arrows indicate planting occasions (Wi, Winter; Sp, Spring; Su, Summer; Au, Autumn). Line-series show monthly rainfall (recorded on site) and the minimum temperature recorded per month at Keurboomsrivier Plantation.

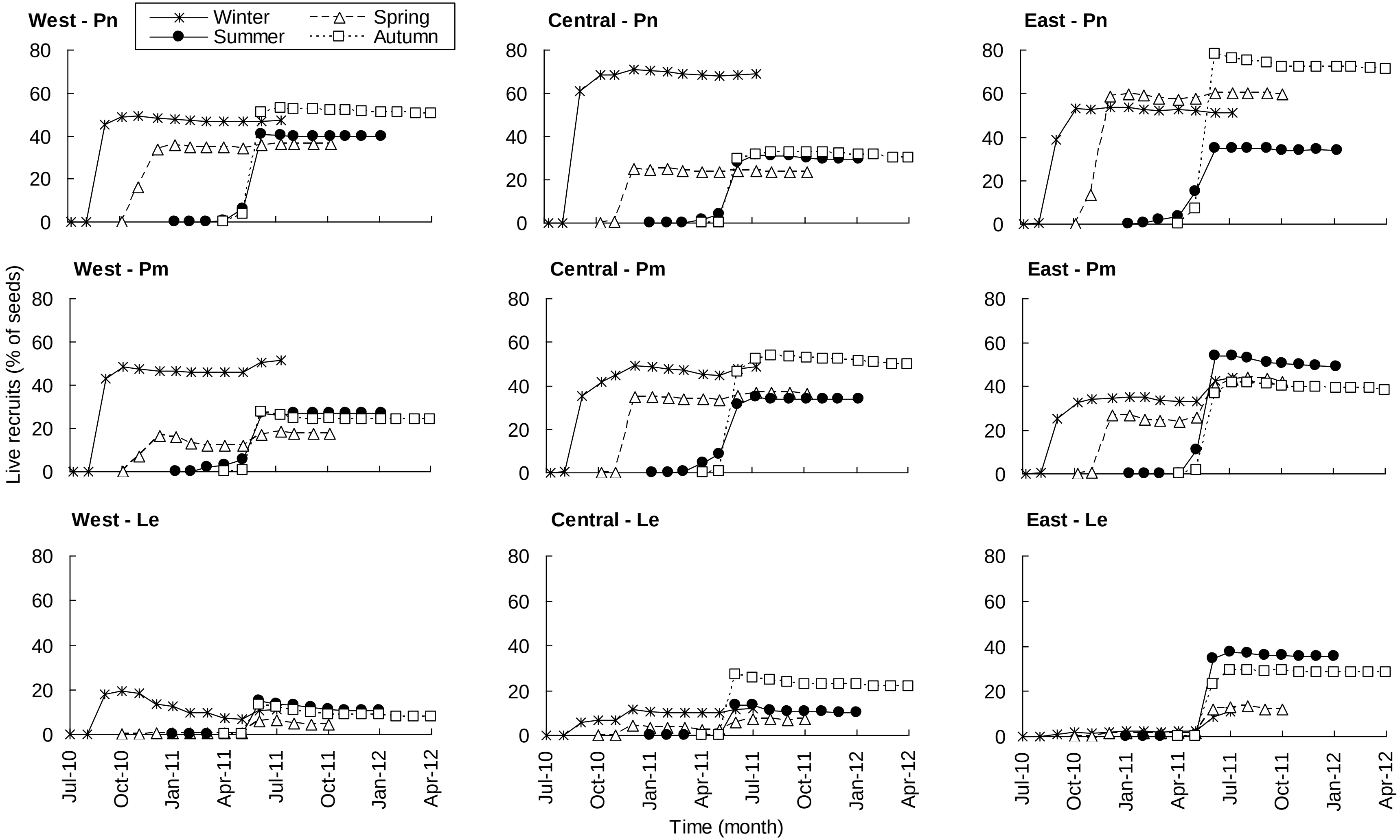

Figure 3: Live recruits of three Proteaceae species (Le, *Leucadendron eucalyptifolium*; Pm, *P. mundii*; Pn, *Protea neriifolia*) observed within the first week of each month, expressed as a percentage of seeds planted under predator-exclosures in four seasons after clearing of above-ground vegetation at three sites (West, Central, East). Zero values at the start of each series mark planting occasions for each of the austral seasons.

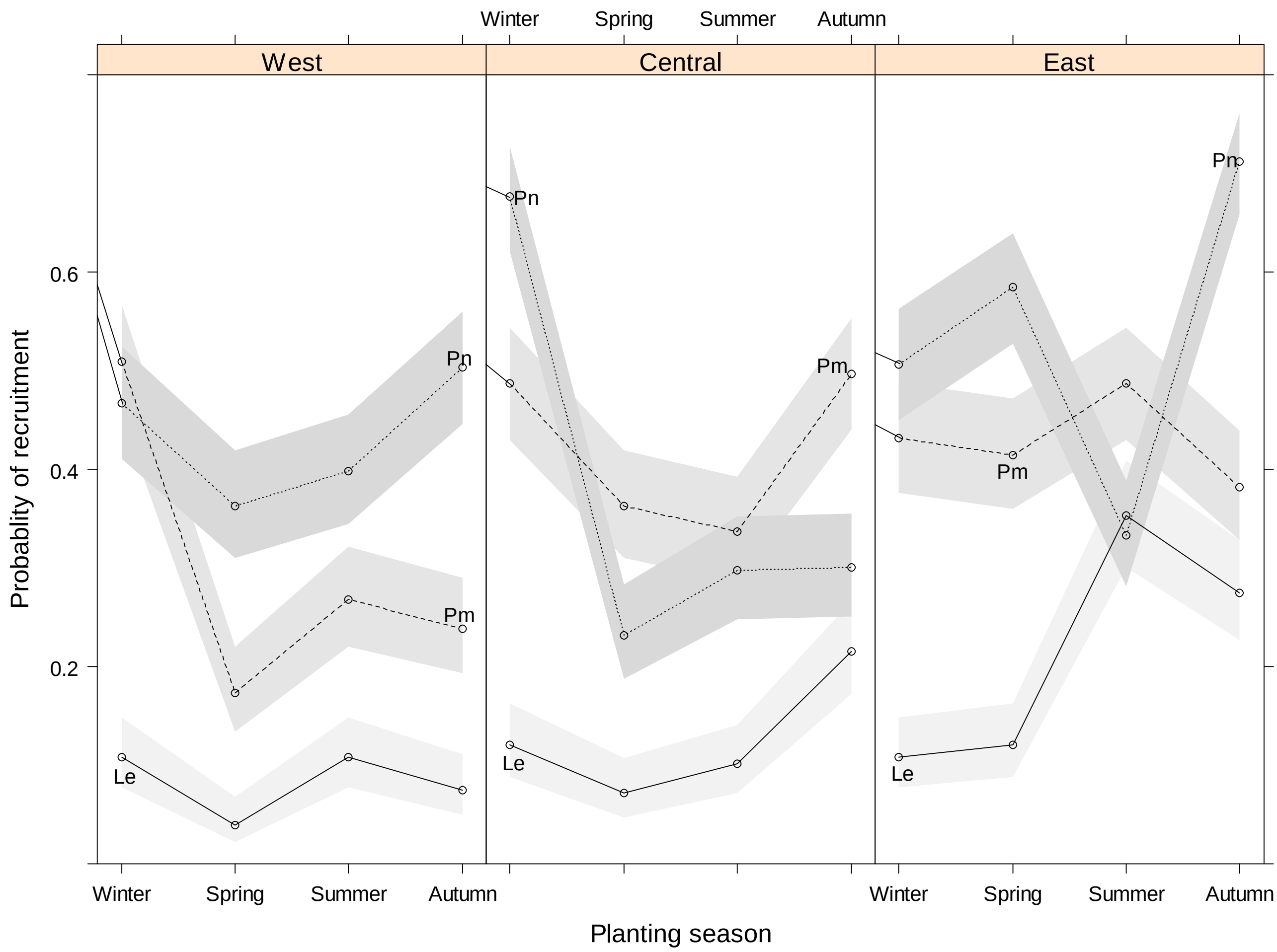

Figure 4: The probability of survival (at one year post-planting) across planting seasons, sites (West, Central, East) and species (Le, *Leucadendron eucalyptifolium*; Pm, *Protea mundii*; Pn, *P. neriifolia*), as estimated by logistic regression model. Bands show 95% confidence intervals.

Table 1: Wald statistics (Type II tests) for the logistic regression model of the effects of planting season, site and species on recruitment (measured as survival at one year post-planting as a proportion of seeds planted).

	Wald χ^2	df	Pr(>χ^2)
Season	108.6	3	<0.001
Site	122.5	2	<0.001
Species	704.4	2	<0.001
Season × Site	97.8	6	<0.001
Season × Species	104.4	6	<0.001
Site × Species	66.9	4	<0.001
Season × Site × Species	174.7	12	<0.001
Residuals		72	

Post-fire recruitment surveys

Of the 46 site-species replicates sampled, six were winter burns, 18 spring, 14 summer and eight autumn burns. Seedling-parent ratios varied widely (0–43, coefficient of variation 115%) within and among seasons, species and regions (Outeniqua *vs.* Tsitsikamma; Fig. 1) (Fig. 5). The RuleFit model fitted the data well without over-fitting (variance explained = 97.7%, normalised root-mean-square error = 0.15, normalised standard deviation = 0.99). The model showed the most important variables affecting recruitment success to be species (estimated relative importance averaged over all predictions = 100%), parent density (56%), post-fire vegetation age (55%) and fire season (39%), while post-fire rainfall (22%) and fire return interval (11%) were unimportant (Fig. 6). Autumn and spring fires resulted in better recruitment than winter and summer fires. Recruitment was negatively related to parent density at densities of <6000 parents/ha and positively related to the post-fire age (>26 months) of the vegetation at the time of assessment. According to the GLM, fire season was significant at the 10% level in affecting post-fire recruitment success ($F_{3,42}$ = 2.53, *P* = 0.07).

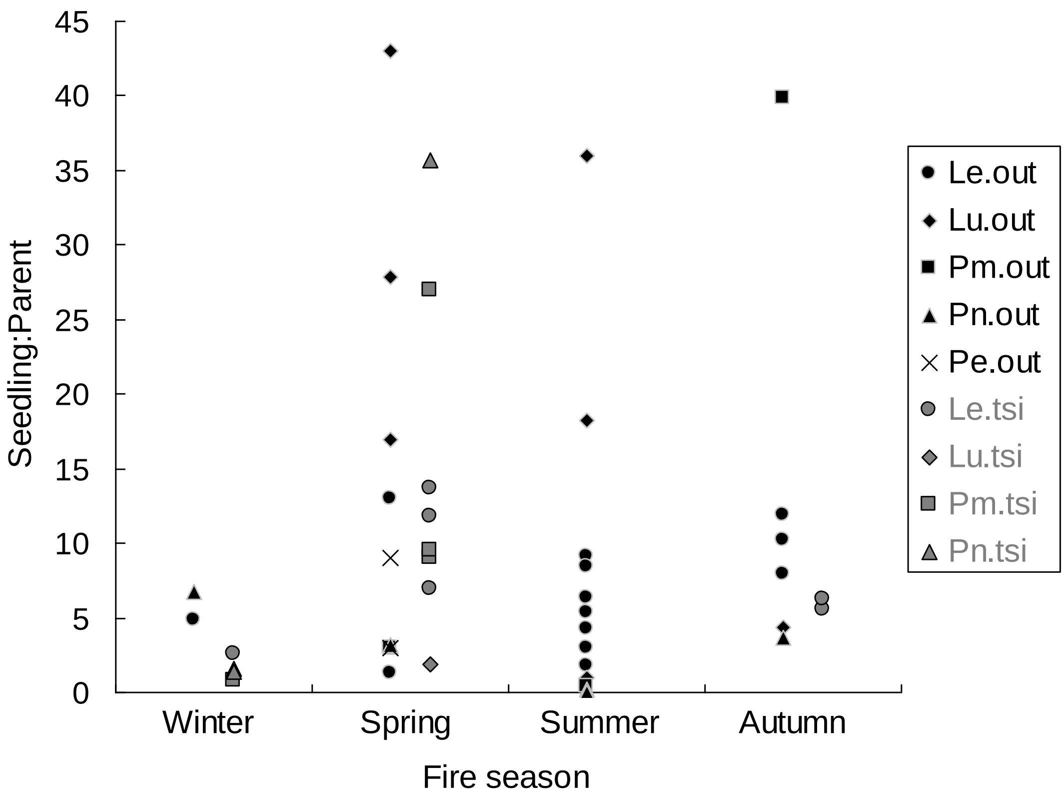

Figure 5: Recruitment success (expressed as seedling-parent ratio) after fires in different seasons, distinguishing between proteoid species (Le, *Leucadendron eucalyptifolium*; Pe, *Protea eximia* Pm, *P. mundii*; Pn, *P. neriifolia*) and the study regions (out, Outeniqua; tsi, Tsitsikamma).

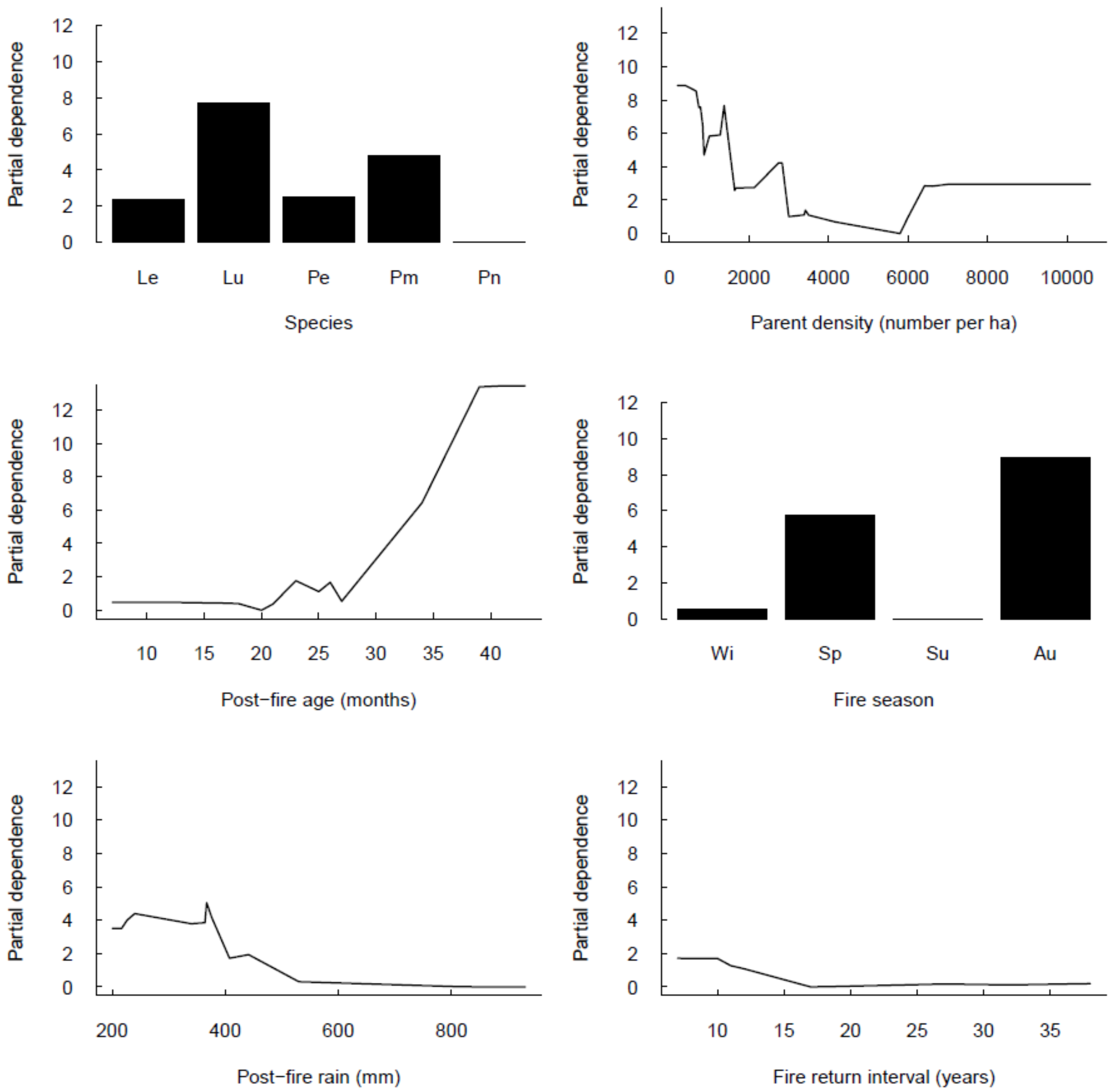

Figure 6: Plots of partial dependence of post-fire recruitment success (measured as seedling-parent ratio) on predictor variables as modelled by a linear plus rule-based ensemble procedure (RuleFit). Panels are arranged row-wise from top left in order of decreasing variable importance: species (Le, *Leucadendron eucalyptifolium*; Pe, *Protea eximia*; Pm, *P. mundii*; Pn, *P. neriifolia*), parent density, post-fire vegetation age at the time of assessment, fire season (Wi, winter; Sp, spring; Su, summer; Au, autumn), post-fire rainfall (during six months post-fire) and fire return interval.

Discussion

Germination and mortality in relation to rainfall and temperature

We found no strong relationships between germination or mortality and rainfall. In the aseasonal environment, germination was generally immediate, and subsequent mortality (16% of germinants during one year) was low. Levels of proteoid germination (20-50%) in our field experiment were comparable to those in other field studies (*c.* 10-60%, Cowling & Lamont 1987;

24%, Midgley, Hoekstra & Bartholomew 1989; 45-80%, Mustart & Cowling 1993) and under optimal laboratory conditions (30-60%, Van Staden & Brown 1977). Distinguishing between fertile and infertile seeds is problematic in *Leucadendron*, unlike in *Protea* (Van Staden & Brown 1977). Ineffective sorting of *Le* seeds may thus have accounted for their comparatively poor germination in our experiment, although poor germination does not appear to be the norm in *Leucadendron* in the field, as seen from our post-fire surveys.

Our results suggest that moisture availability will not constrain proteoid establishment in aseasonal environments, as it does elsewhere in South African and Australian shrublands where seasonal droughts are a feature (Bond 1984; Lamont, Connell & Bergl 1991; Mustart *et al.* 2012). Proteoids show a summer drought-avoiding dormancy in many areas (Deall & Brown 1981; Bond 1984; Midgley, Hoekstra & Barholomew 1989) with germination following a temperature plus moisture cue (Van Staden & Brown 1977) which is met by the cold and wet conditions of winter (Le Maitre 1990). In Mediterranean climates, proteoid germination is thus positively correlated with rainfall (Le Maitre 1988) and negatively correlated with temperature (Cowling & Lamont 1987; Mustart & Cowling 1991), but it was not clear whether these relationships would hold in equable coastal climates where rainfall is evenly distributed throughout the year.

In the semi-arid Swartberg Mountains (inland of the study area, where rainfall is also largely aseasonal, but where summer droughts are more severe due to higher evapo-transpiration associated with higher temperatures and lower humidity; Seydack, Bekker & Marshall 2007) germination of proteoids was strongly correlated with temperature but not with monthly rainfall (Midgley, Hoekstra & Barholomew 1989). We likewise found no correlation between (i) monthly rainfall and the timing of germination (or mortality) in our experiment or (ii) post-fire rainfall and recruitment success in our post-fire surveys, suggesting that post-fire rainfall *per se* is seldom limiting to germination and early survival in the study area. However, we observed a delay in germination following summer-planting which appeared to be due to the absence of low temperatures (minimum monthly temperature <10°C) that are typically needed to stimulate germination in proteoids elsewhere (5°C, Van Staden & Brown 1977; 10°C, Mustart & Cowling 1991). In the aseasonal shrublands of southeastern-Australia, ambient temperature also strongly controlled germination, with high summer temperatures presumably imposing secondary dormancy on seeds irrespective of rainfall (Bradstock & Bedward 1992). Germination thus appears to be prevented during mid-summer when moisture deficits are most likely due to high temperatures rather than the absence of rainfall (as opposed to the combination in Mediterranean climates; Deall & Brown 1981).

In our study, mortality was not affected by planting (fire~) season, unlike in the more arid Swartberg Mountains where summer mortality was higher after winter fires than after summer fires (Midgley 1988). The largest die-off (of very young seedlings) in our study occurred in response to heavy rainfall event(s) during autumn of 2011 (*cf.* De Luís *et al.* 2001) rather than in response to seasonal drought.

Effect of fire season on recruitment

We found that fire season had little effect on post-fire recruitment, which is in strong contrast to the responses to fire season in many shrubland communities elsewhere. Germination largely occurred within two months post-planting, except in the case of summer-plantings which exhibited an additional two–three month delay. This delay did, however, not result in significant suppression of recruitment (mortality of seed did not increase due to extended exposure to decay) or increase in seedling mortality. This was contrary to the observations of others in the more markedly seasonal Swartberg fynbos after spring and summer fires (Bond 1984; Bond, Vlok & Viviers 1984) or in spring-plantings inside rodent exclosures (Midgley, Hoekstra & Barholomew 1989). However, favourable conditions for germination after summer fires are likely to occur sooner or more regularly under a regime of evenly distributed rainfall (compared to winter-rainfall or semi-arid regimes). Because germination in the study area is less rainfall-dependent (see above) than in winter-rainfall fynbos, the germination delay is contracted (implying reduced exposure of seeds to predation or decay) and therefore less influential on recruitment success among fire seasons.

Recruitment success (measured as survival one year after planting) in our seed planting experiment differed significantly among planting seasons, being highest following winter- and autumn-plantings. However, the experimental factors interacted significantly, with the seasonality of recruitment varying greatly among species within sites and within species among sites. Recruitment was thus not consistently superior after disturbance in any particular season.

Post-fire recruitment success measured in our field surveys also differed significantly among seasons, but peaked after autumn and spring fires (as opposed to winter and autumn peaks in our experiment). Heelemann *et al.* (2008), in more inland eastern fynbos, also observed peaks in recruitment after autumn and spring fires, and explained these on the basis of the bimodal (spring-autumn) rainfall regime of the area. However, we question whether this simple relationship adequately explains, and provides evidence of, seasonality in post-fire recruitment in eastern fynbos, particularly in light of a lack of correlation between germination and rainfall in both eastern coastal fynbos (the current study) and further inland (Midgley, Hoekstra & Barholomew 1989). Moreover, rainfall in the study area is not strictly bimodal and may be more appropriately described as aseasonal. Although long-term means reveal peaks in spring and autumn, rainfall occurs throughout the year with marked variation in seasonality among years.

The discrepancy between the seasonality of recruitment in our experiment (winter and autumn peaks) and in our post-fire surveys (autumn and spring peaks), as well as the large variation within and among species and sites in both these datasets, collectively suggests that seasonal patterns in post-disturbance recruitment are weak in eastern coastal fynbos. Good (or poor) recruitment may be expected at any time of the year and may vary considerably between years. A weak seasonal response in recruitment is plausible under an equable, coastal climate with year-round rainfall and is in accordance with the lack of seasonality recorded both in fire danger weather conditions (Chapter 3) and historical fire occurrence (Chapter 2) in the area. In the analogous aseasonal shrublands of southeastern-Australia, the effects of fire season on recruitment are equally unpredictable, given the high level of year to year variation in seasonal rainfall (Bradstock & Bedward 1992). These authors suggested that, in the longer term, the timing of fire relative to sequences of wet and dry years may be of equal importance to fire season in its effect on proteoid populations.

Effects of other factors on recruitment

Our results suggest that recruitment may also vary according to species, the density of parent plants, and the post-fire age of the vegetation at the time of assessment. Large variation in post-fire recruitment, as observed in our study (Fig. 5), is characteristic of fynbos proteoids (van Wilgen & Viviers 1985; Cowling & Gxaba 1990), even within favourable fire seasons (post-summer/autumn fire seedling-parent ratios: 12–19, Bond 1980; 0–21, Bond, Vlok & Viviers 1984; 3–15, van Wilgen & Viviers 1985; 0–9, Le Maitre 1988), and may be caused by a variety of factors. In our study, individual species differed in their recruitment responses (Bond, Vlok & Viviers 1984; Midgley, Hoekstra & Bartholomew 1989), which may be related to wide variation (among species and/or habitats) in post-emergence desiccation tolerance (Mustart *et al.* 2012). Large variability in regeneration within and between species and fire events, suggests that generalisations based on studies of single species or fires should be treated with considerable caution.

In our study, parent density had a greater effect on recruitment success than fire season had. Other studies have found parent density either to have no effect (Cowling & Gxaba 1990), or more (Le Maitre 1988) or less (Bond, Vlok & Viviers 1984; Midgley 1989; Esler & Cowling 1990) effect, than that of fire season. Negative effects of parent density on recruitment have been ascribed to suppressed seed production (Bond, Vlok & Viviers 1984), although evidence is conflicting at the individual and population levels (Esler & Cowling 1990).

Recruitment success increased with post-fire vegetation ages (at the time of assessment) of >26 months. This does not support the notion of increases in seedling mortality with post-fire vegetation age (Bond, Vlok & Viviers 1984). Instead, decay and loss of cones from parent skeletons may have resulted in undercounting of parents in older post-fire ages. Alternatively, small size of seedlings in very young post-fire ages may have resulted in their being undercounted. Restricting the observation window to 1–2 years post-fire should reduce this source of noise in the data. Fire return interval may also affect recruitment success (Bond 1980) through its effect on seed availability, but had no effect in our study as we deliberately excluded data of short (<7 year) interval fires, known to inhibit recruitment (Chapter 4).

Management implications

Prescribed burning is seen as an important management option in fire-prone shrublands globally (van Wilgen, Richardson & Seydack 1994; Morrison, Buckney & Bewick 1996), but its use is constrained by many factors, including the need to burn within acceptable limits of season, frequency, intensity and safety (Bradstock, Williams & Gill 2002; van Wilgen *et al.* 2011). The weak and inconsistent response of proteoid recruitment to fire season implies that season of burn is essentially unimportant in eastern coastal fynbos, and this would remove at least one constraining factor, which should improve the chances of carrying out successful burns. However, various other constraints on fire management remain. Fire return intervals should allow for adequate seed production in slow-maturing obligate reseeders to ensure post-fire regeneration (Chapter 4). Fire intensity needs to be sufficiently high to stimulate seed release and germination in serotinous (Bradstock & O'Connell 1988; Midgley & Viviers 1990) and large or hard-coated, soil-stored seeds (Jefferey, Holmes & Rebelo 1988; Bond, Le Roux & Erntzen 1990; Knox & Clarke 2006). Additionally, there is evidence that variation in fire regimes is necessary to maintain plant diversity in the landscape (Thuiller *et al.* 2007; Gill & McCarthy 1998), and particularly in an unpredictable, aseasonal environment.

Ecological requirements of fire regimes furthermore have to be traded off with the need for safety of human lives and assets (commercial timber plantations, in particular in the study area; Chapter 1), which often present considerable management challenges (Morrison, Buckney & Bewick 1996; van Wilgen, Forsyth & Prins 2012). The number of days per annum with weather conditions meeting both the ecological need for fire intensity and human needs for fire safety, is typically low in fynbos environments (*c.* 10% of days annually; van Wilgen & Richardson 1985). Implementation of further restrictions based on fire season (arising from research suggesting that fynbos recruitment is highly seasonal; Bond, Vlok & Viviers 1984; van Wilgen & Viviers 1985) made prescribed burning of fynbos at a large scale unattainable (van Wilgen 2009). The lack of a seasonal restraint on burning in eastern coastal fynbos therefore has significant and encouraging management implications in affording more flexibility for fire management in this area.

Although prescribed burns contributed little to, and wildfires dominated, the recent fire history of the area (Chapter 2), prescribed burning remains necessary: (i) in key locations to reduce the risk of fire spreading from fynbos to adjacent timber plantations (Chapter 1); (ii) along the wildland-urban interface (Radeloff *et al*. 2005; van Wilgen, Forsyth & Prins 2012); (iii) as a tool in the management of alien invasive plants (Roura-Pascual *et al.* 2009); and (iv) to rejuvenate fragments of fire-dependent vegetation where ignition sources have been reduced or eliminated by transformation of the surrounding landscape . Our findings suggest that prescribed burning may be done in these instances during any season within a framework of adaptive management (van Wilgen *et al.* 2011). Managers furthermore do not have to allocate large amounts of resources to fight wildfires that are burning in the 'wrong' season and may conduct back-burns to contain wildfires during any season.

In conclusion, because the seasonal occurrence of fires may vary over the geographical range of a particular vegetation type, the responses of the vegetation to fires in different seasons clearly need to be documented across the geographical extent of the vegetation type to formulate appropriate guidelines for fire management.

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CHAPTER 6 – Fire regimes in eastern coastal fynbos: imperatives and thresholds in managing for diversity

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Abstract

We synthesised the findings of a research programme focussed on informing ecologically sound management of fire in eastern coastal fynbos shrublands. Until recently, fire ecology was poorly understood in this eastern coastal region of the Cape Floral Kingdom (CFK), South Africa. Rainfall in the area is aseasonal and temperatures are milder and show lower seasonal extremes than in the winter-rainfall and more arid inland parts of the CFK, with implications for the management of fire regimes. We explore potential east-west trends at study area- and CFK-scales in terms of fire season, fire return interval, fire danger weather and lightning incidence to put the fire regimes of the study area into perspective with those of other fynbos regions. The Garden Route National Park was recently established within the study area in a landscape where indigenous forests, fire-prone fynbos shrublands and fire-sensitive plantations of invasive alien trees are interspersed. The institutional history and landscape context of the park pose particular difficulties that need to be addressed by a fire management policy, including high levels of invasion by alien trees, and significant pressure from the adjacent plantation industry to reduce wildfire hazard. We articulate the findings of recent research into ecological thresholds pertaining to the different elements of the fire regime in eastern coastal fynbos, to guide adaptive management of fire in the park. We also make recommendations for a fire management strategy for the park that may address the aforementioned operational considerations within the constraints posed by ecological thresholds. Finally, we highlight future research and monitoring needs.

Keywords: adaptive management; fire-prone shrublands; fire return interval; fire season; Garden Route National Park; prescribed burning; thresholds of potential concern

Introduction

Fire is instrumental in maintaining the species- and endemic-rich fynbos shrublands (Myers *et al.* 2000) of the Cape Floral Kingdom (CFK) of South Africa (Kruger & Bigalke 1984). It may be considered the most important fynbos management practice, being both a key ecological factor and a practical tool for resource manipulation. The fire ecology of fynbos has been well researched in the western, winter-rainfall part of the CFK (Kruger & Bigalke 1984; van Wilgen & Viviers 1985) and in the inland, arid mountains (Bond *et al.* 1984; Midgley 1989; Seydack *et al.* 2007) but was, until recently, poorly understood in the eastern coastal part of the CFK. The climate of the latter is milder with reduced seasonal extremes in temperature, while rainfall occurs year-round. As shown by Heelemann *et al*. (2008) in the inland fynbos of the eastern CFK, overstorey proteoids (non-sprouting, slow-maturing, serotinous Proteaceae) show weak seasonal effects on post-fire recruitment, a consequence of a non-seasonal rainfall and fire regime. We expected similar patterns in our region, as well as faster plant growth and maturation rates of proteoids, a consequence of the region's relatively benign climate. These phenomena will have important implications for the management of fire regimes.

The Garden Route National Park (GRNP; *c.* 130 000 ha) was recently established in the eastern coastal part of the CFK. Situated in a landscape where indigenous forests, fire-prone fynbos shrublands and fire-sensitive plantations of invasive alien trees are interspersed, the park faces considerable ecological and operational challenges pertaining to the management of fire and invasive alien plants (reviewed in Chapter 1). A recent, multi-facetted research programme was undertaken to inform ecologically sound management of fire in eastern coastal fynbos and entailed (i) an assessment of the context within which fire management was practiced during the past century (Chapter 1); (ii) characterisation of the recent fire history and fire regime (1900–2010) in the area (Chapter 2); (iii) characterisation of the seasonality of fire weather and lightning (Chapter 3); (iv) estimation of minimum fire return intervals (FRIs) from juvenile periods and post-fire recruitment success of proteoids (Chapter 4); and (v) determination of the ecologically appropriate fire season from post-fire recruitment seasonality of proteoids (Chapter 5).

Here we synthesise the findings of this research in terms of potential east-west trends within eastern coastal fynbos and at the scale of the entire CFK. We furthermore articulate the findings into ecological thresholds (Biggs & Rogers 2003; van Wilgen *et al.* 2011) pertaining to the different elements of the fire regime in eastern coastal fynbos. Lastly, we recommend a fire management strategy for the GRNP that may address operational considerations (particularly fire risk management and alien plant management) within the constraints posed by ecological thresholds.

Study area

The study area (33.80°S 22.59°E – 34.01°S 24.26°E) comprises the coastal slopes of the Outeniqua Mountains (east of the Touw River) and Tsitsikamma Mountains, of which a large portion occurs within the GRNP (Chapter 1). Owing to maritime influence, the climate of the area is relatively equable (Schulze 1965). Rainfall occurs throughout the year, with winter months being the driest. Mean annual rainfall increases eastwards, from 820 to 1 078 mm in the Outeniqua and Tsitsikamma Mountains, respectively. The proportion of summer rain also increases eastwards (Schulze 1965). The fire-prone and fire-dependent vegetation of the study area largely comprises South Outeniqua Sandstone Fynbos and Tsitsikamma Sandstone Fynbos, in the Outeniqua and Tsitsikamma Mountains, respectively (Rebelo *et al.* 2006). These are tall, medium-dense proteoid shrublands, with an ericoid-leaved shrub understorey (dominated by Ericaceae) and a prominent restioid (Restionaceae) component. More detailed accounts of the climate, vegetation and fire management history of the study area occur elsewhere (Chapter 1, 2, 3, 4).

Fire regimes in eastern coastal fynbos

In Chapter 1 we established that historically, plantation protection enjoyed priority over fynbos conservation, influenced by the large extent of plantations in these mountains. Fynbos close to plantations has most likely been compromised by short-rotation and low-intensity burning in the past, as well as by invasion by alien trees. In terms of area burnt (1900–2010), natural (lightning-ignited) fires dominated the fire regime, particularly in the Tsitsikamma, whereas prescribed burning was relatively unimportant (Chapter 2). Typical FRIs (8–26 years during the period 1980–2010) were comparable to those in other fynbos protected areas (Seydack *et al.* 2007; van Wilgen *et al.* 2010), and appeared to be shorter in the Tsitsikamma (eastern region of study area) than in the Outeniqua (western region) (Chapter 2). Proteaceae juvenile periods (4–9 years) and post-fire recruitment success (following fires in ≥7 year-old vegetation) suggested that for biodiversity conservation purposes, FRIs should be no less than nine years in moist, productive fynbos (Chapter 4; *cf.* Hugo *et al*. 2012). Increases in the total area burnt annually (since 1980) (Chapter 2) that were correlated with long-term increases in average fire danger weather (Chapter 3), suggest fire regime changes related to global change. Collectively, findings on the seasonality of actual fires (Chapter 2) and the seasonality of fire danger weather, lightning (Chapter 3), and post-fire proteoid recruitment (Chapter 5) suggest that the fire regime in eastern coastal fynbos is not limited to any particular season, and therefore management is not constrained, although the ecological requirements for adequate fire intensity (van Wilgen *et al.* 2011) remain.

East-west comparisons at study area- and Cape Floral Kingdom-scales

Seasonality in fire occurrence was less pronounced in the east than in the west of the study area, with fires less concentrated around summer in the Tsitsikamma than in the Outeniqua region (Chapter 2). In the study area as a whole, fire occurrence was less seasonal than in western (van Wilgen *et al.* 2010) and inland (Seydack *et al.* 2007) parts of the CFK, consistent with climatic gradients of increasing winter rainfall and summer drought from east to west and increasing summer evapotranspiration from the coast to the interior. The trend of increasing seasonality in fire occurrence and rainfall from east to west was not reflected in the seasonality of lightning occurrence at either study area- or CFK-scales (Chapter 3). This suggests that, particularly in the western-CFK, fire occurrence is not ignition-limited (Archibald *et al.* 2009). The east-west trend of increasing seasonality in fire occurrence was, however, reflected in the biotic post-fire recruitment response. Fire season had little effect on post-fire recruitment of proteoids in the study area (Chapter 5), in contrast to the strong seasonal response in western (van Wilgen & Viviers 1985; Midgley 1989) and inland (Bond 1984; Bond *et al.* 1984) parts of the CFK, where summer and autumn fires result in optimal recruitment.

FRIs since 1980 appeared to be shorter in the east of the study area (Tsitsikamma region), where rainfall and plant growth rates are higher, than in the west (Outeniqua region) (Chapter 2). However, FRIs for the study area as a whole were broadly comparable to those of other regions in the CFK (van Wilgen *et al.* 2010) suggesting that variation is related to local or regional moisture regimes (Kruger & Bigalke 1984; Seydack *et al.* 2007) rather than an east-west gradient of increasing FRIs across the CFK at large. Given the lack of a consistent gradient in mean annual rainfall from east to west within the CFK (Deacon *et al.* 1992), this result is not surprising. Minimum FRIs to ensure pre-fire maturation and thus successful post-fire recruitment of proteoids in the study area (Chapter 4) were accordingly similar to those from other parts of the CFK (van Wilgen *et al.* 2011).

The total area burnt per annum in the study area has increased significantly since 1980 (Chapter 2) and was correlated with a significant increase over time in weather conditions conducive to the spread of fires (Chapter 3). Increases in fire frequency or extent (Forsyth & van Wilgen 2008) and in the severity of fire danger weather conditions (Wilson *et al.* 2010) have similarly been observed elsewhere in the CFK, although evidence is not unequivocal across all meteorological variables affecting fire danger weather (Hoffman *et al.* 2011).

Managing fire for biodiversity conservation: ecological thresholds

The primary mandate of protected area managers typically is to maintain, on the land under their jurisdiction, all elements of native biodiversity over space and time (SANParks 2008). Adaptive forms of management (Biggs & Rogers 2003) may be adopted whereby targets (or thresholds of potential concern) are formulated to describe the boundaries of the desired state that management aims to achieve. Fire management practices aimed at biodiversity conservation are often in conflict with hazard reduction requirements (Chapter 1), and where such conflict of interest exists, managers need to know the ecological thresholds within which fire may be managed. With adaptive management of fire, thresholds are set in terms of acceptable variations in the elements (frequency, season, intensity, size) of fire regimes, and monitoring regularly assesses whether the fire regimes that arise from various forms of management remain within the specified ranges (van Wilgen *et al.* 2011). We endeavoured to set thresholds for eastern coastal fynbos (Table 1) and particularly in terms of two elements of the fire regime, namely fire frequency (the lower threshold for FRI; Chapter 4), and fire season (Chapter 5).

The adoption of thresholds in terms of elements of the fire regime may at first glance appear to imply that the fire patterns themselves are the desired outcome. However, fire patterns will ultimately manifest themselves in vegetation structure, function and composition, which are assessed in terms of thresholds related to the responses of ecosystems to fire (van Wilgen *et al.* 2011). We distinguished between thresholds pertaining to fire patterns (termed 'operational thresholds' by van Wilgen *et al.* 2011) and those pertaining to ecosystem responses to fires (termed 'ecosystem thresholds' by van Wilgen *et al.* 2011) (Table 1), the ultimate goal being to make the links between fire patterns and ecological outcomes.

Fire return interval

Estimates of optimal fire frequencies are often based on the relationship between plant age and the rate of seed accumulation of the slowest-maturing species. In fynbos and in Australian shrublands, juvenile periods of proteoids are used as indicators of extreme lower limits for FRIs, whereas their longevity indicates extreme upper limits (Bond 1980; Gill & McCarthy 1998). The rule of thumb generally used in fynbos to establish a lower threshold for FRI posits that half of the individuals in a population of the slowest-maturing proteoid species should have flowered in at least three successive seasons before the area may be burnt (Kruger & Lamb 1978; Kruger 1982; van Wilgen *et al.* 2011; Table 1). Recruitment success of proteoids after fires at different intervals may also indicate the ecological suitability of FRIs.

Application of the mentioned rule of thumb to juvenile periods observed in the study area implied a minimum FRI of nine years for moist, productive, Tsitsikamma fynbos, whereas post-fire recruitment of proteoids was always successful following FRIs of ≥7 years (Chapter 4). Considerable variation in juvenile periods, flowering status at given plant ages, and post-fire recruitment success at given FRIs, within and between species and habitats (Chapter 4) suggests that management should not attempt to rigidly and consistently pursue a fixed or narrow range of FRIs. Besides it being practically unattainable (van Wilgen *et al.* 2010), variability in FRIs in nature is inevitable, and where fire management is aimed at conserving biodiversity, variation within established limits is desirable (Gill & McCarthy 1998; Thuiller *et al.* 2007). Variation in FRI (or fire season or fire intensity) will induce variation in the density of overstorey proteoids, which in turn is associated with maintenance of diversity in understorey species (Cowling & Gxaba 1990; Vlok & Yeaton 1999).

Some of the variation in flowering status appeared to be related to local moisture regimes with FRIs being inversely related to rainfall or moisture availability. Due cognisance should therefore be taken of site-specific requirements, with drier habitats (northerly or westerly aspects or shallow soils) generally needing longer intervals between fires. Range-restricted species or habitat specialists may furthermore have very specific FRI requirements (Kruger & Bigalke 1984). Slow-growing, high-altitude species, e.g. *Protea grandiceps* (Near Threatened; Raimondo *et al.* 2009), may be slow to mature (>10 years; J.H.J. Vlok pers. comm. 2012) and thus require longer FRIs.

Although the primary aim was to establish a lower threshold for FRI, the results of Chapter 4 also showed that the upper threshold for FRI is likely to be in excess of 38 years. We concurred with van Wilgen *et al.* (2011) that the occurrence of very old vegetation, and thus the setting of an upper threshold for FRI, is not a key concern in the ecological management of fire in montane proteoid fynbos, both because old vegetation is typically limited in extent (Bond 1980; Chapter 2), and because proteoid recruitment does not appear to be negatively affected by relatively long inter-fire periods (Chapter 4).

The assessment of the recent (1980–2010) history of fires in the study area (Chapter 2) also enabled appraisal of the extent to which the proposed FRI thresholds were exceeded. Generally, the Tsitsikamma region experienced short FRIs more extensively than the Outeniqua. Since 1980, 10.5% of the fynbos of the GRNP burnt at least once at post-fire ages of <7 years. In these areas, proteoids have likely been locally eliminated, as post-fire recruitment success of this guild has been near zero following a 5-year FRI (Chapter 4). Measuring against a minimum FRI threshold of 9 years resulted in much greater area exceeding this threshold, with 27.5% of the study area having burnt at least once at post-fire ages of <9 years. In these areas, seed banks of proteoids have likely been insufficient at the time of fire to have enabled optimal post-fire recruitment. The extent to which proteoid populations may have been compromised in these areas depends on the particular species present, local moisture regimes and plant maturation rates (Chapter 4).

Historical catchment management policies (Chapter 1) furthermore suggest that, prior to 1980, substantial areas, particularly in proximity to timber plantations, were subjected to short interval burns. Short interval fires, which alter vegetation structure (from woody to herbaceous; Kruger 1984; Lloret *et al.* 2003) and thus fuel dynamics, may set up negative feedback loops whereby short FRIs persist in the landscape (Richardson & van Wilgen 1992). Similar effects on fire regimes have occurred after invasion by alien grasses of Californian chaparral (Keeley & Brennan 2012). In large parts of the GRCMs, graminoid sprouters dominate, while proteoids are sparse or absent (Heelemann *et al.* 2010), notably in areas near plantations of alien pine trees (TK, pers. obs.). This likely resulted from frequent and low intensity burning in the past, aimed at protecting timber plantations from fire (Chapter 1). Facilitation of FRIs that would ensure the long-term persistence of proteoids in the GRNP is thus a priority for fynbos conservation management, particularly where this guild has persisted in the landscape. It is therefore important to map the distribution of species that are vulnerable to too frequent fires and to incorporate this information into the fire management plan for the area.

Thresholds may also be set for post-fire age class distributions of the vegetation (Table 1). Relatively equal age class distributions are desirable as these would provide sufficient habitat for a full range of species requiring access to vegetation of different ages, in addition to allowing for manageable amounts of vegetation to be scheduled for prescribed burning or invasive alien plant control each year (van Wilgen *et al.* 2011). The distribution of post-fire vegetation age classes in the GRNP (measured in 2011) was highly skewed towards the younger age classes (Chapter 2), thereby far exceeding proposed thresholds (Table 1) and upsetting invasive alien plant clearing schedules. To correct this situation, increased attempts at protection of GRNP fynbos from extensive burning would be desirable for the next few years.

Fire season

Season of fire has marked effects on floristic composition in fire-prone Mediterranean-climate shrublands (Bond 1984; Enright & Lamont 1989; Midgley 1989). In these winter-rainfall systems, summer-autumn fires lead to optimal recruitment of proteoids, which are key to the conservation

Table 1: Proposed thresholds of potential concern (adapted from van Wilgen *et al.* 2011) relating to fire management of fynbos (*c.* 105 000 ha) in the Garden Route National Park. Thresholds pertaining to fire patterns are informed by monitoring against thresholds related to ecosystem responses to fires.

Area of potential concern	Reason for concern	Measure	Thresholds
Fire patterns:			
Post-fire age distribution will be skewed or uneven.	An unequal distribution of age classes will not provide sufficient habitat for a full range of species requiring access to vegetation of different ages, and will not allow for manageable amounts of vegetation to be scheduled for prescribed burning over time.	Proportion of area in the following post-fire age classes: 0–6, 7–12, >12 years.	The proportion of area in each age class should be >25% and <50%.
Large areas will go without fire for too long.	Fires in older vegetation will lead to poor post-fire reproduction in groups of plants prone to senescence (e.g. serotinous Proteaceae).	Proportion of the area >40 years post-fire.	Proportion of the area >40 years post-fire should be <20%.
Large areas will burn too frequently.	Fires in populations of immature serotinous Proteaceae will lead to poor post-fire regeneration, population declines and local extinction.	Fire return intervals assessed over the past 30 years.	Fire return intervals should be ≥9 years on >80% of the area overall, and on >90% of the area containing proteoids (once mapped).
Fires will consistently occur in a particular season(s).	A lack of variation in fire season in an environment where variation is the norm may consistently promote some species over others thereby reducing diversity.	The proportion of the area that burns in any particular season over the past 15 years.	The area burnt in each season (winter, JJA; spring, SON; summer DJF; autumn MAM) should be >10% and <40%.
Large areas will burn in fires of low intensity or extremely high intensity.	Low fire intensity will fail to stimulate seed release in serotinous plants and germination of large or hard-coated, soil-stored seeds. Extremely high fire intensity will kill small-seeded species with shallow seed banks (e.g. *Erica* spp.) and increase post-fire soil erosion.	Proportion of the area that burnt under low fire danger conditions (FDI≤5) over the past 15 years. Proportion of the area that burnt with excessive fuel loads (e.g. due to alien plant infestations) under high fire danger conditions.	Should be <25%.

Area of potential concern	Reason for concern	Measure	Thresholds
Instead of a similar area being burnt each year, a few large fires, or, alternately, a large number of small fires could occur.	Too many small fires will be difficult and costly to manage. Edge effects (for example predation of seeds by rodents) will be greater with many small fires. Very large fires (>20% of the area of the Park) will upset the desired goal of maintaining an even distribution of post-fire ages.	The distribution of areas of all individual fires over the past 15 years. Adjoining fires that burn in the same season of the same year should be counted as one fire.	The proportion area burnt in fires >1 000 ha should be >80%. Single fires should not exceed 20 000 ha.
Ecosystem responses to fire:			
Insufficient individuals in populations of serotinous Proteaceae will reach maturity and set seed prior to fire.	Fires that occur in relatively immature populations will lead to population declines or local extinction.	Proportion of individual populations that have flowered for at least three successive seasons.	At least 50% of individuals in a monitored population should have flowered for at least three successive seasons before a fire.
Too many individuals in populations of serotinous Proteaceae will reach senescence prior to fire.	Fires that occur in senescent populations will lead to population declines or local extinction.	Proportion of individual populations that show advanced signs of senescence.	No more than 25% of individuals in a monitored population should have advanced signs of senescence before a fire.
Post-fire recruitment in populations of serotinous Proteaceae could be inadequate to replace pre-fire populations.	Fires in ecologically disadvantageous conditions (either post-fire age, low fire intensity, drought or exposure to high levels of seed predation) could lead to failure of adequate populations to establish after fire, leading to population declines of local extinction.	The ratio of seedlings to parent plants measured 1–2 years after a fire.	Seedling to parent ratios should be >2.
Rare or threatened species may be negatively affected by fires.	The existence of disadvantageous fire regimes could lead to population declines or local extinction.	Population counts on fixed areas.	Population declines of >25% in inter-fire periods. Post-fire population sizes should be at least 75% of pre-fire population levels.

of floral diversity overall. In Chapter 5 we established that seasonal patterns in post-fire recruitment of proteoids are weak in eastern coastal fynbos. This implies that season of burn is essentially unimportant, in line with the findings that fire danger weather (Chapter 3) and fire occurrence (Chapter 2) in this area are also largely aseasonal. The lack of a seasonal constraint on burning has encouraging management implications. Managers will not have to allocate large amounts of resources to fight wildfires that are burning in what are considered ecologically undesirable seasons based on patterns from the western and inland fynbos regions; they may also conduct back burns during any season. Instead of the thresholds applicable to fire seasonality in western and inland fynbos (i.e. that >80% of area should burn during summer-autumn and <20% during winter-spring; van Wilgen *et al.* 2011), variability in fire season is considered desirable in eastern coastal fynbos. The thresholds we propose for the study area accordingly relate to a reasonably even distribution of fires among seasons (i.e. the proportion of the area burnt in any particular season should be >10% and <40%; Table 1).

In aseasonal environments such as the study area and southeastern Australia, there is large variation between years in the seasonality of rainfall, and an unpredictable response of proteoid recruitment to season of fire. In the longer term, the timing of fire relative to sequences of wet and dry years may be of equal importance to fire season in its effect on proteoid populations (Bradstock & Bedward 1992). Particularly in these unpredictable, aseasonal environments, variation in fire regimes (including fire season) is necessary to maintain plant diversity in space and time (Gill & McCarthy 1998; Thuiller *et al.* 2007). The range of acceptable variation in fire seasonality that we propose is accordingly wide.

Although removal of the seasonal constraint should expand the window of opportunity and thus improve the chances of implementing prescribed burns, the ecological need for adequate fire intensity remains (Table 1; van Wilgen *et al.* 2011). Fire intensity needs to be sufficiently high to stimulate seed release and germination in serotinous (Midgley & Viviers 1990) and large or hard-coated, soil-stored seeds (Jefferey *et al.* 1988; Bond *et al.* 1990; Knox & Clarke 2006). For instance, a few severely fragmented subpopulations (mostly with <50 individuals each) of the large-seeded, myrmecochorous *Mimetes splendidus* (Endangered; Raimondo *et al.* 2009) occur within the study area, and at least one subpopulation (at Buffelsnek) is known to have been lost due to low intensity fires (J.H.J. Vlok pers. comm. 2012). Ecological requirements of fire intensity are furthermore often in conflict with safety considerations (Morrison *et al.* 1996; van Wilgen *et al.* 2012), presenting considerable management challenges (discussed below).

The assessment of the historical occurrence of fire in the study area (Chapter 2) enabled evaluation of whether the proposed fire season thresholds were exceeded. These were not exceeded when assessed over the entire known history of fires (1900–2010). During this period, the proportional area burnt on record was fairly evenly distributed among seasons (winter 23%, spring 35%, summer 19%, autumn 22%). Neither were the thresholds exceeded when assessed over the past 15 years (1996–2010; *cf.* van Wilgen *et al.* 2011), when the seasonal distribution of fires was also relatively even (winter 20%, spring 35%, summer 19%, autumn 30%). Despite the occurrence of several very large (≥10 000 ha) fires since 1990, fire seasonality remained within the proposed thresholds, suggesting that inappropriate season of fire generally does not jeopardise ecologically sound management of fynbos in the area.

Fire management approach: operational considerations

Various management approaches have been proposed or adopted in the fynbos mountain catchments of the CFK during the past century (Seydack 1992; van Wilgen *et al.* 1994; van Wilgen 2009). The respective systems were mainly distinguished by the extent of intervention pursued, ranging from no manipulation ('natural fire zone management') through selective manipulation ('adaptive interference management') to (attempted) complete control by means of block burning (Seydack 1992). A review of the historical approaches to fire management in the study area (Chapter 1) showed that, by virtue of the large extent of commercial (formerly state-) plantations, the approach has mostly been interventionist; fire risk considerations took precedence over ecological requirements, the goal being to 'tame the fynbos' through extensive block burning at short interval under cool, safe conditions. However, assessments of historical fire regimes in the study area (Chapter 2) and elsewhere (Keeley *et al.* 1999; Moritz 2003; van Wilgen *et al.* 2010) show that rigid control over fire regimes is largely unattainable. Prescribed burning accordingly contributed little to the total area burnt in the study area whereas natural (lightning-ignited) fires accounted for *c.* 60% of the area burnt since 1980 (Chapter 2).

The separation of mountain catchment conservation and forestry functions within South Africa since the 1990s brought about changes in land management authorities and their mandates, necessitating rationalisation of fire management policies (Chapter 1). The perspective of this study is that of protected area management, with specific reference to the GRNP. The key fire management issues presently faced by the GRNP are (i) to reconcile ecological and fire hazard reduction requirements (*cf.* Morrison *et al.* 1996; Gill & McCarthy 1998; van Wilgen *et al.* 2012), especially in the context of neighbouring commercial plantations; and (ii) to integrate fire and invasive alien plant management strategies to optimise biodiversity conservation and ecosystem service delivery (Chapter 1). Here we explore the options for addressing these two main issues within the established ecological constraints.

Fire risk and safety (with emphasis on protecting neighbouring plantations)
In order to minimise wildfire hazards and damage to timber plantations, there is pressure from plantation managers for GRNP authorities to adopt a policy of low-intensity burns at short rotations (4–8 years) in fynbos adjacent to plantations (Chapter 1). Subsequent to substantial legal claims instituted against conservation authorities for fire damage to plantations in recent years, a fire management agreement was drawn up in 2008 between the main plantation holding company, Cape Pine (formerly Mountain to Ocean Forestry), and the GRNP for the Tsitsikamma region (Vermeulen *et al.* 2009). Accordingly, fuel reduction burning is to be undertaken in designated fynbos blocks (45–1178 ha in size) located to the north of plantations where indigenous forest does not form a natural buffer between fynbos and plantations (Chapter 1). The blocks are strategically placed in relation to fire corridors associated with wildfires that burn under hot, dry, bergwind conditions (Geldenhuys *et al.* 1994), and form two parallel fire belts to be burnt on 8-year rotation, such that the vegetation in one of the belts would always be ≤4 years of post-fire age. The block burn system is to be further supported by strategically placed fire breaks as well as controlled fuel reduction burning within plantations, particularly along their boundaries (De Ronde *et al.* 1990).

However, implementation of this system to date has failed for a number of reasons. The rugged terrain, lack of access roads and natural firebreaks, and dense infestations of invasive alien plants (originating from the plantations), make block burning prohibitively expensive and risky. To date, ecological restrictions on fire season (inherited from winter-rainfall fynbos) combined with fire danger weather restrictions reduced the window of opportunity for prescribed burning to only a few days per year (van Wilgen & Richardson 1985). National fire legislation (the Veld and Forest Fire Act of 1998) furthermore acts as a strong deterrent to taking risks with prescribed burning, despite it recognising both the ecological role of fire for maintaining healthy ecosystems and the need to reduce the risks posed by fires (van Wilgen *et al.* 2012).

Even if it were possible to implement prescribed burning according to plan (which may be somewhat more plausible with the relaxation of seasonal constraints; Chapter 5), land managers need to realise that fynbos and plantations cannot be fire-proofed (*cf.* Agee 2002). It has been shown for fire-prone shrublands and forests across the globe that large fires are not strongly dependent on a build-up of fuel, and therefore frequent burning to reduce fuel loads will not necessarily reduce the risk of runaway wildfires (Bessie & Johnson 1995; Keeley *et al.* 1999; Moritz 2003; van Wilgen *et al.* 2010). The most effective strategy for facilitating fire safety where necessary is to focus effort on strategic locations, bearing in mind that fuel breaks are largely effective at facilitating fire management by providing access for fire fighting activities (Syphard *et al.* 2011). Given the mentioned physical, ecological, economical and political constraints, wide-scale implementation of prescribed burning is thus likely to remain unattainable (Keeley *et al.* 1999; van Wilgen 2009; Chapter 1) and ineffective at preventing destructive wildfires (Keeley & Zedler 2009).

Instead of extensive block burning of fynbos in the GRNP, we recommend a system of largely natural fires and minimum interference, but allowing pro-active fire management measures where or when required ('adaptive interference management'; Seydack 1992). The main focus should be on establishing a network of fire breaks where fynbos abuts plantations or other fire-sensitive land uses. In line with the stipulations of the National Veld and Forest Fire Act, the location, specifications (clearing method, width, and maintenance schedule) and maintenance responsibilities pertaining to fire breaks should be formally agreed between neighbouring land managing agencies within the institutional framework of the regional (Southern Cape-) Fire Protection Association. In principle, these fire breaks should provide access and relatively safe conditions for fire fighting along boundaries in areas of high fire hazard. Fire breaks have to be practically aligned with topographical features and need to avoid sensitive habitats, such as mountain ridges, rather than strictly follow property boundaries.

The location and specifications of fire breaks (or other pro-active fire management interventions) will be dynamic in space and time, tracking changes in the vegetation age mosaic and fire risk distribution. Regular assessment of the current situation is essential and may result in the identification of:

(i) Areas where fires should not burn. These include immature fynbos (<9 years post-fire, Table 1); areas of disturbed/transformed forest where forest recovery should be facilitated (Watson & Cameron 2001); and where damage to assets or run-away fires may be anticipated. Such areas should receive priority for intervention during wildfires.

(ii) Areas where fires may be allowed to burn unhindered. These would mainly be inaccessible areas where no immediate threat to assets exists.

(iii) Areas where fires should preferably burn within the next five years. These include senescent fynbos (>40 years old; Table 1) that requires a burn for rejuvenation; areas where excessive fuel build-up pose a fire hazard to human lives or assets; and disturbed areas (primarily decommissioned plantations; Chapter 1) where fire may facilitate the recovery of fynbos (Holmes & Richardson 1999). In these areas prescribed burning should be considered.

Adoption of the outlined approach should afford sufficient flexibility to integrate fire management with the dynamic plantation decommissioning and rehabilitation process (Chapter 1) and with invasive alien plant management (Roura-Pascual *et al.* 2009; van Wilgen 2009).

Other aspects to fire management are preparedness and response or suppression capacity (van Wilgen *et al.* 2012). In areas where fires occur seasonally, (high) fire danger season(s) are typically recognised and fire fighting capacity augmented during this time. Fire managers conventionally regard the fire danger season in the study area to be during autumn-winter (April–October) when rainfall is relatively low and bergwinds often prevail (Le Roux 1969; Geldenhuys 1994; Chapter 1). An analysis of the seasonality of fire-prone weather conditions confirmed that fire danger weather peaks in winter (Chapter 3) although average conditions are mild year-round compared to those characteristic of fire danger seasons elsewhere in the CFK (van Wilgen 1984). The historical occurrence of both lightning- and human-ignited fires in the study area furthermore does not attest to a winter fire regime (Chapter 2), and large fires may occur at any time of the year, even under low or moderate fire danger conditions (Chapter 3). Lightning, as a source of ignition, also occurs throughout the year (Chapter 3). Collectively, these findings suggest that there is no clear fire danger season in the study area that would demand increased preparedness or fire fighting capacity compared to other times of the year.

Fire and management of invasive alien plants

Plant species used in commercial forestry that cause the greatest problems as invasive alien plants are generally those that have been planted most widely and for the longest time (Richardson 1998; De Wit *et al.* 2001). The first state plantations in the study area were established in 1883 (Chapter 1) and the two most widely planted species (*Pinus pinaster* and *P. radiata*) (van Wilgen & Richardson 2012) have become the most problematic invaders in their genus in the study area and elsewhere in the fynbos (Richardson & Higgins 1998). Both are declared invaders (category 2) and ‘transformers’ according to the Conservation of Agricultural Resources Act of 1983 (Henderson 2001).

Key to the invasive success of serotinous pines in fynbos is their response to fire which is similar to that of proteoids (showing marked spatial and temporal post-fire fluctuations in population sizes). However, pines outperform proteoids in two key facets of demography, i.e. seed dispersal and fire-resilience (Richardson & Higgins 1998). Seeds and pollen of pines are exceptionally well dispersed by wind, while isolated pioneers can give rise to colonies by selfing (Richardson & Higgins 1998). Pines furthermore have superior fire-resilience with comparatively short juvenile periods (*c.* 5 & 6 years in *P. radiata* and *P. pinaster*, respectively; Richardson *et al.* 1990) and better adult fire-survival ability than most proteoids. Once pines are established, the fynbos may be transformed into a pine forest over 2–3 fire cycles (Richardson & Brown 1986). Because the life cycles of serotinous pines (and hakeas) are closely linked to fire, integration of fire and alien plant management strategies is essential (Roura-Pascual *et al.* 2009).

The conventional methods of managing invasive pines are slashing or hand-pulling of immature saplings; and ring-barking or felling of large mature trees, allowing time for seeds to be released and subsequent burning of new recruits prior to their reaching maturity (Holmes & Marais 2000; Holmes *et al.* 2000). Equally, where prescribed burning of fynbos is intended, invader plants require pre-fire treatment. In some cases options exist for managing invasions by manipulating disturbance regimes like fire cycles (e.g. Richardson & Higgins 1998 for *Pinus*; Esler *et al.* 2010 for *Hakea*). Unfortunately, potential use of short-rotation fires to control pines is precluded by the fact that juvenile periods of native proteoids in the study area (4–9 years; Chapter 4) are mostly longer than those of pines (see above). However, in fynbos devoid of proteoids (naturally, or due to inappropriate past management of fire), application of a single FRI of <5 years may in some instances provide an inexpensive means of substantially reducing dense infestations of young pine recruits. Otherwise, it would generally be in the interest of invasive plant control to prolong FRIs in order to curb the rate of spread of fire-propagated species like pines and hakeas (Richardson & van Wilgen 1992).

Forestry delivers value, but the collateral damage through invasions may exceed the benefits (Richardson 1998). In the long term, it has been suggested that pine-based forestry be phased out in the Western Cape (Louw 2004; van Wilgen & Richardson 2012; Chapter 1). This would reduce seed pollution and would need to be accompanied be (i) a considerable increase in mechanical control efforts in combination with prescribed burning; (ii) introduction of biological control on invasive pine species (Hoffmann *et al.* 2011); (iii) payment for ecosystem services to co-fund clearing operations (Hutchinson 2010); and (iv) prioritisation, such that limited funds can be utilised where these would achieve optimal outcomes (Roura-Pascual *et al.* 2009; Forsyth *et al.* 2012).

Future research and monitoring needs

Recent research reported here provided understanding of the historical fire regime in the study area and how it has changed during the past century. Ongoing accurate mapping of future fires is necessary to serve as a basis for the design of natural experiments, for fire management decisions and planning (Driscoll *et al.* 2010), and to recognise potential long-term changes in fire regimes (Chapter 2). Ongoing monitoring and regular evaluation of fire regime outcomes in terms of agreed thresholds are essential components of the adaptive management cycle, to enable learning and corrective action where necessary. In cases where thresholds are exceeded, consideration needs to be given to management interventions that will drive the system to be within thresholds, or, alternatively, thresholds may be recalibrated where appropriate. Results from the monitoring of ecosystem responses to fires (ecosystem thresholds in Table 1) should inform the calibration of fire pattern thresholds.

The thresholds we proposed for minimum FRI and fire season are first approximations within which fire managers may attempt to resolve the conflicting demands of fire hazard reduction and biodiversity conservation in eastern coastal fynbos. Further research on maturation rates of slow-maturing reseeding plant species (Lamont *et al.* 1991) and success of post-fire vegetation recovery (Morrison *et al.* 1995) in diverse habitats would be required to refine these thresholds. Substantial variation, both in flowering status and post-fire recruitment, as well as disparity among estimates of minimum FRI based on these measures (Chapter 4), emphasise the need to empirically verify Kruger's (1982) rule of thumb conventionally used to establish the lower threshold for FRI. Verification may be done by relating pre-fire flowering status of proteoid populations to their post-fire recruitment response at corresponding sites (as was done for a single site; Chapter 4) across various species and habitat types. Further research on plant responses to fire intensity and articulation of the findings into ecological thresholds for fire intensity would also be informative in fynbos generally, and especially in environments where weather conditions are variable within seasons and the fire season not clearly delineated. Making the link between past fire regimes, as opposed to single fire events, and their ecological outcomes also remains a major challenge. However, the nature of post-fire fynbos assemblages does not solely depend on the fire survival attributes of constituent species, and greater understanding is required of the effects of dynamic and competitive interactions between overstorey and understorey species (Cowling & Gxaba 1990; Vlok & Yeaton 1999).

The practicalities of complying with fire legislation in the face of conflicting land management objectives (fire risk *vs.* biodiversity conservation) need to be considered. A legal review should clarify the respective responsibilities applicable to the conservation and commercial forestry sectors in terms of fire and invader plant legislation. This should facilitate cross-cutting compliance and cooperation without the need for costly legal action (Chapter 1). Lastly, resource economics research should further explore alternative funding for alien plant clearing initiatives in watersheds. Approaches based on payment for ecosystem services (Hutchinson 2010; van Wilgen & Richardson 2012) should be expanded, targeting major water users, such as agricultural industries, municipalities and the tourism industry.

Concluding recommendations

Recent research aimed to establish what constitutes an acceptable fire regime in eastern coastal fynbos, and we accordingly determined ecological thresholds for fire season and return interval. While prescribed burns do not have to be constrained by season in the study area, other constraints remain, most significant of which are safety requirements and the abundance of fire-adapted invasive alien trees. Because large-scale implementation of prescribed burning is unattainable (Keeley *et al.* 1999; van Wilgen 2009; Chapter 1, 2) and mostly ineffective at ensuring fire safety (Keeley & Zedler 2009) fire managers need to accept that wildfires will remain dominant. Fire management should be adaptive in nature and focussed on (i) managing wildfires to stay within the proposed thresholds; (ii) monitoring to assess actual fire regimes against proposed thresholds or to refine thresholds where appropriate; (iii) protecting boundaries between fynbos and fire-sensitive land uses (such as plantations) through collaborative agreements with neighbours; and (iv) integration of fire and invasive alien plant management, using scarce resources to treat invasive plants and focus prescribed burns in priority areas.

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