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The effects of past management practices for invasive alien plant control on subsequent recovery of fynbos on the Cape Peninsula, South Africa

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Integrated control aimed at reducing impacts of alien woody plant invasions on biodiversity is underway in many parts of the Cape Floristic Region. However, the kinds of control measures applied may themselves affect the recovery of the natural vegetation. In view of this, we investigated the effects of past management practices, viz: 'bulldozing and aerial-spraying', 'aerial-spraying', 'boom-spraying' and 'foliar-spraying' aimed at clearing invasive alien woody plants on subsequent fynbos recovery in the Table Mountain National Park. Changes in soil (pH and depth) and vegetation (species cover, richness, diversity, evenness) properties, the total cover of species representing different dispersal guild, regenerative mode, and life form categories were compared between the differently treated and control plots at three different sites in the reserve. Only partial recovery of fynbos was observed in the 'boom-sprayed' and one of the 'foliar-sprayed' plots where measured species richness was significantly lower than that in control plots. However, marked changes in community structure were observed following 'boom-spraying' and 'foliar-spraying' at one site where a significant reduction in long-lived obligate reseeding species and an increase in the graminoid component was measured, though high fuel loads with possible post-fire erosion may also have aggravated the effects of foliar-spraying. Growth form structure changed the least following 'aerial-spraying' and 'foliar-spraying'. Multivariate analysis of plant functional types indicated a greater similarity between the control plots than the differently treated plots, implying a treatment effect on subsequent fynbos recovery. However, past land use and residual effects of the alien woody invaders may also have contributed to the differential recovery in the treated plots. It is concluded that re-introduction of species in the under-represented guilds may speed up fynbos recovery. The recommendation is a comprehensive seed mix containing the major guilds, and an initial seed mix of fast-growing indigenous species to stabilise the soil.

Introduction

Problems associated with biological invasions have received increased attention from ecologists in the past few decades. One reason for this is the escalating impacts of invasive alien species in natural and semi-natural ecosystems worldwide (D'Antonio and Vitousek 1992, Vitousek *et al.* 1997). The Cape Floristic Region at the southern tip of Africa is no exception, and invasive alien plants are one of the most important threats to biodiversity in this global hotspot (Richardson *et al*. 1996, Rouget *et al*. 2003). The most widespread and damaging invasive alien plant species are trees and shrubs of the genera *Acacia*, *Hakea* and *Pinus*. These species have invaded large tracts of land in both the mountains and the lowlands of the fynbos biome (Richardson *et al*. 1992, Rouget *et al*. 2003). Such invasions bring about many changes to ecosystems, including a marked change to the amount, distribution, and properties of combustible biomass, increased litter fall, and altered nutrient cycling patterns (Richardson and Van Wilgen 2004, Yelenik *et al.* 2004).

Substantial progress has been made in research relevant to the management of alien plant invasions in the fynbos. Recent innovations in invasive alien plant control have led to the integrated use of biological, chemical and mechanical methods of control. Mechanical control of woody invasives in fynbos involves felling the trees/shrubs using mechanical tools. Fire and/or chemical control are usually applied after initial clearing using mechanical means. Three main categories of mechanical control are used: 1) 'cut and burn', 2) 'cut and leave', and 3) 'burn standing'. Fire is an integral part of alien plant control in fynbos (Van Wilgen *et al.* 1992). It stimulates the release of seeds of serotinous invaders such as hakeas and pines, and stimulates germination of the soil-stored seeds of acacias (Richardson *et al*. 1992). Hand-pulling of seedlings and/or herbicide application is required as follow-up to the initial mechanical measures and fire. Herbicides used in these operations can selectively target grasses or broad-leaved species, leaving other species unharmed (Van Wilgen *et al*. 2000). Biological control, using species-specific insects and diseases from the region of origin of the alien plant, is an integral part of control programmes for all the major invaders in fynbos (Olckers 2004).

Despite the advances in our understanding of the ecology of plant invasions in fynbos and the implementation of systematic control programmes in many areas, managers still face many challenges due to the large areas requiring treatment and shortage of resources, mixtures of species requiring different treatments, unplanned wildfires that disrupt planning, and poorly understood differences in the success of control operations in different areas. Despite the best attempts at controlling invaders in some areas, some control operations have exacerbated the problem, caused further damage to native communities (Richardson and Van Wilgen 1986, Breytenbach 1989, Holmes *et al.* 2000, Holmes 2001a). Because of the lack of detailed records of control operations, managers are often forced to base plans for control on their personal knowledge and experience.

A key element of current alien management programs is the restoration of sites after removal of the invaders (Hobbs and Mooney 1993, Holmes and Richardson 1999, Holmes *et al.* 2000, Holmes 2001b). Good information is therefore needed on the extent to which different control measures affect the capacity of the site to self-repair following the removal of the invasive alien. This is because the management itself has the capacity to alter the rate at which a site potentially may return to a condition approximating the pre-invasion state. Such insights are needed in order to know, amongst other things, the level of resources to allocate to proactive restoration measures, such as the introduction of keystone species to speed up succession. Thus, it is important to know what types of restoration practices should be applied with each type of control method in order to promote vegetation recovery.

Distinguishing between the net effects of invasive alien plants and control measures, and naturally occurring differences between sites is problematic. Fynbos plant species are not distributed uniformly or randomly across landscapes, but are concentrated in small nodes (Kruger and Taylor 1979, Simmons and Cowling 1996). Such localised distribution patterns, and the high turnover of species, even over short distances, and also the large number of plant species within identifiable 'functional groups' (Cowling *et al*. 1994, Richardson *et al*. 1995) means that comparing the species composition of different sites is not very helpful when seeking indicators of the impact of a particular management treatment. The problem lies in determining whether any differences in species composition are 'natural' (i.e. due to the normal pattern of species turnover), or due to the elimination or addition of species due to invasions and/or management interventions. Consequently, the approach taken in this study was to investigate changes to measures of biodiversity (i.e. abundance, species richness, diversity, evenness) and vegetation structure, rather than comparing species composition across sites.

This paper reports on the recovery of fynbos vegetation following four typical alien-control treatments applied to dense stands of invasive alien acacias. All alien stands were burnt standing as the initial treatment, with first follow-up treatment as: 1) 'bulldozing and aerial-spraying', 2) 'aerial-spraying', 3) 'boom-spraying', and 4) 'foliar-spraying'. No scientific work has been conducted on the relative susceptibility of fynbos plant species or functional groups to any of the treatments applied. Hence it was not feasible to draw detailed hypothesis relating the various functional types to the above treatments. This study was therefore largely exploratory and descriptive, and aimed at determining whether: 1) the management practices employed have affected species richness, diversity, evenness, density and total cover, 2) treatments have changed the representation of plant functional groups in the vegetation, and 3) whether information from 1) and 2) could be used to make recommendations on functional types that should be re-introduced into the community following management, to promote the recovery of fynbos.

Methods

Study area

The study was conducted in the Cape of Good Hope Nature Reserve section of the Table Mountain National Park (previously known as the Cape Peninsula National Park), which is situated at the south-western corner of the Cape Floristic Region. This section of the park covers 7 750ha (Figure 1). The natural vegetation and flora (Taylor 1969, 1983, 1984a, 1984b, Fraser and McMahon 1994, Privett 1998, Privett *et al*. 2001) and the invasive alien flora (Taylor and Macdonald 1985, Taylor *et al*. 1985, Macdonald *et al*. 1987, 1989, Fraser and McMahon 1994, Richardson *et al*. 1996) have been well documented. The reserve was therefore considered ideal for this study, as it is one of the very few areas in the Cape Floristic Region for which reasonable data (some dating back to 1941) was available on the history of invasive alien plant management.

Plot location

Plot location was based on a thorough review of the study area history using information obtained from published accounts and ranger's reports (dating back to 1963), consultations with managers, and field visits. A database of the various alien plant control measures employed in the reserve was compiled and the information mapped using Geographical Information System (GIS; ArcView version 3.1). Using this information, 10 main plots, each comprising $5m^2$ x $50m^2$ sub plots randomised along a transect through each main plot, were located at three different sites

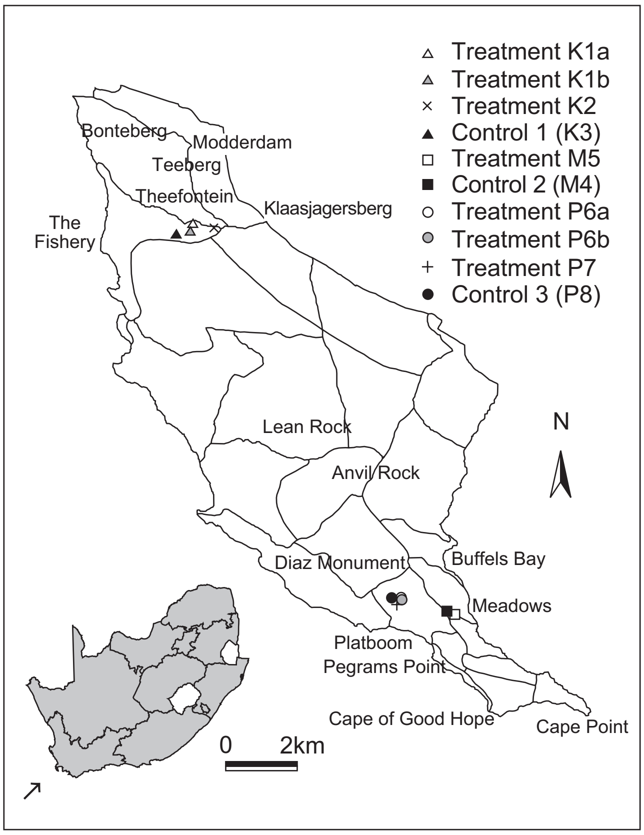

Figure 1: Map of the Cape of Good Hope Nature Reserve Section of the Table Mountain National Park. The symbols show the locations of the study plots

(Klaasjagersberg, Meadows and Platboom) in the reserve (Figure 1). Seven of these main plots (treatments) had in the past supported dense stands (>70% cover) of invasive alien woody species which had been subjected to different combinations of bulldozing, aerial-, foliar- and boom-spraying to eradicate the aliens. The remaining three main plots (controls), one at each site, had no record of dense stands of woody alien species but had a similar fire history to that of corresponding treatment plots (Table 1).

Vegetation properties

Species abundance in each sub-plot was ranked according to Acocks' (1975) scale, namely: 1 (occasional) = 1–4 individuals; 2 (fairly frequent) = 5–10 individuals; 3 (frequent) = 11–50 individuals; 4 (common) = 51–100 individuals; 5 (abundant) = >100 individuals. Estimates of plant density were based on the median value of each cover abundance class.

Species richness was measured at two different scales by counting the total numbers of perennial taxa present in both a $1m^2$ quadrat positioned at the centre of each sub plot and in the entire $50m^2$ sub plot. The projected percentage canopy cover of each species and the proportion of bare ground in each sub plot were visually estimated. Estimates of less than 1% of the total sub plot area were given an arbitrary value of 0.1%.

Species diversity (H) and evenness (J) indices in each sub plot were calculated using the Shannon-Wiener formulae (Begon *et al*. 1995):

$$H = -\sum P_i \log P_i \qquad (1)$$

where P_i is the proportion of total individuals (density) present in each sub plot represented by species P

$$J = H/H_{(max)} \qquad (2)$$

where $H_{(max)}$ is the maximum diversity if all species in the plot had equal numbers of individuals.

Soil properties

Three soil samples were collected at random within each sub plot. The samples were air-dried and the pH measured in a 30g sample of soil suspended in 75ml of deionised-distilled water using a pH meter (WTW 320 pH meter, Germany). Average soil depth was estimated by hammering a steel rod into the soil until reaching an impenetrable layer, at five random points within each sub plot.

Statistical analyses

Species richness and abundance measurements were log transformed to reduce inequality of variance in the raw data. Canopy cover percentages were arc-sine transformed to correct non-normality in proportions. Species were also grouped into different dispersal guilds, regenerative modes and life form categories (functional groups) based on their attributes listed in Goldblatt and Manning (2000), Van Wilgen and Forsyth (1992) and Trinder-Smith (1995). The total percentage covers of species representing each of 13 delineated functional groups, viz: passive-dispersed, ant-dispersed, wind-dispersed, bird-dispersed, sprouter, long-lived-seeder, short-lived seeder, low shrub (<1m), mid-sized shrub (1–2m), tall shrub (>2m), graminoid and forb (inclusive of geophytes) were summed in each sub plot. Differences in measured vegetation properties and covers of different functional groups within and between treatments and controls were tested with a single factor analysis of variance (ANOVA). Differences in measured soil properties between treatments and controls were tested with a non-parametric Mann Whitney U-test.

Multivariate analyses

Detrended Correspondence Analysis (DCA) (Gauch 1982) examined the degree of similarity between the treatment and control plots and between the different functional groups. The data were detrended by segments (unimodal option for detrending). DCA was done using the program CANOCO for Windows (Ter Braak and Smilauer 1998).

Results

Soil and vegetation properties

Comparison of within site treatments against controls (Table 2) revealed significantly ($P \leq 0.05$) smaller plant densities

Table 1: Historical details for 10 experimental plots (7 treatments and 3 controls) distributed over three study sites in the Cape of Good Hope Nature Reserve section of the Table Mountain National Park

Sites	Klaasjagersberg				Meadows		Platboom			
Dominant aliens	*A. saligna* (*A. cyclops*, *A. longifolia*, *Eucalyptus lehmannii*, *Pinus pinaster* present prior to 1963)				*A. cyclops*		*A. cyclops*			
Plots	K1a	K1b	K2	K3: Control	M5	M4: Control	P6a	P6b	P7	P8: Control
1963	Fire	Fire	Fire	Fire	–	–	–	–	–	–
1986	Fire	Fire	Fire	Fire	–	–	–	–	–	–
1986 (Feb–Mar)	Bulldozing	Bulldozing	–	–	–	–	–	–	–	–
1986 (Oct)	Aerial-spraying	Aerial-spraying	Aerial-spraying	–	–	–	–	–	–	–
1988	Foliar-spraying	Foliar-spraying	Foliar-spraying							
1990	Weeding + herbicide	Weeding + herbicide	–	–	–	–	–	–	–	–
1991 (Mar)	–	–	–	–	–	–	Fire	Fire	Fire	Fire
1991	Weeding	Weeding	Weeding	–	Weeding	Weeding				
1991	Foliar-spraying	Foliar-spraying	Weeding + herbicide	–	–	–	–	–	–	–
1992 (Apr)	–	–	–	–	Fire	Fire	–	–	–	–
1992 (Sep)	–	–	–	–	Burnt heaps	–	–	–	–	–
1993 (Feb)	–	–	–	–	–	–	Boom-spraying	Boom-spraying	Foliar-spraying	–
1993	Weeding	Weeding	Weeding	–	–	–	–	–	–	Weeding
1993	Weeding + herbicide	Weeding + herbicide	Weeding + herbicide	–	–	–	–	–	–	Weeding + herbicide
1993 (Sep)	–	–	–	–	Foliar-spraying	–	–	–	–	–
1994	–	–	–	–	–	–	–	–	–	Weeding
1995	Weeding + herbicide	Weeding + herbicide	Weeding + herbicide	–	–	–	Foliar-spraying	Foliar-spraying	–	–
1995	–	–	Weeding	–	–	–	–	–	–	–
1996	–	–	–	–	–	–	Weeding	Weeding	Weeding	Weeding
1997	Weeding	Weeding	Weeding	Weeding	Weeding	Weeding	–	–	–	–

Table 2: Means ± standard errors for measured soil and vegetation properties in differently treated plots and controls, and U-statistics and F-ratios for within and between site treatment comparisons against controls. Significantly different at * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001

Site	Plot	Treatment	Soils			Vegetation					
			Bare soil %	pH	Depth cm	Plant density	Canopy cover %	Species 50m^{-2}	Species 1m^{-2}	Diversity index (H)	Evenness index (J)
Klaasjagersberg											
	K1a	Burnt, bulldozed and aerial-sprayed	11.0 ± 4.3	4.7 ± 0.4	57.4 ± 10.9	120 ± 30.8	89.0 ± 4.3	10.4 ± 1.4	3.2 ± 0.7	0.6 ± 0.0	0.6 ± 0.0
	K1b	Burnt, bulldozed and aerial-sprayed	5.4 ± 2.8	4.6 ± 0.6	52.9 ± 11.5	234 ± 34.5	94.6 ± 2.8	13.2 ± 1.5	3.4 ± 0.4	0.8 ± 0.0	0.7± 0.0
	K2	Burnt and aerial-sprayed	13 ± 4.4	4.1 ± 0.2	78.1 ± 4.3	209 ± 26.4	87.0 ± 4.4	15.8 ± 1.4	3.7 ± 1.2	0.8 ± 0.1	0.7 ± 0.0
	K3	Control	9.8 ± 3.5	4.2 ± 0.2	74.8 ± 11.4	131 ± 27.6	90.2 ± 3.5	15.0 ± 1.8	4.4 ± 0.6	0.9 ± 0.1	0.7 ± 0.1
Meadows											
	M5	Burnt and foliar-sprayed	27.4 ± 17.6	7.5 ± 0.1	91.6 ± 8.2	144 ± 33.8	72.6 ± 17.6	9.0 ± 2.5	2.6 ± 0.8	0.4 ± 0.1	0.4 ± 0.1
	M4	Control	7.8 ± 1.9	7.3 ± 0.1	79.6 ± 5.3	247 ± 50.9	92.2 ± 1.9	23.2 ± 2.3	8.2 ± 1.2	1.1 ± 0.1	0.8 ± 0.0
Platboom											
	P6a	Burnt and boom-sprayed	22.4 ± 9.5	6.8 ± 0.4	99.4 ± 1.6	133 ± 36.1	77.6 ± 9.5	8.0 ± 0.8	3.4 ± 0.4	0.5 ± 0.1	0.6 ± 0.1
	P6b	Burnt and boom-sprayed	22 ± 9.9	5.3 ± 0.4	101.0 ± 0.0	134 ± 28.4	78.0 ± 9.8	9.6 ± 1.9	2.8 ± 0.5	0.5 ± 0.1	0.5 ± 0.1
	P7	Burnt and foliar-sprayed	20.6 ± 7.6	4.6 ± 0.2	79.2 ± 9.5	130 ± 34.1	79.4 ± 7.6	13.0 ± 1.8	4.8 ± 0.7	0.8 ± 0.0	0.8 ± 0.0
	P8	Control	14.6 ± 2.6	4.7 ± 0.1	94.6 ± 6.0	203 ± 31.4	85.4 ± 2.6	23.6 ± 5.3	8.0 ± 1.4	1.04 ± 0.1	0.8 ± 0.0
Statistical Analyses			U-statistics			F-ratios					
All treatments and Controls (df = 9)						1.5	0.8	5.8***	4.7***	7.6***	2.5*
Within site treatment vs Controls (df = 1)											
Klaasjagersberg		(K1a and K1b) vs K3	10	10	6	0.6	0.1	1.6	1.8	2.8	0.7
		K2 vs K3	10	9.5	11	1.4	0.6	1.6	0.3	0.6	0.0
Meadows		M5 vs M4	11	10*	6	4.0*	2.1	22.2***	22.1***	35.4***	11.7***
Platboom		(P6a and P6b) vs P8	11	4*	6.5	2.2	0.1	23.6***	15.1***	26.5***	6.0*
		P7 vs P8	11.5	8	4.0	2.1	0.2	5.7*	3.1	3.3	0.1
Between site control comparisons (df = 1)											
Klaasjagersberg vs Meadows (K3 vs M4)			–	–	–	3.0	0.0	3.8	4.8*	3.4	0.3
Platboom vs Meadows (P8 vs M4)			–	–	–	0.2	0.5	0.1	0.1	0.1	0.1
Klaasjagersberg vs Platboom (K3 vs P8)			–	–	–	3.0	0.1	4.5*	6.1*	3.7	0.3
Within site treatment comparisons (df = 1)											
Klaasjagersberg (K1a and K1b) vs K2			–	–	–	0.1	0.7	0.1	0.2	0.1	0.1
Platboom (P6a and P6b) vs P7			–	–	–	0.1	0.1	4.4*	3.5	9.2**	5.0*

and significantly ($P \leq 0.05$) more alkaline soils in the burnt and foliar-sprayed plots than control plots at the Meadows site. In the burnt and foliar-sprayed plots at this site and in the burnt and boom-sprayed plots at the Platboom site, species richness at both $1m^2$ and $50m^2$ scales, and species diversity and evenness were all significantly ($P \leq 0.05$) lower than in corresponding control plots. Also, soils were significantly ($P \leq 0.05$) more alkaline in the burnt and boom-sprayed plots than control plots at the Platboom site. However, only species richness at the $50m^2$ scale was significantly ($P \leq 0.05$) lower in the burnt and foliar-sprayed plot than in the control plot at the Platboom site.

Between site comparison of control plots (Table 2) showed significantly ($P \leq 0.05$) lower species richness at the $1m^2$ scale at the Klaasjagersberg site than the Meadows and Platboom sites, and also significantly ($P \leq 0.05$) lower species richness at the $50m^2$ scale at the Klaasjagersberg site than the Platboom site.

Within site treatment comparisons (Table 2) indicated significantly ($P \leq 0.05$) lower species richness at the $50m^2$ scale, and significantly ($P \leq 0.05$) lower species diversity and evenness in the burnt and boom-sprayed plots than in the burnt and foliar-sprayed plot at the Platboom site.

Dispersal guilds and regenerative modes

Comparison of within site treatments against controls (Table 3) revealed a significantly ($P \leq 0.05$) smaller proportion (% cover) of species with wind- and bird-dispersed seeds, as well as a significantly ($P \leq 0.05$) smaller proportion of species with both long-lived and short-lived seeds in the burnt and foliar-sprayed plot than in the control plot at the Meadows site. At the Platboom site, there was a significantly ($P \leq 0.05$) greater proportion of sprouters and species with short-live seeds, and *vice versa* in species with long-lived seeds, in the burnt and boom-sprayed plots than in the control plot. Also, a significantly ($P \leq 0.05$) smaller proportion of species with long-lived seeds were observed in the burnt and foliar-sprayed plot than in the control plot at this site.

Between site comparison of control plots (Table 3) showed significantly ($P \leq 0.05$) smaller proportions of species with wind- and bird-dispersed seeds as well as short-lived seeds at the Klaasjagersberg site than the Meadows site, the Klaasjagersberg site also containing a significantly ($P \leq 0.01$) smaller proportion of species with ant-dispersed seeds than the Platboom site. Also, a significantly greater proportion of species with bird-dispersed and short-lived seeds occurred at the Meadows site than the Platboom site.

Within site treatment comparisons (Table 3) indicated a significantly ($P \leq 0.05$) higher proportion of sprouters and a significantly ($P \leq 0.05$) smaller proportion of species with wind-dispersed and long-lived seeds in the burnt and boom-sprayed plots than in the burnt and foliar-sprayed plot at the Platboom site.

Life form categories

Comparison of within site treatments against controls (Table 4) revealed significantly ($P \leq 0.001$) smaller proportions (% cover) of low and tall shrubs, but a significantly ($P \leq 0.05$) greater proportion of graminoids in the burnt and foliar-sprayed plot than in the control plot at the Meadows site. Similarly, at the Platboom site there was a significantly ($P \leq 0.01$) smaller proportion of small and mid-sized shrubs as well as a significantly ($P \leq 0.05$) greater proportion of graminoids in the burnt and boom-sprayed plots than in the control plot. However, only low shrub forms had a significantly ($P \leq 0.05$) smaller cover in the burnt and foliar-sprayed plot than in the control plot at this site.

Between-site comparisons of control plots (Table 4) showed a significantly ($P \leq 0.01$) smaller proportion of mid-sized shrubs but a significantly ($P \leq 0.01$) higher proportion of large shrubs at the Klaasjagersberg site than the Meadows site. In contrast, the Platboom site contained a significantly ($P \leq 0.01$) greater proportion of mid-sized shrubs, but a significantly ($P \leq 0.05$) smaller proportion of tall shrubs than the Meadows site.

Within site treatment comparisons (Table 4) indicated significantly ($P \leq 0.01$) smaller proportions of low and mid-sized shrubs, but significantly ($P \leq 0.01$) greater proportions of graminoids and forbs (including geophytes) in the burnt and boom-sprayed plots than in the burnt and foliar-sprayed plots at the Platboom site.

Detrended correspondence analysis

The DCA, which explained 58% of the total variance in the data showed a distinct clustering of all control plots and treated plots. The exception was the 'foliar-sprayed' plot at the Platboom site, which was positioned closer to the control plots than treatment plots (Figure 2a). The ordination of different functional groups (Figure 2b) indicated that resprouters and graminoids were more closely associated with the treatment plots than the control plots. In contrast, low, medium-sized and tall shrubs had a higher representation in the control plots and in the 'foliar-sprayed' plot at the Platboom site. Noteworthy, was a close association of several 'boom-sprayed' plots with high covers of short-lived seeders (e.g. *Vellereophyton dealbatum* and *Plecostachys serpyllifolia*).

Discussion

Effects of alien control methods on diversity and abundance

In all cases discussed below, the impacts of alien control methods represent an integration of the earlier impacts of invasion by dense acacia stands and fire at a particular site, together with the subsequent impact of post-fire alien control treatment.

Plant species richness at both the $1m^2$ and $50m^2$ scales were significantly lower for most of the alien-cleared areas, except for the 'bulldozed and aerial-sprayed' and the 'aerial-sprayed' treatment sites. Although the richness in these two areas were not significantly impacted, two widespread and weedy grasses (*Stenotaphrum secundatum* and *Cynodon dactylon*) that are indicative of disturbance (Bromilow 1995), were dominant. The impact of the bulldozing may also have been kept to a minimum since the blade was kept 1.5m above the ground. Holmes and Cowling (1997a, 1997b) also observed decreases in species richness, diversity and

Table 3: Average percentage covers ± standard errors of different dispersal guilds and regenerative modes in differently treated plots and controls, and F-ratios for within and between site treatment comparisons against controls. Significantly different at * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001

Site	Plot	Treatment	Dispersal guild				Regenerative mode		
			Passive	Wind	Ant	Bird	Sprouter	Long-lived seeder	Short-lived seeder
Klaasjagersberg									
	K1a	Burnt, bulldozed and aerial-sprayed	71.5 ± 16.0	32.9 ± 15.1	0.1 ± 0.1	0.0 ± 0.0	48.9 ± 17.6	41.5 ± 17.0	2.7 ± 1.3
	K1b	Burnt, bulldozed and aerial-sprayed	87.1 ± 5.7	17. 8± 4.9	0.0 ± 0.0	0.0 ± 0.0	47.2 ± 22.2	28.9 ± 10.0	34.1± 10.7
	K2	Burnt and aerial-sprayed	65.3 ± 10.8	22.4 ± 10.7	0.2 ± 0.2	0.0 ± 0.0	41.2 ± 12.2	42.6 ± 12.2	5.4 ± 1.7
	K3	Control	60.2 ± 7.6	30.1 ± 6.3	5.2 ± 5.2	0.0 ± 0.0	23.4 ± 6.1	68.4 ± 11.1	3.6 ± 1.8
Meadows									
	M5	Burnt and foliar-sprayed	68.5 ± 18.1	2.9 ± 1.7	2.4 ± 1.5	0.0 ± 0.0	67.6 ± 17.1	4.1 ± 2.3	4.1 ± 1.7
	M4	Control	36.7 ± 8.3	57.8 ± 8.1	7.5 ± 2.1	1.1 ± 1.0	30.7 ± 5.4	56.6 ± 8.2	15.7 ± 4.6
Platboom									
	P6a	Burnt and boom-sprayed	39.9 ± 21.3	17.3 ± 3.3	28.7 ± 12.3	0.0 ± 0.0	64.1 ± 11.6	3.9 ± 1.7	17.9 ± 2.8
	P6b	Burnt and boom-sprayed	62.3 ± 17.2	12.5 ± 5.2	13.2 ± 7.3	0.0 ± 0.0	60.1 ± 16.5	27.2 ± 11.1	2.6 ± 1.4
	P7	Burnt and foliar-sprayed	48.4 ± 7.8	36.1 ± 7.8	3.6 ± 1.1	0.0 ± 0.0	20.4 ± 4.0	63.6 ± 8.5	4.1 ± 2.6
	P8	Control	60.9 ± 11.7	31.6 ± 5.4	22.3 ± 6.9	0.1 ± 0.1	26.6 ± 11.1	87.7 ± 6.7	0.9 ± 0.6
Statistical Analyses			F-ratios				F-ratios		
All treatments and Controls (df = 9)			1.2	4.3***	14.2**	2.9*	1.4	9.0***	6.86***
Within site treatment vs Controls (df = 1)									
Klaasjagersberg		(K1a and K1b) vs K3	1.6	0.1	1.0	0.0	2.1	7.3	6.1*
		K2 vs K3	0.2	0.2	0.02	0.0	0.1	0.1	1.1
Meadows		M5 vs M4	1.9	30.0***	1.32	14.7***	2.3	16.8***	5.4*
Platboom		(P6a and P6b) vs P8	0.3	3.5	0.6	0.2	4.5*	42.8***	7.2*
		P7 vs P8	0.5	0.1	6.0*	0.1	0.1	4.7*	0.57
Between site control comparisons (df = 1)									
Klaasjagersberg vs Meadows (K3 vs M4)			1.0	4.7*	2.0	14.7***	0.1	0.7	6.1*
Platboom vs Meadows (P8 vs M4)			0.2	1.2	2.3	6.1*	0.1	2.5	7.6**
Klaasjagersberg vs Platboom (K3 vs P8)			0.1	0.02	9.0**	0.1	0.01	3.2	1.2
Within site treatment comparisons (df = 1)									
Klaasjagersberg (K1a and K1b) vs K2			1.0	0.1	0.1	0.0	0.3	0.5	3.2
Platboom (P6a and P6b) vs P7			0.1	5.1*	4.0	0.0	5.5*	16.3***	3.3

Table 4: Average percentage covers ± standard errors of five life forms in differently treated plots and controls, and F-ratios for within and between site treatment comparisons against controls. Significantly different at * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001

Site	Plot	Treatment	Low shrub	Mid shrub	Tall shrub	Graminoid	Forb (including geophytes)
Klaasjagersberg							
	K1a	Burnt, bulldozed and aerial-sprayed	5.1 ± 2.9	30.4 ± 14.4	3.5 ± 2.7	49.5 ± 18.0	4.5 ± 2.5
	K1b	Burnt, bulldozed and aerial-sprayed	26.5 ± 15.0	9.1 ± 5.8	1.8 ± 1.3	63.4 ± 16.4	6.3 ± 6.0
	K2	Burnt and aerial-sprayed	15.0 ± 6.4	19.1 ± 11.1	7.4 ± 2.3	45.3 ± 12.2	2.4 ± 0.6
	K3	Control	54.8 ± 9.1	16.7 ± 4.0	11.2 ± 8.6	12.5 ± 3.4	0.2 ± 0.2
Meadows							
	M5	Burnt and foliar-sprayed	8. 2 ± 3.4	0.1 ± 0.1	0.7 ± 0.4	66.4 ± 16.7	0.5 ± 0.4
	M4	Control	49.8 ± 5.6	0.0 ± 0.0	31.4 ± 10.1	16.3 ± 5.3	5.4 ± 2.9
Platboom							
	P6a	Burnt and boom-sprayed	5.5 ± 3.7	0.0 ± 0.0	2.4 ± 1.6	64.1 ± 11.6	13.9 ± 4.4
	P6b	Burnt and boom-sprayed	14.6 ± 9.4	9.2 ± 4.8	16.4 ± 6.1	57.5 ± 17.6	2.2 ± 2.0
	P7	Burnt and foliar-sprayed	33.2 ± 10.8	29.6 ± 6.2	9.6 ± 5.3	15.5 ± 3.6	0.1 ± 0.1
	P8	Control	67.3 ± 7.2	26.6 ± 6.6	3.0 ± 2.3	19.3 ± 5.5	1.1 ± 0.5
Statistical Analyses					F-ratios		
All treatments and Controls (df = 9)			7.8***	5.2***	4.1***	2.9*	2.7*
Within site treatment vs Controls (df = 1)							
Klaasjagersberg		(K1a and K1b) vs K3	16.4	0.1	1.7	8.2	3.0
		K2 vs K3	1.2	0.1	1.5	0	0.3
Meadows		M5 vs M4	12.9***	0.0	21.1***	5.7*	2.6
Platboom		(P6a and P6b) vs P8	32.1***	11.6**	1.45	6.9*	3.6
		P7 vs P8	6.5*	0.1	1.7	0.04	0.7
Between site control comparisons (df = 1)							
Klaasjagersberg vs Meadows (K3 vs M4)			0.2	8.5**	9.1**	0.1	3.4
Platboom vs Meadows (P8 vs M4)			0.1	12.2**	6.3*	0.1	1.2
Klaasjagersberg vs Platboom (K3 vs P8)			1.0	1.0	0.9	0.2	0.3
Within site treatment comparisons (df = 1)							
Klaasjagersberg (K1a and K1b) vs K2			0.1	0.0	2.5	0.1	0.0
Platboom (P6a and P6b) vs P7			7.4**	13.85***	0.1	8.1**	8.4**

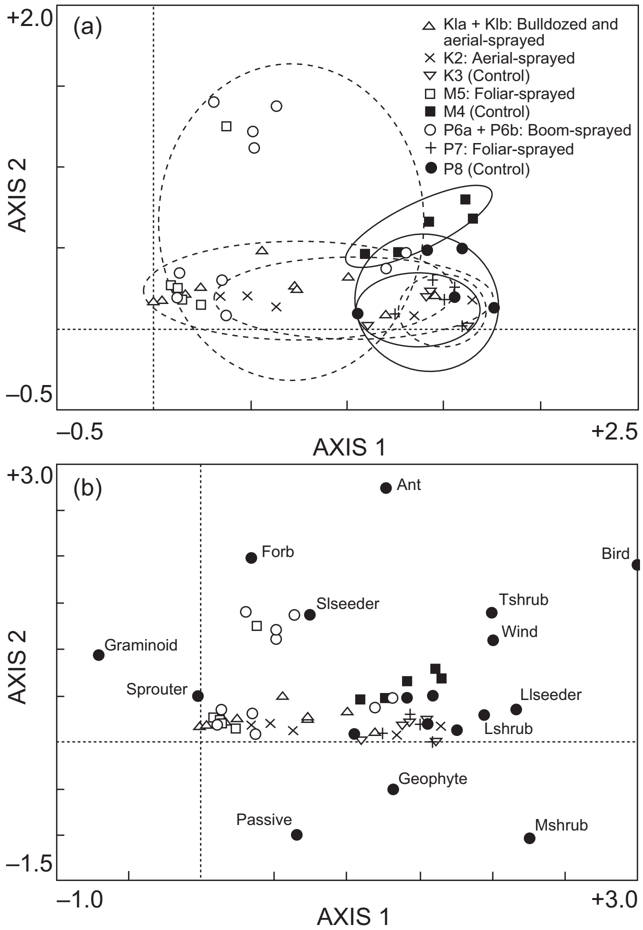

Figure 2: Detrended correspondence analysis of (a) the various guilds into which vegetation was classified with symbols encircled with solid lines representing the controls and those encircled by stippled lines represent the treatments, (b) plant percentage covers of the thirteen functional groups, namely (Lshrub = low shrub, Mshrub = medium shrub, Tshrub = tall shrub, Slseeder = short-lived seeder and Llseeder = long-lived seeder)

abundance in previously invaded sites and attributed this to reduced seed input under alien trees and the gradual attrition over time of the soil-stored seed banks.

Results of this study indicate that herbicide application impacts on fynbos communities to varying degrees. The most detrimental impacts of alien clearing on fynbos recovery occurred at the Meadows site. High fuel loads, due to the accumulation of extensive brush piles from past clearing operations (Wood 1993) as well as stack burns, probably led to an unnaturally severe fire with some visual evidence of soil erosion and poor post-fire fynbos recruitment (Richardson and Van Wilgen 1986, Holmes *et al*. 2000). Recruitment may have been further impacted by the follow-up foliar-spraying.

The foliar-spraying treatment at Platboom caused a significant reduction in species richness at the sub-plot scale (50m^2) and boom spraying of alien vegetation was also found to have a negative effect on the recovery of fynbos vegetation, as it significantly reduced the species richness at both quadrat and plot scales. Boom-spraying (with the boom approximately 1m above ground) involved very direct contact of herbicide with both alien and indigenous vegetation as the vehicle traversed the 2-year-old patch of alien plants. A report by ranger Alex Wood (February 1993) indicated that boom-spraying was hampered to a certain extent by strong south-easterly winds. There would thus have been some drift of the herbicide onto indigenous vegetation, probably resulting in higher indigenous plant mortality and creating a plant community that was very unevenly distributed. Ellis *et al*. (unpublished) also concluded that wind direction and strength were important factors contributing to the mortality of indigenous species following spraying of alien *Acacia cyclops*.

By contrast, the aerial-spraying treatment had a similar species richness to the control community. The taller (eight-month old) *Acacia* canopies probably intercepted the blanket application of herbicide (Triclopyr), thus lowering mortality of indigenous plants in the understorey. A small-scale study conducted within the Cape of Good Hope Nature Reserve, looking at the effect of foliar-spraying on fynbos, showed proteoids, ericoids and, to a lesser degree graminoids, to be sensitive to the chemicals (Triclopyr) used in control operations (Ellis *et al*. unpublished).

The exceptionally low richness in the Klaasjagersberg region compared to the other controls may be due to historical factors unrelated to alien plant management (Opie 1967, Taylor 1969, Hallinan 1992), since other studies conducted by Van Wilgen (1981) and Holmes and Cowling (1997a) showed higher richness values for similarly-aged fynbos vegetation.

Representation of plant functional types

The range of dispersal syndromes, regenerative modes and growth forms, were well represented in the controls and the 'foliar-spraying' treatment at Platboom compared to the other treatment sites. The implication is that most of the clearance methods may have impacted the representation of functional types in the treatment areas, and exacerbated the impact caused by the alien invasion itself. Most species recorded in this study utilise both passive and wind-dispersal more than ant- and bird-dispersal. Plant species using wind- and passive-dispersal mechanisms generally produce small seeds that are distributed closer to the soil surface. In the 'foliar-sprayed' treatment site at the Meadows, failure of the various categories of plants (such as the low shrubs, tall shrubs and the long-lived seeders) to re-establish may have been as a consequence of a higher intensity fire that killed off the small-seeded guild. Holmes *et al*. (2000) found that following a 'fell and burn' treatment through *Hakea*, which resulted in a high intensity fire, guild structure was severely affected. Only myrmecochores persisted relatively well, since seeds of these species are buried by ants.

'Boom-spraying' and 'foliar-spraying' caused a significant reduction in the long-lived obligate reseeding species (mainly overstorey Proteaceae). This guild forms a dominant component of uninvaded fynbos, but does not persist long in dense acacia (Holmes and Cowling 1997b). The overstorey is thought to maintain understorey diversity in the long term

(Vlok and Yeaton 1999). Loss of this guild may thus threaten diversity and ecosystem functioning.

In most treatments, there was a decrease in the low shrub and an increase in the graminoid (predominantly grass) component of the vegetation. This may be attributed to the fact that Triclopyr targets only dicotyledonous plants. Growth-form structure changed least following 'aerial-spraying' and 'foliar-spraying' at Platboom. In the latter case, the growth form structure remained constant, despite changes in species richness.

Implications for management

Recent research by Holmes and Cowling (1997a) into the restoration potential of mountain fynbos has shown that this vegetation type is relatively resilient to disturbance such as alien plant invasion. Although 70% of the flora disappeared from the standing vegetation following two fire cycles in areas invaded by alien *Acacia saligna*, representatives of all the major growth forms survived in the seed bank as soil-stored propagules. Thus, following the clearance of dense alien stands and fire, indigenous vegetation was stimulated to re-establish, primarily from the soil seed bank (Holmes and Marais 2000).

Species re-introductions may be needed where guilds have been eliminated or are under-represented, to improve the long-term resilience of the restored community (Holmes and Richardson 1999). In treatments such as the 'bulldozed and aerial-sprayed' and the 'boom-sprayed' treatment, as well as the 'foliar-sprayed' treatment at the Meadows, where groups such as long-lived seeders, tall shrubs, medium shrubs and low shrubs have been significantly reduced, re-introduction of those groups would accelerate recovery.

Since the majority of obligate reseeding species have soil-stored seeds it may be necessary to augment recruitment from the seed bank by sowing seed harvested from another site in the area, first giving seeds a smoke treatment to stimulate germination (Brown 1993). Species such as serotinous Proteaceae that store seeds in the canopy and which have been eliminated by invasion may be re-introduced if local seed sources are far away (>1km) and natural recolonisation would be slow. Such introductions into the ecosystem would accelerate recovery and lead to a greater probability of a structurally diverse and more functional ecosystem re-establishing. It is important to realise however that dormant soil seed banks are cued to germinate after a fire. Thus, re-introduction by seed will only be successful after fire or on bare ground since seed germination cues are tied to the post-fire environment. Cues such as a direct heat pulse (Cocks and Stock 1997), smoke from a fire (Brown 1993) and an increase in diurnal temperature fluctuation due to vegetation removal (Pierce and Moll 1994) all play a role in stimulating germination in the post-fire environment.

In the bulldozed area, sowing could be conducted after the treatment itself, but in the case of 'boom-spraying', it may be necessary to wait for another fire-cycle, after applying this treatment, to meet the ideal 'post-fire' fynbos recruitment environment.

At the Meadows site, high fuel loads coupled with possible soil erosion may have exacerbated the effect of post-fire 'foliar-spraying'. The impact of this treatment would have been lower following a burn under cooler weather conditions or following removal of fuel following felling to reduce the intensity and severity of the fire. Also, surface erosion could be reduced using logs pegged across steeper slopes and sowing with fast growing fynbos pioneers to provide early plant cover to protect the soil (Holmes and Richardson 1999, Holmes *et al*. 2000). At this site where the soil seed bank has been lost, the restoration of a structurally representative community would require the sowing of a comprehensive seed mix containing the major groups such as graminoids, forbs, low shrubs, and overstorey shrubs.

The 'aerial-spraying' treatment and the 'foliar-spraying' at Platboom caused the least change to the vegetation. Thus, natural recovery is adequate and no seed additions are required. If the former treatment is to be used in future management plans, practitioners need to ensure that herbicidal applications (using crop-dusting aircraft) are delayed until the faster growing alien species have created a dense canopy above the regenerating indigenous species. This would reduce the possibility of herbicidal drift killing the fynbos understorey. When 'foliar-spraying' of alien plant species is conducted using handheld mistblowers, chemical drift plays a role in the mortality of indigenous vegetation. Thus, there is a need to explore alternative application methods. Currently, a new method of application in which the herbicide is wiped directly onto the foliage of the target plants is being tested. This method should minimise mortality of non-target species since there is no dripping or spray-drift.

'Boom-spraying' reduced the species richness and altered the structure of the vegetation. Triclopyr selectively kills dicotyledonous plants and this method of application is less selective than foliar-application.

Priorities for future research

Herbicidal application has been used for many years in the control of invasive alien plants. Foliar-spraying as well as blanket herbicidal applications have been conducted in parts of the CFR, but very little research has been done to determine the side effects of this treatment. Trials pertaining to the impacts of different methods of herbicidal application, including timing and season of application on alien vegetation after a fire would be particularly useful. This will enable managers to improve the efficiency of their follow-up methods and potentially aid the natural recovery of the ecosystem.

The bulldozing treatment should be re-assessed in a site where farming is not a contributing factor. Managers need to know beforehand whether this is a viable method for eradicating burnt alien vegetation to enable adequate recovery of a site.

In conclusion, this study found that the impacts of herbicide application methods vary considerably among sites and depend partly on factors such as earlier land-use impacts and the direct and indirect impacts of the alien acacias at particular sites. Poorest recovery was recorded at a site where the impacts of a severe fire through acacias were implicated. Best recovery was recorded at a site where herbicide application was timed to minimise contact with indigenous species.

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