Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration

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Abstract   The recovery of fynbos vegetation after invasion by dense stands of alien trees, and clearing by either 'burn standing', 'fell and burn', or 'fell, remove and burn' treatments, was investigated in two watersheds in the Western Cape Province, South Africa. Native plant density, cover, functional and biological guilds and species richness were compared with matched control sites that were not invaded, but were burnt in the same fires. Species richness was lower for invaded sites compared to controls, at all scales measured (up to 2000 m^2). Species area curves for invaded sites did not converge with those of controls, indicating that lower richness at smaller scales was not compensated by increased species survival at a larger scale. Indigenous plant density and cover were lower for invaded sites compared to controls. Overall, treatment differences were non-significant, but the 'burn standing' treatment caused the least change to vegetation variables, and the 'fell, remove and burn' and 'fell and burn' treatments caused greater, similar changes. Changes to the guild structure of the recovering fynbos stands differed among treatments, and indicated that the 'fell and burn' treatment had the greatest negative effect on guild survival. In the 'fell and burn' treatment, which resulted in an exceptionally intense fire, only non-mycorrhizal graminoids (predominantly myrmecochores) persisted relatively well. Because of practical problems associated with the 'burn standing' and 'fell, remove and burn' treatments, managers often have little option but to apply the 'fell and burn' treatment. Our results illustrate the dangers of this, and highlight the need for intervention before areas become densely invaded. They also highlight the need for effective biological control agents to reduce rates of spread of aggressively invasive species.

Key words: ecological restoration, functional guilds, species richness, watershed management, weed species.

INTRODUCTION

Invasive, alien organisms are a major global environmental problem (Vitousek *et al.* 1997) and are considered to be the second most significant threat to biodiversity following direct habitat destruction (Rubec & Ledd 1996). In South Africa, invasive alien trees and shrubs threaten both the floristically distinctive fynbos vegetation and water resources (Richardson *et al.* 1997). The realization that dense stands of alien invasive trees could lead to substantial reductions in stream flow has prompted government initiatives to deal with the problem, and multimillion dollar weed control programmes have been embarked upon (Van Wilgen *et al.* 1998). Many of these programmes are taking place in the mountains of the Western Cape Province,

which support fynbos shrublands typical of the Cape Floristic Region (Cowling & Holmes 1992). The most widespread invasive aliens in mountain watershed areas are species of *Pinus* and *Hakea*, with *Acacia* species being more restricted to riparian zones (Richardson *et al.* 1997).

Once alien trees have established, they grow faster and taller than indigenous species, and after one or two fire-cycles form closed stands with reduced light penetration and altered nutrient cycling patterns, litterfall and fuel properties (Richardson *et al.* 1997). Such stands typically replace fynbos vegetation and their impacts intensify with time elapsed since invasion (Holmes & Cowling 1997a).

Fynbos vegetation is fire-prone and fire-adapted (Van Wilgen *et al.* 1992), but regular fires also promote the spread of invasive trees (Richardson *et al.* 1992). In order to clear infestations of invasive trees, these are felled prior to burning; seeds are released from *Pinus* and *Hakea* cones following felling and their resultant seedlings are killed by the fire (Van Wilgen *et al.* 1992).

This management strategy relies on the recruitment properties of the remaining indigenous plants and propagules, because recovery mostly results from surviving plants in the area, soil-stored seed banks and medium-distance wind dispersal (Holmes & Richardson 1999). However, the 'fell and burn' clearing treatment carries the risk of unplanned fires, which may burn under extreme weather conditions (Richardson & Van Wilgen 1986a). The additional fuel loads situated close to the soil surface can lead to extreme fire intensities, which have detrimental effects on the soil (Scott & Van Wyk 1990) and on soil-stored seed banks.

In many cases the 'fell and burn' strategy has been successful in the re-establishment of a functional cover of fynbos vegetation, but managers may need to consider alternative approaches where there is a threat of fire in areas with high fuel loads. Although there is as yet no fynbos restoration policy, there may be a need to initiate such a programme after clearing operations (Holmes & Richardson 1999). Without good indigenous vegetation recovery, soils will be susceptible to erosion and future colonization by indigenous species may be slow. Furthermore, a sustainable cover of fynbos vegetation is required to ensure continued high water quality and yields into the future. An understanding of the impacts and consequences of alternative treatments will contribute towards improving watershed management.

We report on the recovery of fynbos vegetation following three distinct treatments in dense alien stands. These were (i) 'fell and burn', in which an accidental fire under severe weather conditions had burned through high loads of dead plant material (felled *Hakea* fuel) close to the soil surface; (ii) 'fell, remove and burn', areas that had been cleared of *Pinus* plantations by felling and removing the timber before burning (thereby reducing fuel loads and fire intensity considerably); and (iii) 'burn standing', areas where stands of *Pinus* trees had burnt while still standing, prior to clearing (thus with relatively high biomass but lacking high loads of dead material close to the soil surface). We set out to establish: (i) which of the treatments had the greatest impact on species richness, density, cover and functional composition of the vegetation; (ii) whether the treatments impacted more on certain biological and functional guilds than others; and (iii) whether any guilds would need re-introduction into the community in order to restore a functional cover of fynbos vegetation.

An understanding of these issues is fundamental to the sound management of watershed areas that need to be cleared of invasive trees and restored to fully functional indigenous ecosystems.

METHODS

Study sites

The study was conducted in two watershed areas in the Western Cape Province: Jonkershoek (33°59′S, 18°57′E) and Wemmershoek (33°51′S, 19°10′E), which lie 21 km apart. The Jonkershoek valley was afforested with *Pinus radiata* between 1949 and 1965, whereas the Wemmershoek valley supported dense stands of the invasive *Hakea sericea*, a tall shrub from Australia that grows to 5 m in South Africa (Table 1). Both areas experienced accidental wildfires. At Jonkershoek, some of the mature pines were burnt standing during a fire in February 1996, while other sites had been cleared, the logs removed, and replanted prior to the fire. The Jonkershoek treatments can be likened to treating invasive trees, because the pines were planted originally into pristine fynbos. At Wemmershoek the hakeas had been felled six months before a fire in January 1984. The heavy fuel loads and the warm, dry and windy weather conditions resulted in a very intense fire. Recovery of indigenous vegetation was monitored for 19 months after the 1984 fire (Richardson & Van Wilgen 1986a).

Table 1. Description of study sites

Watershed	Site	Invader species	Aspect and slope	Treatment
Jonkershoek	1	*Pinus radiata*	N, >20°	'Burn standing'; planted 1951, burnt February 1996, felled and replanted 1996.
Jonkershoek	2	*Pinus radiata*	NE, 10–20°	'Burn standing'; planted 1949, burnt February 1996, felled and replanted 1996.
Jonkershoek	3	*Pinus radiata*	NE, >20°	'Fell, remove and burn'; planted 1950, felled and replanted 1993, burnt February 1996, replanted 1996.
Jonkershoek	4	*Pinus radiata*	Valley bottom	'Fell, remove and burn'; planted 1965, felled and replanted 1994, burnt February 1996, replanted 1996.
Wemmershoek	5	*Hakea sericea*	W, 10–20°	'Fell and burn'; dense invasion, felled 1983, burnt January 1984.
Wemmershoek	6	*Hakea sericea*	SW, 10–20°	'Fell and burn'; dense invasion, felled 1983, burnt January 1984.

Both watersheds support structurally similar Proteoid Fynbos vegetation (Cowling & Holmes 1992), on sandy soils derived from granite and sandstone parent materials. Mean annual rainfall approximates 1500 mm at both watersheds. At Jonkershoek, four sites were investigated that encompassed both the steep hill slopes and the valley bottom (altitudinal range 280–540 m, Table 1). At Wemmershoek two sites in similar gently sloping terrain were studied (altitudinal range 480–540 m, Table 1). Matched control sites were established in adjacent fynbos vegetation, which had also burnt in the respective fires, but which had never been invaded. Distances between alien-invaded and matched control sites were a maximum of 200 m at Jonkershoek and 700 m at Wemmershoek.

Sampling was 18 months post-fire at Jonkershoek and 13 years post-fire at Wemmershoek. Although vegetation structure changes with time elapsed since fire, as ephemerals die back and long-lived species become more dominant (Kruger & de Bigalke 1984), all fynbos species regenerate within the first year after a fire, and the later-maturing species were represented at both watersheds. Thus, the main difference expected between the two watersheds owing to post-fire age was a lower representation of short-lived species at Wemmershoek compared to Jonkershoek.

Vegetation sampling

Three square 25 m^2 plots were positioned at each of the invaded and control sites (36 plots in total). During May and June 1997 all species within the plots were listed, and the number of individuals (termed the density) and the projected canopy cover were recorded for each species, as well as the total canopy cover for the entire plot. Species richness was recorded in a 1 m^2 quadrat placed at the centre of the plot. Additional species occurring in the 1 m strip around the perimeter of the plot (an additional 24 m^2) were noted as were all additional species occurring outside the plots at the site (an area of about 50 m diameter). Voucher specimens of all unknown species were collected, pressed and identified to species level if possible, in local herbaria. Follow-up field visits to collect further material of unidentified species took place in November and December 1997. Botanical nomenclature in this paper follows Bond and Goldblatt (1984).

Data analysis

The effects of previous invasion on a range of vegetation variables were tested by one-way ANOVA. We compared the effects of the different clearing treatments on the vegetation variables using ANCOVA, with data from the matched control sites serving as the covariates. This approach is valid because burning is a natural phenomenon in fynbos, triggering recruitment, and the control sites represent the status of the vegetation in the absence of invasion and clearing. Because individual treatment plots could not be matched to individual control plots, other than arbitrarily, sites were taken as the true replicates and the results averaged across the three plots used in the analyses. This approach greatly reduced the number of degrees of freedom, hence we have raised the significance level to $P < 0.1$. In order to meet the required assumptions of normality, cover and density values were arcsin and log transformed, respectively.

To investigate whether guild structure remained constant following invasion and subsequent burning, indigenous species were assigned to categories with respect to their growth form, leaf size, dispersal mode, seed storage and regeneration mode, and nutrient acquisition mode (Table 2). The categorization of species was based on data in Bond and Slingsby (1983), Bond and Goldblatt (1984), Van Wilgen and Forsyth (1992), Cowling et al. (1992), Trinder-Smith (1995) and our own field observations. It has been postulated that the major ecosystem functions, such as water and nutrient cycling, can be typified by the balance of disparate guilds, especially the various growth forms, regeneration modes and nutrient-acquisition modes (Holmes & Richardson 1999). Thus, we used a combination of these three attributes to define functional guilds, but included only the later-maturing species (lifespans >4 years) in the analyses in order to minimize potential differences between the watersheds owing to post-fire age. Some of these combinations did not occur in our samples, or contained too few species for meaningful analysis. The three root-nodulating shrub guilds had to be combined with the equivalent mycorrhizal shrub guilds in order to meet minimum cell sizes for the contingency table analyses (nine out

Table 2. Plant species attributes used to classify fynbos plants at two watershed areas. Combinations of growth form, regeneration mode, and nutrient acquisition mode were used to define functional guilds

Plant species attribute	Range of possibilities considered
Growth form	Geophyte, graminoid, forb, shrub
Height (m)	<0.25, 0.25–<1, 1–2, >2
Leaf size	Leptophyll, nanophyll, microphyll, mesophyll
Seed dispersal mode	Wind, vertebrate, ant, ballistic, passive
Regeneration mode	Sprouter, seeder
Pollination mode	Bird, insect, wind
Seed storage mode	Soil, canopy, none
Nutrient acquisition mode	Mycorrhizal, non-mycorrhizal, N-fixing

of 11 functional guilds were used). We tested the null hypothesis that cover and density in each biological attribute and functional guild remains constant following clearing treatments. The assumption is that density is a more sensitive measure of change, but that ecosystem function is more likely to be driven by changes in plant cover (as a surrogate measure for biomass). Thus changes in plant cover for a particular guild are more likely to indicate a possible change in function as a result of the treatments. Data were analysed separately for each treatment (BMDP PROGRAM 4F, Dixon 1992). Where the guild structure of the stands differed significantly, adjusted standardized deviates were examined for significant cells (those with an absolute value exceeding 3.0; Haberman 1973).

We used detrended correspondence analysis (DCA; Gauch 1982) to assess shifts in functional guild composition of the vegetation in relation to invasion and fire. We used the sum of cover values for all species within 11 functional guilds, including only the later-maturing species.

RESULTS

Species richness, cover and density

Species richness was lower for invaded areas than controls at all scales measured (Table 3). There was no marked difference in the slope of the log-transformed species area curves between controls and invaded sites for any treatment (Fig. 1). Although differences among treatments were not significant, relatively large F-values were obtained at the 25 m^2 and 49 m^2 scales (Table 4). In order of greatest impact on richness, treatments were 'fell, remove and burn' > 'fell and burn' > 'burn standing'.
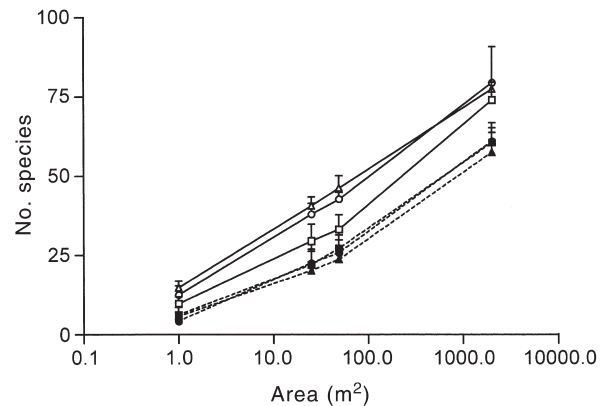

Fig. 1. Species area curves for the three treatment and control sites. Means and standard deviations are shown ($n = 6$ for the three smallest areas, $n = 2$ for the community area); BS, 'burn standing'; FRB, 'fell, remove and burn'; FB, 'fell and burn'. (□) BS control; (△) FRB control; (○) FB control; (■) BS invaded; (▲) FRB invaded; (●) FB invaded.
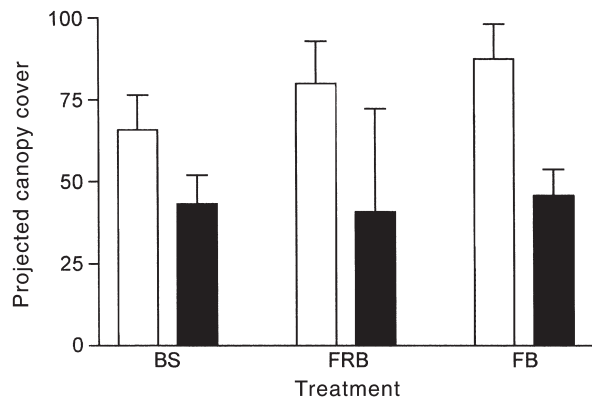

Fig. 2. The effect of different clearing treatments on indigenous vegetation projected percentage canopy cover (±SD, $n = 6$). Invaded (■) and control (□) sites are significantly different ($F = 12.9$, $P = 0.005$).

Table 3. Species richness in vegetation plots following different clearing treatments and fire; data are means ± SD ($n = 6$, or $n = 2$ for combined and community data). Results of one-way ANOVAs comparing invaded and control sites are shown (**$P < 0.01$, ***$P < 0.001$)

Treatment	1 m^2	25 m^2	49 m^2	[a]75 m^2	[a]147 m^2	[b]Community
Burn standing						
Control	9.67 ± 2.25	29.5 ± 5.39	33.2 ± 4.58	50.5 ± 2.12	53.0 ± 1.41	74.0 ± 16.9
Invaded	6.17 ± 2.48	22.0 ± 6.93	27.2 ± 6.85	43.5 ± 12.0	48.5 ± 10.6	60.5 ± 6.36
Fell, remove and burn						
Control	14.8 ± 2.04	40.7 ± 2.73	46.3 ± 3.88	64.0 ± 5.66	66.5 ± 3.54	77.5 ± 2.12
Invaded	5.67 ± 4.37	20.2 ± 6.73	23.7 ± 7.79	39.5 ± 10.6	42.5 ± 13.4	57.5 ± 7.78
Fell and burn						
Control	12.5 ± 2.88	38.0 ± 3.46	42.7 ± 2.25	64.0 ± 5.66	67.0 ± 7.07	79.5 ± 0.71
Invaded	4.17 ± 2.71	22.5 ± 3.83	25.8 ± 4.07	43.0 ± 4.24	44.5 ± 3.54	61.0 ± 2.83
One-way ANOVA	MS F	MS F	MS F	MS F	MS F	MS F
Between (d.f. = 1)	145.6 23.3***	629.3 21.1**	690.1 18.1**	918.7 15.2**	867.0 13.1**	901.3 20.1**
Within (d.f. = 10)	6.2	29.8	38.2	60.6	66.0	44.7

[a]Combined data from three plots (not contiguous); [b]Community size, approximately 2000 m^2 contiguous area.

Table 4. ANCOVA results for indigenous species richness at different scales. The covariate was richness at the matched control sites

Source	1 m² MS	F	25 m² MS	F	49 m² MS	F	75 m² MS	F	147 m² MS	F	Community MS	F
Covariate (d.f = 1)	3.995	0.723 (NS)	105.56	10.77*	119.03	10.62*	55.21	0.502 (NS)	21.80	0.154 (NS)	27.34	0.67 (NS)
Treatment (d.f. = 2)	3.883	0.703 (NS)	50.12	5.11 (NS)	64.46	5.75 (NS)	36.40	0.331 (NS)	25.11	0.177 (NS)	8.61	0.21 (NS)
Error (d.f. = 2)	5.525		9.80		11.21		109.89		141.85		40.83	

NS, not significant; *$P < 0.1$.

Indigenous plant cover and density were significantly lower in invaded areas compared to controls (Fig. 2, Table 5). There was no significant increase overall in the density of herbaceous alien plants with invasion (Table 5). There were no significant differences among clearing treatments with respect to plant cover or
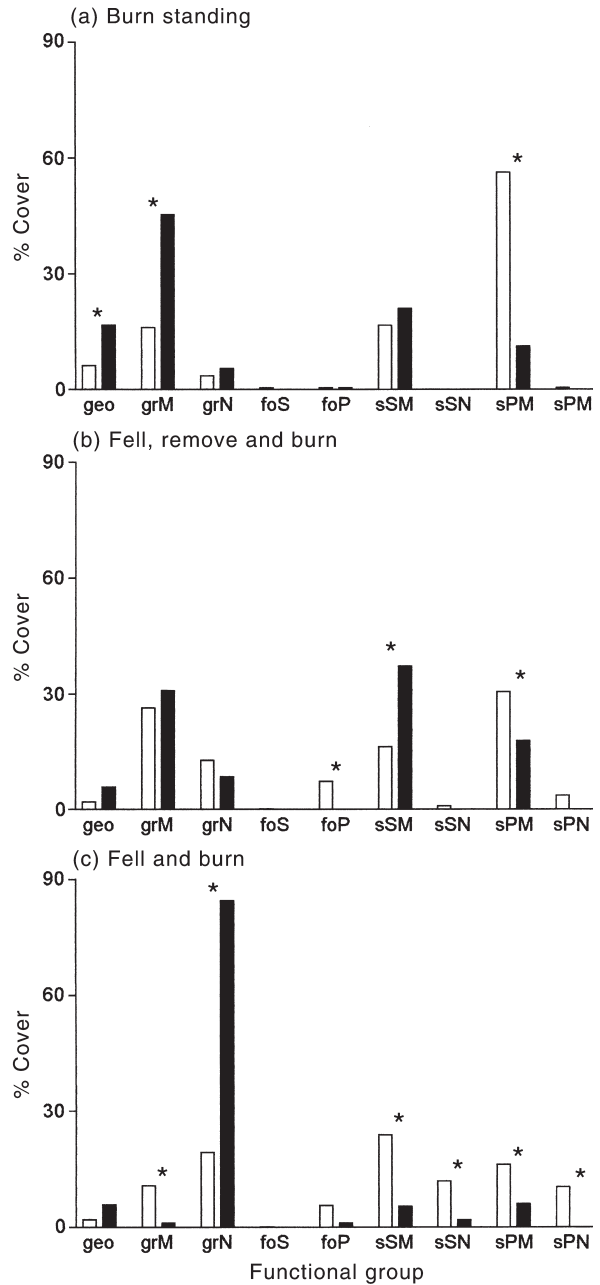

Fig. 3. The impact of different clearing treatments on the relative cover of plant functional guilds (long-lived (>4 years) species only); (a)'burn standing', $\chi^2 = 132.3$***; (b) 'fell, remove and burn', $\chi^2 = 80.8$***; (c) 'fell and burn', $\chi^2 = 363.2$. Numbers are Pearson χ^2 values, ***$P < 0.001$; *adjusted standardized deviates >3.0. Geo, geophyte; gr, graminoid; fo, forb; s, shrub; S, seeder; P, sprouter; M, mycorrhizal; N, non-mycorrhizal. □, control; ■, invaded.

Table 5. Plant density in vegetation plots following different clearing treatments and fire; $n = 6$ (25 m² plots)

Treatment		Native density (mean ±SD)	Alien densityª (mean ± SD)
Burn standing	control	314.5 ± 73.4	4.2 ± 4.9
	invaded	204.6 ± 97.4ᵇ	40.3 ± 37.7
Fell, remove and burn	control	561.2 ± 233	0.17 ± 0.41
	invaded	300.3 ± 262.1	6.0 ± 5.2
Fell and burn	control	213.7 ± 49.1	0.17 ± 0.41
	invaded	81.7 ± 33.5	0.17 ± 0.41
One-way ANOVA		MS F	MS F
Between groups (d.f. = 1)		1.86 3.79★	27.08 3.11 NS
Within groups (d.f. = 1)		0.49 8.72	

ªPredominantly herbaceous species, excludes study alien species (*Pinus* and *Hakea*); ᵇone plot excluded owing to the unusual presence of 1375 individuals of *Phylica pubescens*; NS, not significant; ★$P < 0.1$.

Table 6. Results of the ANCOVAs for projected canopy cover, indigenous plant density and herbaceous alien density. The covariate was the equivalent datum from the matched control site

Source		Cover		Indigenous density		Alien density	
		MS	F	MS	F	MS	F
Covariate	(d.f. = 1)	0.104	2.61 (NS)	2.342	67.01★	3.185	1.17 (NS)
Treatment	(d.f. = 2)	0.026	0.64 (NS)	0.307	8.77 (NS)	17.130	6.28 (NS)
Error	(d.f. = 2)	0.040		0.035		2.726	

NS, not significant; ★$P < 0.1$.

density, although the *F*-value for indigenous density is close to significant (Table 6). In order of greatest impact, the treatments were 'fell, remove and burn' > 'fell and burn' > 'burn standing'.

Guild structure

Functional guilds

Changes in the relative cover of the nine functional guilds in response to invasion and clearing differed among treatments (Fig. 3). Following the 'burn standing' and 'fell, remove and burn' treatments, cover of mycorrhizal graminoids increased, and sprouting shrubs decreased. In the 'burn standing' treatment, cover of geophytes increased and in the 'fell, remove and burn' treatment sprouting forbs decreased in relative cover. In the 'fell and burn' treatment the cover of most functional guilds decreased, except for non-mycorrhizal graminoids (Restionaceae and Cyperaceae), which increased dramatically in relative cover following invasion. The functional guild ordination indicated overlap among control plots, reflecting the structural similarity of the vegetation at all sites (Fig. 4). Previously invaded 'fell and burn' plots are clearly separated from controls and other treatments, suggesting that 'fell and burn' differs in its impact on guild structure from the other treatments.

Biological Attributes

Significant changes in relative densities were found for nearly all the biological attributes investigated, but not all of these translated into changes in relative cover, and occasionally the direction of change reversed for relative cover (data available on request from the corresponding author). For 'burn standing' and 'fell and burn' treatments, graminoid relative cover increased and shrub cover decreased, whereas for the 'fell, remove and burn' treatment the main change was a decrease in forb cover. Few shrubs survived the 'fell and burn' treatment, resulting in no significant changes in woody plant height and leaf size guilds. Shrubs of lower stature (<1 m) decreased following 'burn standing' and 'fell, remove and burn' treatments whereas medium or tall shrubs increased in relative cover. Changes to leaf size differed between the two treatments, with leptophylls decreasing in 'burn standing' and nanophylls decreasing in 'fell, remove and burn' relative to other guilds.

All treatments resulted in an increase in the relative density of ant-dispersed species, but this translated into a significant increase in relative cover for only the 'fell and burn' treatment. All other dispersal guilds decreased following this treatment. Species with ballistic dispersal decreased in relative cover following all treatments, whereas species with passive dispersal increased following 'burn standing' and 'fell, remove and burn' treatments. The relative density and cover of canopy seed storage species decreased, and soil storage species increased, following all treatments, although

this trend was not significant for the 'burn standing' treatment. Sprouting plants decreased and seeding plants increased in relative density and cover following 'burn standing' and 'fell, remove and burn' treatments, but the inverse occurred following the 'fell and burn' treatment. Changes in pollination mode guild structure were similar for 'fell, remove and burn' and 'fell and burn' treatments, with bird and insect pollination guilds decreasing and the wind pollination guild increasing.

DISCUSSION

Richness, density and cover

Vegetation recovery following invasion depends on recruitment from persistent propagules in the soil, as long-distance dispersal is rare in fynbos (le Maitre & Midgley 1992). Over 75% of fynbos species with dormant soil-stored propagules were found to persist at the community level in sites invaded by *Acacia saligna* after two fire cycles (about 30 years; Holmes & Cowling 1997b). This study documents a similar degree of persistence in previously invaded areas. Species area curves for invaded sites did not converge with those for control sites, suggesting that species losses at the plot scale were not compensated for at the community scale. This is contrary to the notion that potential refugia for vulnerable species would increase with scale. Lower fynbos plant densities in previously invaded areas resulted from reduced seed rain under alien trees and gradual attrition of soil-stored seed banks (Holmes & Cowling 1997b).

The lower plant density and higher cover in 'fell and burn' controls reflect the greater post-fire age of vegetation at these sites. At 13 years post-fire, short-lived species will have died and vegetation cover will have matured. However, Richardson and Van Wilgen (1986b) found that indigenous plant cover for the 'fell and burn' treatment was only 13.3% at 18 months post-fire at the same site, which is much lower than the 40.8% and 43.3% recorded, respectively, for 'fell, remove and burn' and 'burn standing' treatments at the same post-fire age. The 'fell and burn' treatment yielded very high fire intensities (Richardson & Van Wilgen 1986a). Fuel was concentrated near to the ground, and heat penetration into the soil was probably high with temperatures attained in excess of the lethal range for many indigenous seeds. Breytenbach (1989) found that fire intensity in stands of felled *Hakea* was much higher than predicted from heat release models and suggested that the models may underestimate the biological impacts of such fires. Serious soil erosion occurred during the first heavy winter rains following the fire on sites 5 and 6 (Richardson & Van Wilgen
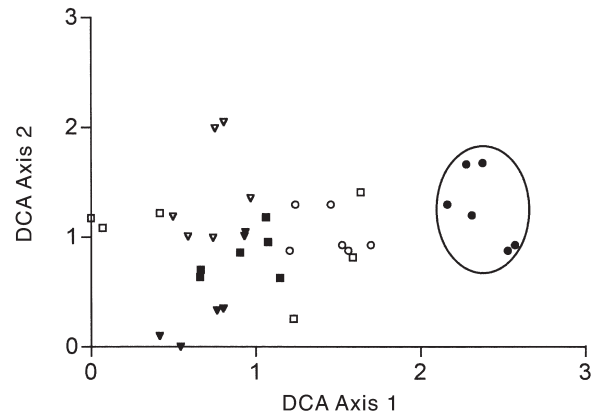

Fig. 4. Detrended correspondence analysis ordinations of the functional guild composition of plots following different clearing treatments. Only the later-maturing species included (lifespans >4 years). □, burn standing control; ■, burn standing invaded; ▲, fell, remove and burn control; ▼, fell, remove and burn invaded; ○, fell and burn control; ●, fell and burn invaded.

1986a). Although we observed interfire recruitment of seeder species, much lower plant densities and cover persisted after felling and burning.

Guild composition

Only the non-mycorrhizal graminoids persisted relatively abundantly following the 'fell and burn' treatment. Species in this guild had relatively large ant-dispersed seeds, which are stimulated to germinate by direct or indirect fire-related germination cues (Bond *et al.* 1991; Keeley & Bond 1997). Fynbos ant-dispersed seeds are buried to a median depth of 50 mm (Bond *et al.* 1991), which would give sufficient protection from heat generated by the most intense fires (Bond & Van Wilgen 1996). Seed-regenerating species without ant dispersal are generally distributed nearer to the soil surface and are killed by intense fires. Many of these species are small-seeded and would have insufficient resources to emerge from greater depths in the soil.

Geophytes were relatively persistent in response to invasion, as they can survive for many years as dormant storage organs under an alien stand (Richardson & Van Wilgen 1986b). After fire, most geophytes emerge to flower and set seed before being overgrown by the vegetation (le Maitre & Midgley 1992). However the 'fell and burn' treatment may have killed some of the geophytes, as found by Breytenbach (1989).

Mycorrhizal shrubs persisted well in response to the 'burn standing' and 'fell, remove and burn' treatments, whereas they fared badly following the 'fell and burn' treatment. The extreme 'fell and burn' fire conditions may have sterilized the upper layers of soil, so that

obligately mycorrhizal species (e.g. *Erica* species) may have failed to establish.

The loss of species and the changes in relative abundance of different functional guilds after invasion by alien trees and subsequent clearing operations are likely to have implications for ecosystem functioning. Biodiversity plays an important role in buffering the ecosystem against the loss of functionally important components following a variety of perturbations (Richardson *et al.* 1995). Thus a fynbos community deprived of certain functional guilds may be less resistant to disturbance than a richer community. Although community richness in previously invaded areas exceeds 75% of that within control areas, some guilds have been disproportionately affected by the treatments. The relative reduction in sprouter abundance and cover may threaten watershed stability in the immediate post-fire phase. The elimination of serotinous species by invasive trees results in significant structural change by removing the dominant overstorey. Fynbos overstorey shrubs have been shown to maintain understorey richness (Vlok 1996) and their long-term absence from the community may threaten community diversity, which in turn may affect ecosystem function.

Management implications

Of the three treatments applied, 'burn standing' caused the least change to vegetation variables. The 'fell, remove and burn' and 'fell and burn' treatments caused similar reductions in fynbos species richness and density, but 'fell and burn' caused the greatest change to cover and guild structure. The 'fell and burn' treatment is the standard for the control of non-sprouting trees and shrubs with canopy-stored seeds (such as *Pinus* and *Hakea* species, Van Wilgen *et al.* 1992). However, our results (and those of Breytenbach 1989) indicate that the risks associated with this management strategy may become unacceptable if the felling operations produce excessive amounts of dead fuel. The 'fell, remove and burn' option, while producing more desirable results, may be feasible in limited areas only, where large logs and access to roads allow for marketable wood to be removed and sold to offset costs. In many areas, however, the rugged, inaccessible terrain will preclude this as a practical option, which then leaves managers with a choice to either 'fell and burn', or 'burn standing'.

The results clearly indicate that the 'burn standing' treatment best promotes fynbos recovery. Unfortunately, this method also facilitates the spread of alien propagules and the re-invasion of cleared sites or initiation of new invasions, and the standing dead trees that are left reduce accessibility to sites for the follow-up weeding of alien seedlings (Richardson & Van Wilgen 1986a; Pieterse & Boucher 1997). For these reasons, 'burn standing' is unpopular with managers and this emphasizes the need for alternative and long-term solutions to the problem, such as finding suitable biological control agents for alien plants. There have been numerous successes where such control agents have been introduced (Dennill & Donnelly 1991; Kluge & Neser 1991; Morris 1991). It also emphasizes the need for rapid action. Many areas are currently only lightly invaded and 'fell and burn' treatments in such areas have few detrimental effects, as fuel loads are relatively low. However, the continued spread and densification of alien trees will begin to foreclose this option over the next decade or two, with severe results for the ecosystem and the services it delivers (Van Wilgen *et al.* 1996).

Following a high intensity fire through dense alien slash, some restoration actions are recommended to speed up the recovery of indigenous guild structure and ecosystem function. Erosion should be combated with physical structures and the sowing of non-invasive, fast-growing herbs. To restore guild structure, locally harvested indigenous seed should be sown over the area in early autumn to augment recruitment from persistent soil-stored seed banks (Holmes & Richardson 1999).

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