

Spontaneous succession of riparian fynbos: Is unassisted recovery a viable restoration strategy?

M.K. Reinecke^{a,*}, A.L. Pigot^{b,*}, J.M. King^c

^a *Ecologic Environmental Consulting cc, PO Box 16386, Vlaeberg, Cape Town, South Africa*

^b *Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom*

^c *Freshwater Research Unit, Zoology Department, University of Cape Town, Rondebosch 7707, Cape Town, South Africa*

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Abstract

The invasion of alien trees is a major threat to the freshwater resources and biodiversity of South Africa. The Working for Water (WfW) Program was initiated in 1995 in order to control the growth and spread of woody alien species in riparian zones, but the extent to which the indigenous vegetation naturally recovers following alien clearance remains poorly understood. In this study spontaneous succession of riparian vegetation following wild fires and alien clearing was monitored over a number of years at two sites on the Cape Peninsula: a pine plantation in an upland plateau and an *Acacia* spp.-invaded valley floodplain. After clearing, the vegetation at the pine site was successfully recovering along a trajectory towards Afromontane forest and as a result it is suggested that no active restoration is required. By contrast, our results show that areas cleared of *Acacia* spp. may be less resilient, with extensive regeneration of woody aliens and only a negligible recovery of indigenous trees. We propose that the absence of riparian trees may have been responsible for precipitating the transition to a community dominated by weedy nitrophilous grasses, and find evidence that this may be perpetuated through the continued removal of *Acacia* spp. It is hypothesized that this grass-dominated state may be resilient to natural restoration and thus represents an additional constraint to the recovery of riparian communities. Under such circumstances, we argue that active restoration would be required in order to re-instate the riparian community.

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1. Introduction

The restoration of degraded ecosystems is recognised as an essential component in stemming the global loss of biodiversity (Hobbs and Harris, 2001). As one of the primary drivers of species extinction (Vitousek et al., 1997) the control of invasive species is a central task of restoration ecologists (D'Antonio and Meyerson, 2002). In common with riparian ecosystems throughout the world, the riparian vegetation of the Western Cape of Southern Africa has been heavily invaded by exotic species (Richardson et al., 1992). The most damaging invaders

in this region are trees and woody shrubs in the genus *Acacia*. These species out-compete indigenous plants and disrupt ecosystem functioning by altering the fire regime, patterns of sedimentation and erosion, the availability of water (Galatowitsch and Richardson, 2005; Richardson et al., 2007) and soil nutrient levels (Yelenik et al., 2004).

Following the recognition that alien trees threatened the supply of freshwater resources, large areas previously invaded have been cleared under the auspices of the Working for Water (WfW) Program (Van Wilgen et al., 1998). A number of clearance techniques are employed (see Blanchard and Holmes, 2008-this issue), with follow-up treatments often implemented to remove regenerating aliens. In order to save costs, however, no active intervention to assist the recovery of indigenous species is carried out. The extent to which the indigenous vegetation recovers and resists re-invasion by woody aliens, is critical for the long term success of the WfW Program (Holmes et al., 2005).

* Corresponding authors. M.K. Reinecke is to be contacted at Tel.: +27829258309.

E-mail addresses: karlreinecke@gmail.com (M.K. Reinecke), alexander.pigot@imperial.ac.uk (A.L. Pigot).

Riparian community composition and structure are determined by, and in turn influence, a variety of factors including; channel morphology, discharge, flood regime (Naiman et al., 2005) and the frequency and intensity of fires (Kruger, 1978; Sieben, 2003). In the Western Cape, it has been hypothesized that site moisture levels and vulnerability to fires are key abiotic determinants of riparian community structure. In addition, soil type (texture and pH), creates a feedback loop of community structure and composition on fire frequency by promoting certain growth forms of different flammability and resistance to fire. Western Cape riparian vegetation is dominated by broad-leaved woody species of scrub, predominantly perennial shrubs and small trees, but also includes characteristic fynbos elements such as species of Restionaceae and Ericaceae (Cowling and Holmes, 1992). The understorey comprises forbs and graminoids, with continual recruitment of perennials and woody species occurring within the sub-canopy. In steep kloofs sheltered from fire, large tree species may establish leading to succession towards Afromontane forest (Taylor, 1978).

Few studies have investigated the resilience of riparian communities in the Western Cape to the invasion and clearance of alien trees (but see Blanchard and Holmes, 2008-this issue; Vosse et al., 2008-this issue). There is evidence that the recovery of indigenous woody riparian species may be extremely limited, with extensive regeneration of woody aliens (Galatowitsch and Richardson, 2005). In this paper, we monitor the spontaneous succession of riparian vegetation following alien clearing in a single river catchment over a number of years. Although focussing on a single case study may trade generality for detail, analysis of vegetation change at a single locality through time may offer new insights into whether spontaneous succession of riparian communities in the Western Cape is a viable restoration strategy. For example, failure of woody riparian species to re-establish following clearance may be due to either a degenerate seed bank, a lack of propagule supply, or high levels of juvenile mortality associated with the clearing practices; each of which may require a different restoration strategy. The dynamics of spontaneous succession in the process of riparian vegetation recovery following alien removal thus warrants further investigation.

1.1. Study site

The Silvermine River catchment, located on the Cape Peninsula is contained within the boundaries of the Table Mountain National Park (Fig. 1). Extensive stretches of the river were invaded or planted with a number of alien species, including *Pinus pinaster* D. Don, *Acacia saligna* (Labill.) H.L. Wendl., *Acacia longifolia* (Andrews) Willd., *Populus X canescens* (Ait.) Sm. (pro sp.), *Lantana camara* L. and *Paraserianthes lophantha* (Willd.). In January 2000, wild fires burned large areas of the Cape Peninsula, incinerating the majority of the vegetation in the Silvermine River catchment and leaving only a few large trees standing. The remaining alien trees and regenerating aliens were cleared by WfW personnel over successive follow-up treatments. In line with WfW policies, no re-vegetation strategies were employed.

2. Methods

2.1. Data collection

Two sites were selected along the course of the Silvermine River. The first site was a *P. pinaster* (Cluster Pine) plantation in the mountain stream zone (hereafter Site 1), while the second was located in the foothill zone (hereafter Site 2) and supported dense stands of *A. longifolia* (Long-leaved Wattle) and *A. saligna* (Port Jackson willow) (Reinecke and King, 2003). Given that these two sites occur under different hydro-geomorphological settings (see Rowntree and Wadson, 1999), they represent alternative case studies and are not compared directly. Analysis of aerial photographs indicated that alien trees had formed closed canopies at these sites approximately 20 years prior to sampling.

At each site, two belt transects were used to survey the vegetation. These were positioned approximately 15 m apart, and ran perpendicular to the river channel, extending into the mountain fynbos on each side of the valley. This allowed the riparian community to be delimited statistically on the basis of species composition rather than by eye. The four belt-transects consisted of contiguous metre-square plots within which the aerial cover of each species was estimated, and the maximum height of each species measured: between 49 and 78 plots were sampled along each transect. A permanent beacon cemented at each end of the transects enabled the same plots to be accurately resurveyed during summer (January through March) of year one, two and four following the fire in January 2000. All vegetation data were entered into the vegetation database TURBOVEG V1.99 (Hennekens, 1996). Along each belt transect, the valley topography was surveyed using an electronic theodolite (Leica TC307 model) and a standard Leica prism and staff. The position of high water during the winter flood of July 2001 was recorded to aid in delineating the boundary of the riparian vegetation.

2.2. Statistical analysis

Non-parametric statistics were used to delimit the riparian community. Species-cover data were 4th root transformed to achieve a balance between the influences of common and rare species (Clarke and Warwick, 2001). For each belt transect, the Bray–Curtis similarity coefficient was used to convert the cover data to a matrix of similarity between plots (a method which does not take into account joint absences). Similarity was then compared between plots using Non-metric Multi-Dimensional Scaling (MDS) graphs and CLUSTER dendrograms implemented in PRIMER (Clarke and Warwick, 2001). Plots belonging to the riparian zone were identified as the contiguous plots that grouped together in both 2001 and 2002. These plots fell within the marked floodline on the surveyed cross-sections, validating delineation of the riparian community.

At each site, the plots of the two belt transects that were identified as riparian were combined. The number of indigenous and alien species and their mean richness within each plot were calculated, and measures of species diversity and equitability were also calculated for indigenous species. In order to identify

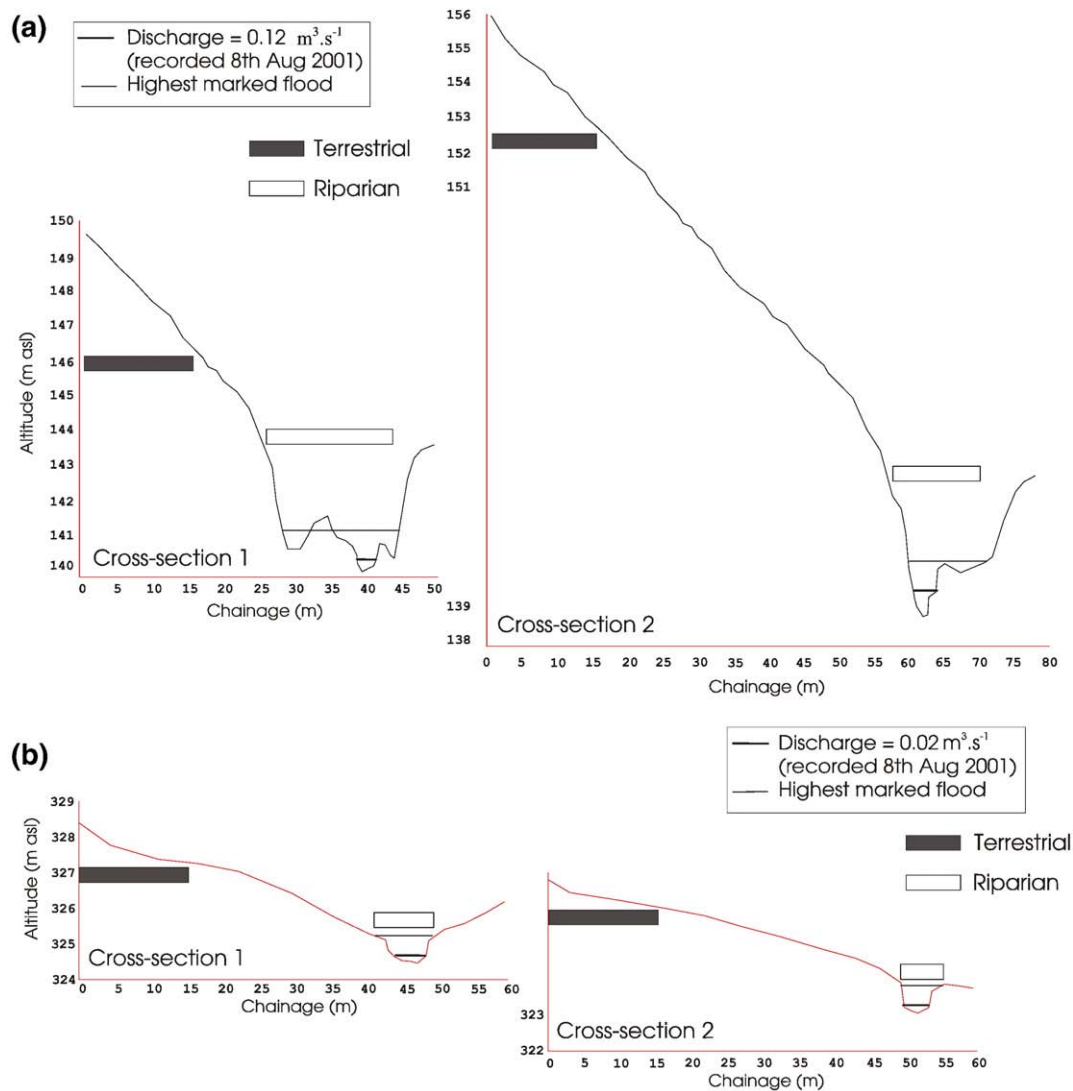


Fig. 1. Cross-sections depicting the channel shape surveyed at Sites 2 (a) and 1 (b). The location of summer low flow (discharge in cumecs), the position of the winter high flow flood line and the location of terrestrial and riparian sample plots are indicated. Riparian plots are located within the flood line in both cases.

the dominant species at each site, species-cover data were ranked by frequency of occurrence (100% = a species occurred in all plots at a site) and total cover (the average over all plots within a site).

Given that funds for clearing are limited, the extra costs required for any active intervention, in order to fast track recovery, must be justified if the goal of alien clearing programmes is succession towards naturally functioning riparian communities that can buffer against further invasion. Plant species attributes

and life history strategies are important in determining which riparian lateral zone a species may occupy and hence the structure and composition of different riparian communities (Holmes et al., 2005). Some preliminary work on community composition and structure was done by Reinecke et al. (2007) who hypothesized a trajectory of recovery for Riparian Scrub stands between one and ten years of age following alien clearing or fire. Their model described the frequency of growth forms at different life stages of

Table 1
The six growth forms used to classify species groups, with heights referring to the adult of the species

Growth form	Definition
1 Forb	A broad leafed herbaceous plant other than graminoids.
2 Graminoid	Plants in the family Juncaceae, Cyperaceae, Poaceae and Restionaceae.
3 Ericoid	Shrubs with ericaceous leaves.
4 Shrub	A low or medium sized woody perennial plant often with multiple stems (<1 m).
5 Small tree	A large woody perennial plant usually with multiple stems or with main trunk (2–10 m).
6 Tree	A tall woody plant with main trunk, branches and a distinct elevated crown (>10 m).

Growth form nomenclature follows Goldblatt and Manning (2000).

common Riparian Scrub species on Western Cape riverbanks, some of which tended to occur at predictable elevations.

They found that a description of the frequency of growth forms at different life stages was appropriate in order to characterise community structure and assess recovery. On this basis, each species was classified into one of the six growth forms (Table 1) according to Goldblatt and Manning (2000), and the number of species and the total plant cover belonging to each group was summed. Vegetation structure also provides an important measure of community recovery, given its key role in regulating the susceptibility to fire and its hypothesized role in attracting vertebrate dispersers (Richardson et al., 2007). To investigate changes in vegetation structure, the maximum height of each species occurring within each plot was measured and assigned to one of four vertical strata (m): <0.5, 0.5–2.0 m, 2.0–5.0 and >5.0 m (Galatowitsch and Richardson, 2005). The total plant cover occurring in each height class was calculated for each site. The tallest stratum with more than 25% of the total vegetation cover was assigned as the dominant height class, and the number of occupied strata and relative cover in each was used to calculate a simple measure of plant height diversity using the Shannon–Weiner diversity index. Although not all of the plants foliage may

fall within the assigned stratum, for the purposes of this paper, this limitation was accepted.

Invasion of woody alien species into the Silvermine catchment was so extensive that few, if any, areas were suitable to serve as appropriate reference sites against which recovery could be assessed. Prior to the fires (January 2000), mature Afromontane forest occurred along the river at Site 1, while at Site 2, the more open valley and susceptibility to fires suggest that Riparian Scrub would naturally predominate (Taylor, 1978). Acknowledging the difficulties in assigning appropriate restoration targets, the recovery of the riparian vegetation was assessed by comparing the species composition of each site at four years post-fire to a reference condition database for Riparian Scrub in mountain stream and foothill reaches of Western Cape rivers (Table 4; Reinecke et al., 2007).

At Site 2, there was a dramatic expansion in the cover of the perennial grass *Ehrharta setacea* between the 2001 and 2002 survey, coincident with the follow-up clearance programmes that removed regenerating *Acacia* spp. A *post-hoc* analysis of the change in percentage cover of *Acacia* spp. and *E. setacea* between 2001 and 2002 was performed, using ordinary least squares regression implemented in the R programming

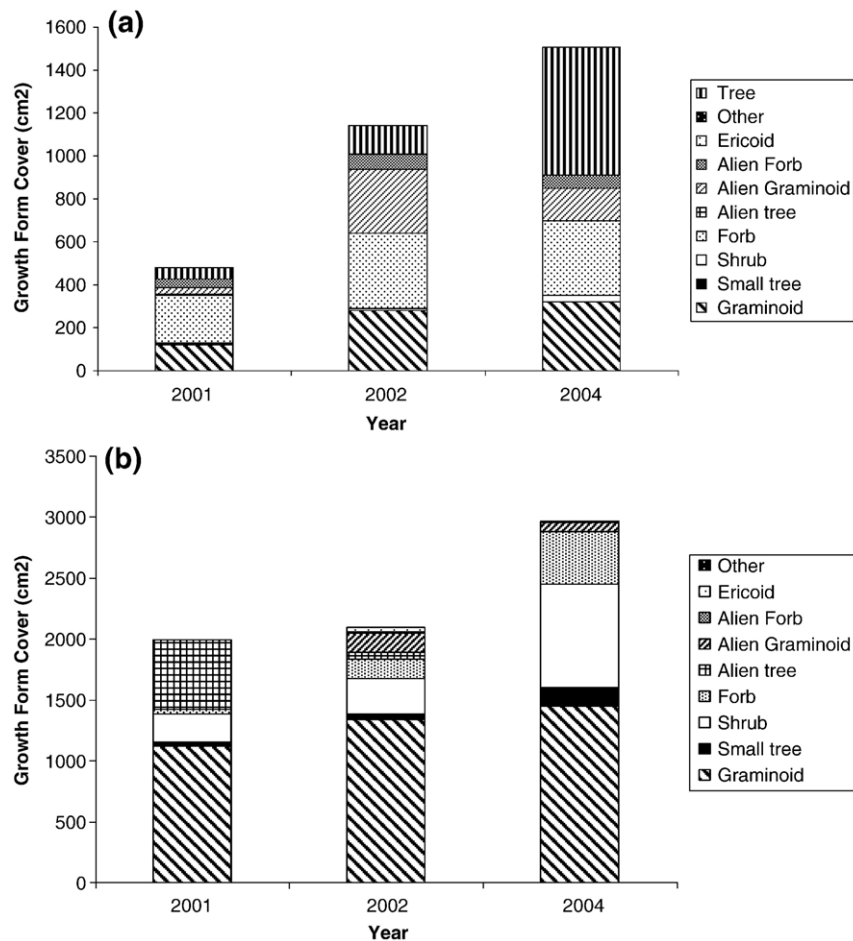


Fig. 2. The changes in the total growth form cover between 2001 and 2004 at (a) Site 1 and (b) Site 2. At Site 1, non-indigenous annual graminoids peaked and subsequently decline, while there were steady increases of indigenous trees, forbs and graminoids. In contrast, at Site 2, there was an immediate increase in perennial graminoids and alien trees in the immediate post-fire environment. There was a gradual increase in the cover of shrubs and forbs, while perennial graminoids remained dominant.

environment (R Development Core Team, 2004). In order to meet with the assumptions of constancy of variance and normality of errors, the percentage data was arc-sine transformed prior to analysis (Crawley, 2002).

3. Results

Using cluster analysis and MDS ordination, 18 plots at Site 1 and 32 plots at Site 2 were demarcated as belonging to the riparian communities (Fig. 2). Vegetation recovery was highly disparate between the two sites, with differences in the relative contributions of the various growth forms, the identity of the dominant species, and the resulting vegetation structure.

3.1. Cover and species richness of indigenous and non-indigenous species

3.1.1. Site 1

In the immediate post-fire year, 13 indigenous species were recorded in the riparian zone, with a mean richness per plot of $1.94 \pm 1.55/m^2$ (Table 2). Between 2001 and 2004, the total number of indigenous species remained approximately constant but there was a consistent increase in mean plant cover (Fig. 2a) and species richness per plot. Levels of diversity declined, reflecting the increased dominance of a few common species. The almost

constant total indigenous species richness over the 4-year study period masked a high level of turnover in species composition, with only 50–60% of species shared between successive years (Table 3). 7 alien species were present in the immediate post-fire year at low cover. The cover of aliens increased up to the 2002 survey but subsequently declined to low levels by 2004.

3.1.2. Site 2

There was a rapid increase in plant cover in the first year following the fire (Fig. 2b). Although predominantly driven by indigenous species, alien species also contributed substantially (Table 2). In the following year, total plant cover increased only marginally due to a decline in the cover of alien species balancing the increase in the cover of indigenous taxa. The cover of aliens continued to decline to 2004, while there was large increase in the cover of indigenous species. There was little change in species richness (measured at either the site or plot level), diversity and equitability over the study period.

3.2. Trends in growth form and species composition

3.2.1. Site 1

In the first year following fire, the recovering vegetation was dominated by indigenous forbs and graminoids (Fig. 2a). A number of ephemeral alien species including *Taraxacum*

Table 2
Descriptive biodiversity and vegetation statistics at both sites for each year

Year	Site 1 (plots=18)			Site 2 (plots=32)		
	2001	2002	2004	2001	2002	2004
<i>Species richness (n)</i>						
Total	20	21	18	29	31	28
Native	13	16	13	26	24	24
Alien	7	5	5	3	7	4
<i>Mean species richness (n)</i>						
Total	3 ± 2.11	3.5 ± 2.50	3.44 ± 1.92	5.03 ± 3.4	3.91 ± 2.57	3.69 ± 2.31
Native	1.94 ± 1.55	2.56 ± 1.76	2.72 ± 1.45	3.78 ± 3.15	3.03 ± 2.07	3.28 ± 2.16
Alien	1.06 ± 0.87	0.94 ± 1.26	0.72 ± 1.01	1.25 ± 0.72	0.88 ± 0.98	0.41 ± 0.76
<i>Mean vegetation cover (cm²)</i>						
Total	26.7 ± 34.3	63.4 ± 53.7	83.7 ± 44.3	62.3 ± 57.2	65.6 ± 39.3	92.6 ± 54.3
Native	22.6 ± 29.4	43 ± 36.3	71.7 ± 37.6	44.4 ± 45.2	58.6 ± 38.1	90.3 ± 55.9
Alien	4.1 ± 5.8	20.4 ± 35.4	12 ± 25.2	17.8 ± 24.6	6.9 ± 12.4	2.3 ± 6.1
<i>Shannon–Weiner</i>						
Species diversity (H)	2.497	2.59	2.28	2.29	2.48	2.37
Equitability (E)	0.833	0.85	0.79	0.680	0.72	0.71
<i>Simpson's Index</i>						
Species diversity (H)	9.52	11.49	7.67	7.02	5.78	6.35
Equitability (E)	0.48	0.55	0.43	0.24	0.19	0.23
<i>Plant height diversity (H)</i>						
Dominant height class (m)	0.97	0.96	1.35	0.95	0.71	0.84
	0.5–2	0.5–2	>5	0.5–2	0.5–2	0.5–2

At Site 1, the cover of indigenous vegetation and richness increased from 2001 to 2004. Species richness, diversity and equitability remained relatively constant and there was no increase in plant height diversity and dominant height class over the four years at Site 1. At Site 2, the removal of the regenerating *Acacias* between 2001 and 2002 changed the structural complexity from 0.95 to 0.71. Due to a lack of indigenous woody species the vegetation structure remained stunted (dominant height class 0.5–2 m) and lower plant height diversity over the four years.

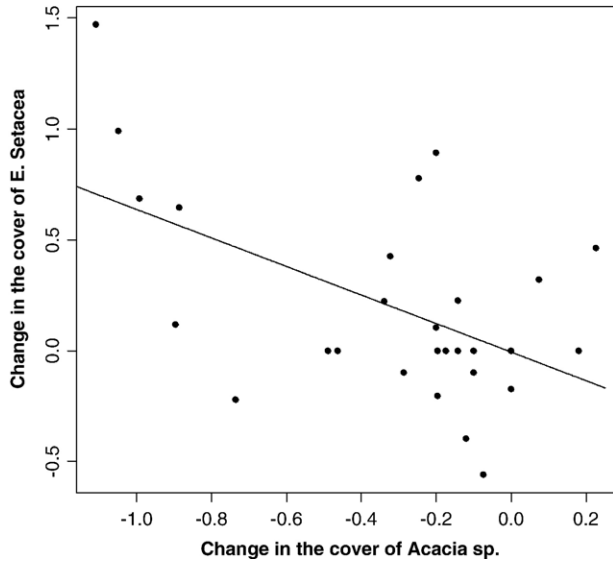


Fig. 3. Comparison of *Acacia* cover (arc-sine transformed) and corresponding growth in perennial grasses (notably *Ehrharta calycina*) between 2001 and 2002. As cover of *Acacia* was reduced, the cover of perennial grasses increased significantly, ($r^2=0.3$, slope= -0.64 , $p=0.001$).

officinale and *Briza maxima* were present throughout the site. Numerous indigenous tree seedlings successfully germinated from the seed bank including; *Cunonia capensis*, *Virgilia oroboides*, *Curtisia dentata* and *Psoralea pinnata*. By contrast, only a few *P. pinaster* seedlings were present and these were subsequently removed by follow-up clearing treatments.

In the following year, there was a large increase in the cover of large trees due primarily to the rapid growth of *V. oroboides* seedlings. Two indigenous tree species, a large and small tree respectively, *C. dentata* and *P. pinnata*, were present in 2001 but absent by the 2002 survey. By 2004, the community was characterised by a dense canopy of large *V. oroboides* and *C. capensis* trees, with an understorey of graminoids and resprouting forbs. Six of the most common species present are considered to be typically Afromontane (Table 4), while there was an obvious lack of ericoids, restioids, shrubs and small trees (Fig. 2a). There was a high level of plant structural complexity, and a dominant height class of >5 m (Table 2).

3.2.2. Site 2

The rapid regeneration in the immediate post-fire year was driven by perennial graminoids and alien *Acacia* spp. which accounted for more than 50% and 25% of the vegetation cover

Table 3
Sørensen's similarity index reflecting turnover in species composition over four years

Years compared	Site 1	Site 2
2001 × 2002	0.63	0.67
2002 × 2004	0.51	0.61
2004 × 2002	0.53	0.56

There was a high level of turnover in species composition, with only 50–60% of species shared between successive years, though species richness remained fairly constant (Table 2).

Table 4

Species commonly found in Riparian Scrub and Afromontane Forest communities (Reinecke and King 2007)

Riparian Scrub	Site		Afromontane Forest	Site	
	1	2		1	2
<i>Brabejum stellatifolium</i> (ST)			<i>Asparagus scandens</i> (FO)		
<i>Brachylaena neriifolia</i> (ST)			<i>Blechnum capense</i> (FO)		
<i>Calopsis paniculata</i> (GR)			<i>Blechnum punctulatum</i> (FO)		+
<i>Cannamois virgata</i> (GR)			<i>Canthium ventosum</i> (TR)		
<i>Diospyros glabra</i> (SH)			<i>Cunonia capensis</i> (TR)		+
<i>Elegia capensis</i> (GR)			<i>Diospyros whyteana</i> (TR)		
<i>Erica caffra</i> (ST)			<i>Ehrharta erecta</i> (GR)		
<i>Freylinia lanceolata</i> (ST)			<i>Halleria lucida</i> (TR)		
<i>Halleria elliptica</i> (SH)			<i>Histiopteris incisa</i> (FO)		+
<i>Juncus lomatoophyllus</i> (GR)			<i>Ilex mitis</i> (TR)		
<i>Metrosideros angustifolia</i> (ST)			<i>Juncus effusus</i> (GR)		+
<i>Morella serrata</i> (ST)			<i>Kiggelaria africana</i> (TR)		+
<i>Prionium serratum</i> (SH)		+	<i>Podocarpus</i> sp. (TR)		
<i>Psoralea pinnata</i> (ST)		+	<i>Pteridium aquilinum</i> (FO)		+
<i>Pteridium aquilinum</i> (FO)		+	<i>Rapanea melanphloeos</i> (TR)		+
<i>Rhus angustifolia</i> (ST)			<i>Secamone alpinii</i> (FO)		
<i>Salix mucronata</i> (ST)			<i>Todea barbara</i> (FO)		+
<i>Todea barbara</i> (FO)		+	<i>Virgilia oroboides</i> (TR)		+

ST = Small tree, FO = forb, GR = graminoid, SH = shrub and TR = tree.

+ indicates the species was present at one of the sites.

respectively (Fig. 2b). *Acacia* spp. were ubiquitous throughout the site (*A. longifolia* alone was present in over 80% of plots) and formed a closed canopy that rapidly overshadowed the other species; some individuals growing to 2.5 m in height in a single year. In contrast, there was only a limited regeneration of a few small indigenous tree species scattered across the site (*Erica caffra* and *P. pinnata*) and no large tree species.

Follow-up clearances between the 2001 and 2002 surveys removed most of the regenerating *Acacia* spp. Coincident with this was a large increase in the cover of *E. setacea*, which by 2002 comprised approximately 40% of the total plant cover (total graminoid cover increased only marginally because of the death or decline of a number of other species). Plots with the greatest reduction in cover of *Acacia* spp. during this period exhibited significantly greater increases in cover of *E. setacea* ($r^2=0.3$, slope= -0.64 , $p=0.001$, Fig. 3).

During the study period, there was a gradual increase in the cover of shrubs and forbs, of which the most common species were; *Berzelia lanuginosa*, *Oftia africana*, *Pteridium aquilinum* and *Vellereophyton dealbatum*. The cover of indigenous small trees increased only marginally, while by 2004 large indigenous tree species remained completely absent from the site. Furthermore, the small tree guild was represented by only a single species, *P. pinnata* (Fig. 2a): this species has been categorized by previous authors as either a small tree, or as a shrub by Goldblatt and Manning (2000). The only other member of this guild, *E. caffra*, had perished. The increase in cover of the shrub and small indigenous tree guild was driven by the growth of those individuals that had initially regenerated, rather than continued recruitment.

Reflecting the lack of indigenous woody species, there was no increase in the dominant height class over the study period, remaining at 0.5–2 m. Plant height diversity declined between

2001 and 2004 due to the removal of regenerating *Acacia* spp. (Table 2). Reinecke et al. (2007) re-sampled the site in 2005 and found that, with the exception of *P. pinnata*, indigenous trees remained absent from the site. Perennial grasses on the other hand, such as *E. setacea*, maintained a high cover and frequency.

4. Discussion

4.1. Temporal patterns in post-clearance regeneration

Analysing the temporal patterns of community assembly, following the clearance of alien invasive trees, provided a number of insights into the dynamics of riparian communities with implications for their management and restoration. It was apparent that all species of indigenous trees (large and small) and shrubs, the dominant guilds in Riparian Scrub, that emerged from the seed bank did so within the first few years following clearing (also see Vosse et al., 2008-this issue). This suggests that despite the relatively long time frame of community development expected in such systems (Reinecke et al., 2007), it is possible to assess the likely trajectory of recovery and determine the need for active restoration shortly after the initial clearing operations. Indeed, within our 4-year study period, it was evident that the recovery of vegetation at the two study sites was proceeding along markedly different trajectories.

Where *P. pinaster* was cleared, the riparian vegetation recovered rapidly forming a community dominated by large indigenous trees with an understorey of graminoids and re-sprouting forbs. Although the community was relatively depauperate, lacking a number of species characteristic of Afromontane forest (Table 4), the high structural complexity of the vegetation, dense canopy cover, and stable substrates should provide optimal conditions for the immigration and establishment of these taxa (Galatowitsch and Richardson, 2005). As a result, we suggest that no active restoration will be required at this site.

The burning of the dense stands of *A. saligna* and *A. longifolia* was followed by germination of woody aliens *en masse* from the soil-stored seed banks. Few indigenous tree seedlings were present in the post-fire community, which was instead dominated by herbaceous species and, to a lesser extent, shrubs. This supports the previous findings of Galatowitsch and Richardson (2005) and suggests that the limited resilience of riparian trees to prolonged invasion and clearance operations is largely due to their absence from the soil-stored seed bank. Our results also show however that a high mortality of juvenile riparian small trees may contribute to their rarity following alien clearance (see below).

Although the accelerated increase in the cover of the small tree and shrub guild between 2002 and 2004 suggests that woody species are becoming a more prominent component of the community at Site 2, this was driven by the growth of the few individuals that had initially regenerated. Consequently, as their growth declines, we expect future increases in the cover of these guilds to be minimal. Given that the seeds of many riparian trees are dispersed by birds, the low structural complexity of the vegetation resulting from a lack of woody species may inhibit the potential for future recovery and render this site susceptible to chronic re-invasion of woody aliens.

Development of the vegetation at both sites was characterised by a high level of turnover in species composition. Although this was principally driven by ephemeral species, our study also identifies the enigmatic loss of a number of long-lived woody taxa (*C. dentata*, *P. pinnata* and *E. caffra*). The most likely explanation for the coincident mortality of these species is that they were removed during the follow-up clearance operations. Given the rarity of woody riparian taxa in the post-clearance community, the removal of only a few individuals may have a disproportionate impact on future vegetation recovery. Ensuring that WfW teams are adequately trained in the removal of alien species must be a priority as this will reduce the need for active re-vegetation, for which the costs may be prohibitive.

4.2. Secondary grass invasion and the prospects for future recovery

In addition to the absence of characteristic woody riparian species, the most notable feature of the vegetation at the site cleared of *Acacia* spp. was the exceptionally high cover of perennial graminoids, particularly *E. setacea*. Although this species is native to the fynbos biome, it does not comprise a dominant component in undisturbed riparian communities (Reinecke et al., 2007; Table 4). The trend for weedy perennial grasses to proliferate following the removal of *Acacia* spp. has been documented in terrestrial fynbos communities and has been attributed to the nutrient enriched soils resulting from nitrogen fixation by the *Acacia* spp. (Yelenik et al., 2004). A similar trend of nutrient poor shrub lands shifting to a grass-dominated state has been widely documented for European heathlands subjected to atmospheric nitrogen deposition (Bobbink et al., 1998).

In contrast to nutrient poor terrestrial fynbos, riparian zones are noted for their relatively fertile soils. Indeed this is thought to accelerate the growth of indigenous trees and the development towards forest (Manders et al., 1992). The higher availability of nutrients would also be expected to promote the growth of perennial grasses, and yet under natural conditions this guild typically forms only a minor component of the initial post-fire riparian community (Reinecke et al., 2007). Given this context, elevated levels of soil nitrogen resulting from *Acacia* spp. invasion would seem to provide an inadequate explanation for the abundance of weedy grasses documented in this study. Instead we suggest that following fires the regeneration of Riparian Scrub and the associated reduction in light availability act to suppress the growth of perennial grasses. Where disturbance has been intense however, and the recovery of Riparian Scrub is limited, higher light availability can lead to the rapid increase in the cover of grasses. The significant association between the expansion in the cover of *E. setacea* and the removal of regenerating *Acacia* spp. supports this.

Despite mean *Acacia* spp. cover in 2001 being 'only' 21%, the reduction in *Acacia* cover explained approximately 30% of the variance in the change in *E. setacea* cover. We suspect that had regeneration of the *Acacia* spp. been more advanced, the effects of their removal would have been much more

pronounced. This raises the possibility that follow-up clearing programmes may inadvertently perpetuate the dominance of weedy grasses, adding to a growing body of literature regarding the unintended, and often undesirable, consequences of attempting to control invasive species (Zaveleta et al., 2004).

The proliferation of perennial grasses in systems, where they have previously been rare, can lead to dramatic changes in community dynamics (Levine et al., 2003). For example, exotic grasses may out-compete indigenous tree seedlings (D'Antonio and Mack, 2001) and through their rapid growth rates and availability of fine fuel, may initiate a self-perpetuating cycle of invasion by promoting more frequent fires (D'Antonio and Vitousek, 1992). It is unlikely that the high cover of perennial grasses was a factor limiting the recovery of other riparian elements in this study, since the regeneration of most species took place prior to the expansion of *E. setacea*. However, given the dominance now attained by perennial grasses, we suspect that their regeneration from meristems and the soil seed bank, following future fires, is likely to be both more pronounced and rapid (Milberg and Lamont, 1995). This may adversely effect the seedling recruitment of woody riparian species decreasing the diversity of the community over successive fire cycles. Furthermore, given that Riparian Scrub development is inhibited by short fire cycles (Galatowitsch and Richardson, 2005) the possible effects of *E. setacea* on fire dynamics may be particular important.

Through such self-reinforcing feedbacks (Suding et al., 2004), invasion by perennial grasses into recently-cleared areas may represent an additional constraint to those identified by Galatowitsch and Richardson (2005) already inhibiting Riparian Scrub recovery. If the key factor precipitating the dominance of perennial grasses is the absence of riparian trees, we recommend re-instating this guild in order to catalyse recovery. In contrast to the measures proposed for the fynbos (Yelenik et al., 2004), reducing nutrient levels in riparian ecosystems naturally characterised by fertile soils would seem neither desirable nor achievable and is unlikely to succeed in reducing the dominance of perennial grasses. Additionally, the potential for perennial grasses to inhibit woody seedling survival suggests that the planting of indigenous trees may be more successful at catalysing recovery than sowing seeds in areas where the cover of perennial grasses is high. Future research should attempt to identify both the factors promoting the proliferation of weedy grasses and their effects on the regeneration of both indigenous and alien woody species.

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