Composition of the soil seed bank in alien-invaded grassy fynbos: Potential for recovery after clearing

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Abstract

Indigenous soil seed banks play a very important role in facilitating the natural recovery of indigenous fynbos vegetation after clearing invasive alien vegetation. In densely invaded areas, there is a reduction in fynbos cover and seed production, and these ecosystems rely heavily on the remaining soil seed bank as a reservoir of plant propagules. This study used the seedling emergence approach to assess recovery potential based on the soil seed banks of riparian and hillslope grassy fynbos communities that had been densely invaded for three decades, with *Acacia longifolia* as the dominant alien species. Forty-eight species (of which five were aliens), representing 30 genera and 18 families, emerged from the soil seed bank, with Asteraceae and Cyperaceae being best represented. The mean density of indigenous seedlings for the study area was 1582 seedlings/m^2. *Senecio rigidus* exhibited the highest density, with 274 seedlings/m^2, followed by *Chironia baccifera* (151 seedlings/m^2) and *Rumohra adiantiformis* (136 seedlings/m^2). Forbs were the most numerous growth form. Two other alien species exhibited comparable seedling densities, i.e. *Solanum nigrum* (181 seedlings/m^2) and *Conyza canadensis* (98 seedlings/m^2). *A. longifolia* seed densities of up to 4528 seeds/m^2 were found by sieving the soil. Results revealed that alien-invaded grassy fynbos had a diverse and viable soil seed bank with relatively high seed densities. Pioneer species were well represented, as well as graminoids in the riparian zone. Species representing some guilds were missing; e.g. serotinous species from the genera *Leucadendron* and *Protea*, and few geophytes were present in the hillslope soil seed bank, although ericoid shrubs were well represented. Riparian species such as *Cliffortia graminea* and common Cyperaceae and Restionaceae species were also not represented in the seed bank. It would appear from this data that the soil seed bank would be adequate to enable a functional cover of indigenous vegetation to re-establish after clearing. In order to improve vegetation structure and composition, the addition of some missing guilds would facilitate restoration, provided that post-clearing follow-up treatments do not prevent or hinder the establishment of these indigenous species.

1. Introduction

The invasion of indigenous ecosystems by alien plants poses a threat worldwide, with major impacts on ecosystem functioning and biodiversity (Richardson and Van Wilgen, 2004). In 1998, it was estimated that about 8% of South Africa had been invaded (Versfeld et al., 1998). Riparian ecosystems are vulnerable to invasion (Galatowitsch and Richardson, 2005; Holmes et al., 2005), and in response to the negative impact of invasion on water resources, a government programme, Working for Water, was initiated in 1995 to clear woody alien species from catchment areas.

Implicit in the alien plant removal programme is the assumption that indigenous ecosystems will recover naturally after the removal of invasive species. However, especially in long and heavily invaded systems, vegetation resembling the pre-invasion structure and composition does not recover naturally, and these areas are often further degraded through soil erosion and reinvasion.

One of the factors influencing the recovery of natural vegetation is the nature of the indigenous soil seed bank, and its persistence may play a very important role in facilitating the recovery of ecosystems after the clearance of invasive alien vegetation. Seed banks act as a reservoir of plant propagules (Clemente et al., 2007), and it is generally assumed that soil seed banks contribute to vegetation recovery after disturbance such plant invasion (Holmes, 2001; Holmes and

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Newton, 2004; Sakai et al., 2005). In densely invaded ecosystems, there is a rapid reduction in fynbos cover and seed production, and these ecosystems rely heavily on the persistent soil seed bank for recovery. A persistent seed bank remains in the soil for more than one season, and is a common strategy in areas where the probability of adult survival and reproduction may vary temporally (Kalisz and McPeek, 1993; Holmes and Cowling, 1997a,b), such as in fire-dependent ecosystems.

Fynbos, including riparian fynbos, is adapted to periodic fire events and adaptations for the survival of species during these events also, to a degree, equip fynbos species to survive invasion. During fire events, several plant species are killed by fire and depend on germination of the seeds stored in the soil or canopy for the regeneration of their populations (Cowling, 1992; Van Wilgen and Forsyth, 1992; Clemente et al., 2007). Species which have life cycles shorter than the fire return interval have persistent soil-stored seeds which are fire-stimulated (Van Wilgen and Forsyth, 1992). Although most fynbos species are adapted to cope with regular fire, the increased biomass in invaded systems can cause extreme temperatures during the fire which can damage the soil and cause erosion (Scott, 1993). These fires may also kill resprouters and seeds near the soil surface.

A number of studies in South Africa have investigated the soil seed bank in fynbos (Musil, 1991; Pierce and Cowling, 1991; Holmes and Cowling, 1997a,b), including the effect of alien invasion on the indigenous soil seed bank (Vosse et al., 2008-this issue). However, no studies have looked at the effect of invasive species on the soil seed banks in grassy fynbos communities of the Eastern Cape. A decline in seed bank density has been recorded for invaded areas (Holmes and Cowling, 1997a,b), generally declining with increasing invasion age. Holmes and Foden (2001) found that although a viable soil seed bank is present in invaded areas for up to 30 years, by comparison the soil seed bank from areas that have been invaded for more than 40 years is impoverished. Thus there may be an irreversible threshold of good recovery potential for invaded fynbos ecosystems.

This study aims to assess the recovery potential of a riparian and adjacent terrestrial fynbos community, based on the soil seed bank composition, in an area that has been densely invaded for approximately 30 years.

1.1. Study area

The study area is located in the upper reach of the Palmiet catchment, a tributary of the Kariega, in the Albany District near Grahamstown (33° 20′S, 26° 29′E) (Fig. 1).

The original vegetation in the area consisted of grassy fynbos on the hillslopes, dominated by *Erica chamissonis* and *E. demissa* (Martin, 1966; Richardson et al., 1984), with a patch of Afrotemperate forest at the top of the catchment, 200 m upstream. There are no detailed accounts of the pre-invasion riparian vegetation of this catchment, but riparian vegetation in nearby similar catchments is dominated by Restionaceae and Cyperaceae such as *Carpha* spp. and *Eleocharis* spp, as well as *Cliffortia graminia*, interspersed with woody species such as *Halleria lucida*, *Burchellia bubalina*, *Rapanea melanophloeos*, and *Erica brownleea*.

By 1974, the south-facing slopes in the catchment were covered almost entirely by alien species (*Pinus* species, *Hakea sericea*, *A. longifolia*, *A. saligna* and *Solanum mauritianum*) (Jacot-Guillarmod, 1983). At that time, it was estimated that most of the pine trees were from 15 to 17 years old, and many of them from 45 to 60 years in age. The remaining grassy fynbos was in poor condition, with straggly *Protea cynaroides* and *Erica* species under the alien canopy.

A section of the south-facing slopes adjacent to the study area was cleared during a 12 month period, and was almost
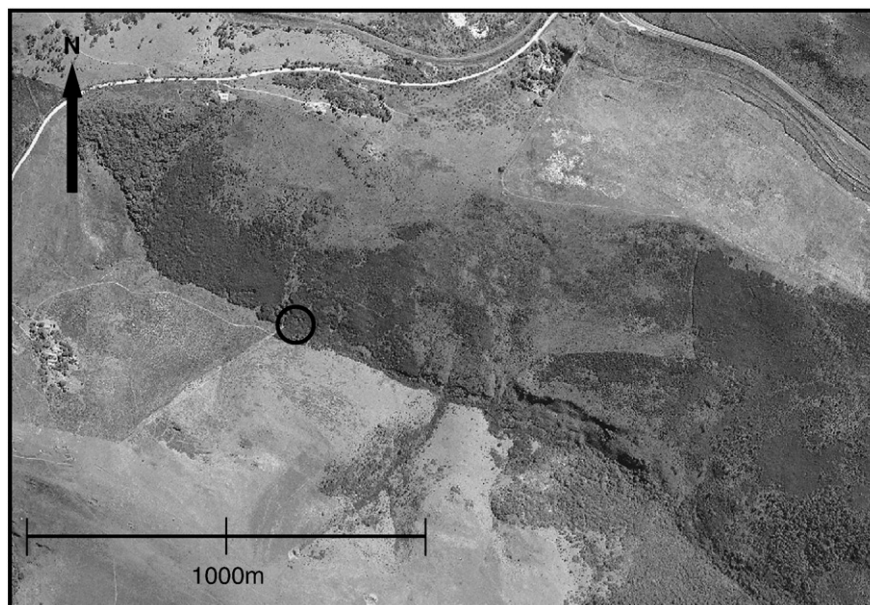

Fig. 1. The Palmiet catchment, indicating the study area (circled in black). The darker patches are dominated by the invasive alien tree *Acacia longifolia* (Chief Directorate: Surveys and Mapping, 2003).

entirely free of aliens by 1980, except for a strip towards the south-western boundary near the river, where some large alien trees remained. During August 1980, a hot wildfire ran through the valley. After the fire, a survey of the re-appearance of indigenous and alien vegetation over time was undertaken (Richardson et al., 1984) and documented 143 indigenous species. After the fire, all alien species re-appeared, except for *H. sericea*.

Aerial photographs indicate that the area was re-invaded fairly rapidly after this fire, and by 1990 a closed alien stand had re-established. Another wildfire went through the valley in 1996, with a repeat of the post-fire re-establishment of alien vegetation. The study area has thus experienced two fire cycles resulting in closed-stand aliens.

A strip approximately 150 m wide, running from the southwest across the stream and upslope towards the northeast, thus encompassing riparian and terrestrial fynbos communities, was cleared by WfW in 2000. Follow-up clearance was not done, and regrowth of the invasive vegetation was such that by 2004 a closed-canopy stand of trees of up to 6 m in height had re-established, consisting of mainly *A. longifolia*. The strip was cleared again in June 2004, after which this study was initiated.

2. Methods

2.1. Sampling

In spring 2004, the strip was divided into a grid of 6 m × 6 m blocks (Fig. 2), with the corner of each block marked with a 10 mm diameter roundbar rod. Some of the rows were longer than others, as some areas were inaccessible due to the steepness of the slope or the height of the slash piles. A total of 118 blocks were demarcated, to allow the long-term monitoring of

post-recovery under field conditions after clearing, which can be correlated against with the results of this soil seed bank study. The blocks were grouped into latitudinal zones (riparian, north-facing dry bank, south-facing dry bank, lower hillslope and upper hillslope), depending on their aspect and proximity to the stream. In the centre of each block, a soil sample was taken during October and November 2004, using a 15 cm × 15 cm square metal frame (Holmes, 2002). The metal frame was hammered into the soil to a depth of 4 cm, after which the soil was carefully removed and placed in paper bags. The frame was then hammered in to a depth of 8 cm, and the process repeated. Each sampling point therefore had soil excavated at two 4 cm depth layers.

2.2. Soil processing and emergence monitoring

The soil was air dried and sieved though a 2 mm diameter sieve to remove stones and pieces of roots and wood, as well as *Acacia* seeds. Any seeds, other than *Acacia* seeds, were returned to the sieved samples. The *Acacia* seeds from each sample were counted and viability tested using the standard tetrazolium chloride test (Association of Official Seed Analysts, 1998).

In January 2005, the sieved soil was spread to a depth of 1.5 cm on top of a 7 cm layer of a mix of Hygromix and sterile compost (to prevent the loss of sample soil) in seedling trays and placed randomly in a small nursery. Twenty control trays containing the sterile growth medium were also placed in the nursery to test for seed contamination. The nursery was completely covered in shade-cloth and open to ambient weather conditions and events like rain.

The samples were exposed to a smoke treatment, by covering the nursery with a large PVC sheet, and making a fire in a metal drum in a wheelbarrow. Once the fire was burning strongly, green fynbos branches were placed on the fire, and the
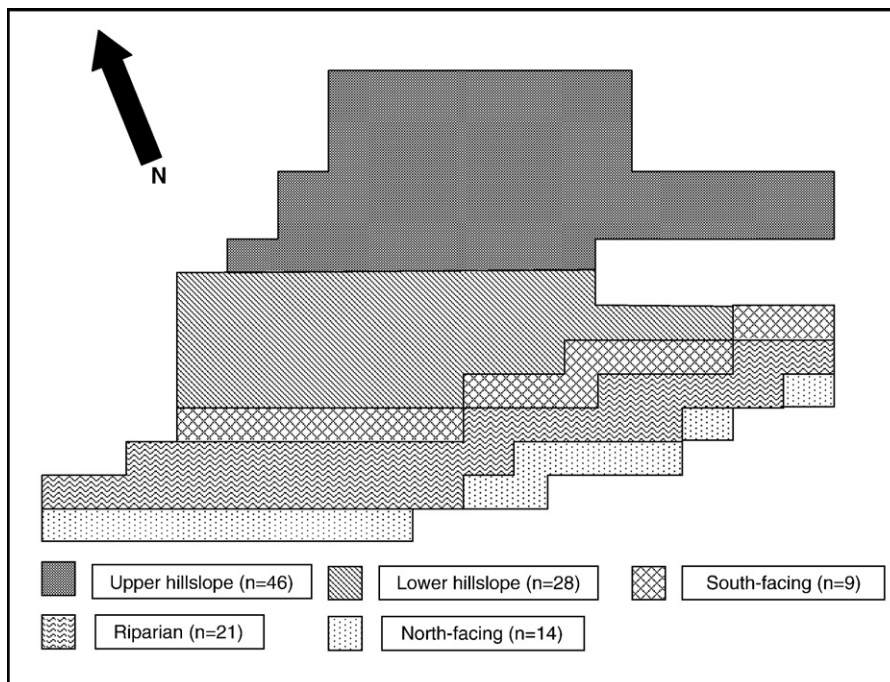

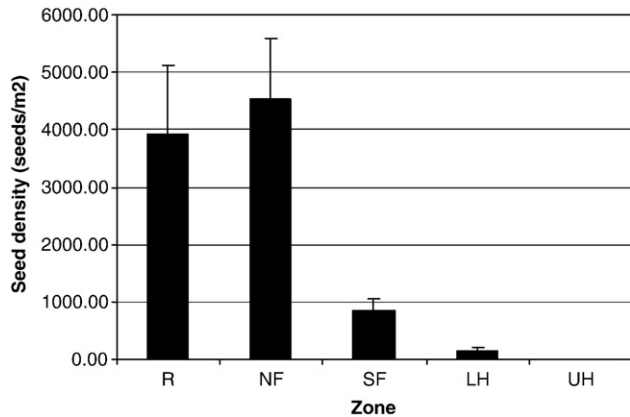Fig. 2. Sampling grid and zones (*n* = number of samples).

Fig. 3. Density of *Acacia longifolia* seeds within soil seed bank (mean + SE) (R = Riparian, $n=21$; NF = North-facing, $n=14$; SF = South facing, $n=9$; LH = Lower hillslope, $n=28$; UH = Upper hillslope, $n=46$).

wheelbarrow was wheeled inside the nursery. This was repeated for an hour, and thick smoke was captured in the nursery.

The seedling trays were watered by hand whenever required, and emerging seedlings identified and removed from the trays. Seedlings which could not be identified were potted into black bags and grown on until a positive identification could take place. Monitoring continued until December 2005, when germination of any new species had ceased. Nomenclature follows Goldblatt and Manning (2000).

2.3. Estimation of soil seed bank

Data were analysed according to species, genus and family to assess floristic composition of emergent species. Species densities and distribution for the study area as well as densities

of species per habitat type (zone) were calculated. For the purpose of this paper, data were not analysed according to the 2 depths, but only total seed density per sample (up to 8 cm depth).

Multivariate analysis was undertaken using the community analysis package, Primer (Clarke and Warwick, 2001), to assess habitat groupings, by means of multidimensional scaling (MDS). An analysis of similarity (ANOSIM) was undertaken to establish differences between the zones, and a SIMPER analysis was undertaken to assess the contribution of individual species in defining the differences between the zones, using Primer (Clarke and Warwick, 2001).

3. Results

3.1. Invasive alien soil seed bank

A. longifolia seeds within the soil seed bank were most abundant in the riparian (3912 ± 1217 seeds/m^2) and north-facing zone immediately adjacent to the river (4528 ± 1075 seeds/m^2). *Acacia* seed densities declined rapidly on the south-facing side of the river and moving upslope (Fig. 3). 99% of the *Acacia* seeds were viable.

3.2. Species composition

A total of 5294 seedlings emerged in the greenhouse, representing 48 species (Appendix A), of which 5 were alien species (contributing 1093 seedlings to the overall number).

Alien species represented three families: Fabaceae (*A. longifolia*), Asteraceae (*Conyza canadensis* and *Pseudognaphalium luteoalbum*) and Solanaceae (*Solanum nigrum* and *S. mauritianum*). A total of 30 indigenous genera were distributed over 18

Table 1
Seed density of the 10 most dominant indigenous species for each zone

Species	Riparian ($n=21$)			North facing bank ($n=14$)			South-facing bank ($n=9$)			Lower hillslope ($n=28$)			Upper hillslope ($n=46$)		
	D	R	F	D	R	F	D	R	F	D	R	F	D	R	F
Rumohra adiantiformis	567±379	1	38	143±99	2	29									
Senecio rigidus	559±237	2	81	321±181	1	93	410±102	1	100	248±43	1	93	120±25	3	70
Conyza pinnata	290±184	3	57	124±58	4	50	173±80	2	78	111±32	4	46	66±11	7	28
Ficinia oligantha	241±112	4	52				35±24	6	33						
Cyperus esculentis	121±48	5	57	76±35	8	43									
Halleria lucida	119±104	6	14	83±55	7	29	25±15	9	33						
Erica brownleeae	116±53	7	52	48±21	9	50									
Helichrysum sp.	104±35	8	57	111±40	5	79	25±15	8	44						
Helichrysum epapposum	102±37	9	38												
Isolepis cernua	93±27	10	52	89±69	6	29									
Cheilanthes viridis				140±58	3	43	104±62	4	33	162±65	2	36			
Helichrysum petiolare				44±13	10	57	138±47	3	100	52±18	7	43			
Chironia baccifera							44±22	5	44	143±34	3	64	278±44	1	78
Anthospermum herbaceum							35±16	7	44	73±36	6	39	62±15	8	50
Hypoxis argentea							20±13	10	22	41±30	8	18	60±20	9	41
Selago corymbosa										83±35	5	39	160±28	2	72
Erica chamissonis										38±19	9	32	96±28	4	52
Eragrostis obtusa										37±14	10	36	57±18	10	43
Lobelia tomentosa													91±27	5	41
Helichrysum cymosum													80±16	6	61
Total density of zone	2753±553			1435±392			1146±163			1217±141			1400±102		

$n=$ number of samples, $D=$ seed density (mean + SE); $R=$ ranking within the zone, $F=$ % frequency.

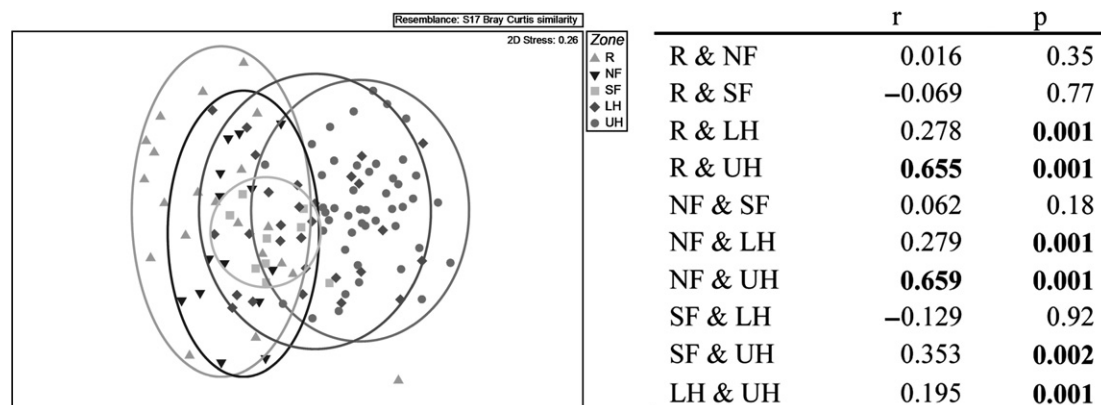|	r	p
R & NF	0.016	0.35
R & SF	−0.069	0.77
R & LH	0.278	**0.001**
R & UH	**0.655**	**0.001**
NF & SF	0.062	0.18
NF & LH	0.279	**0.001**
NF & UH	**0.659**	**0.001**
SF & LH	−0.129	0.92
SF & UH	0.353	**0.002**
LH & UH	0.195	**0.001**

Fig. 4. Multi-dimensional scaling plot of the soil seed bank species for different zones. Analysis of similarity between zones is given on right of figure (R = Riparian, $n=21$; NF = North-facing, $n=14$; SF = South facing, $n=9$; LH = Lower hillslope, $n=28$; UH = Upper hillslope, $n=46$).

families, the families Asteraceae (13 species), Cyperaceae (6 species) and Poaceae (4 species) being the most species rich (Appendix A).

The mean density of indigenous seedlings for the study area is $1582\pm129/m^2$. The species exhibiting the highest density is *Senecio rigidus* (Asteraceae), with a mean density of 274 seedlings/m^2 (±51), followed by *Chironia baccifera* (151 seedlings/m$^2\pm22$) and *Rumohra adiantiformis* (136 seedlings/m$^2\pm70$). Most of the species identified were forbs. Two alien species exhibited densities comparable to the commonest indigenous species, i.e. *S. nigrum* (181 seedlings/m$^2\pm70$) and *C. canadensis* (98 seedlings/m$^2\pm9$).

Seed densities for the indigenous species in each zone are given in Table 1. Although there is a gradual shift in community composition upslope from the riparian zone, *S. rigidus* and *Conyza pinnata* remained dominants within all the zones. The propagule densities ranged between 567 ± 379 propagules/m^2

(*R. adiantiformis*) in the riparian zone and 20 ± 13 seeds/m^2 (*Hypoxis argentea*) in the south-facing zone, for the 10 most abundant species. The highest species richness was found in the riparian and upper hillslope zone (both 34), while the lowest species richness was found in the south-facing zone (26).

The highest indigenous seed density was found in the riparian zone ($2753/m^2\pm533$), followed by the north-facing zone ($1435/m^2\pm392$) and the upper hillslope zone ($1400/m^2\pm102$). Patchiness was greatest in the riparian and north-facing zone, as evidenced by the high variance, with some samples exhibiting densities of up to 7688 seedlings/m^2 (*R. adiantiformis*), 4666 seedlings/m^2 (*S. rigidus*) and 3910 seedlings/m^2 (*C. pinnata*). Some alien species also exhibited high densities in patches, e.g. *S. nigrum*, with up to 7021 seedlings/m^2.

The multidimensional scaling analysis of species data (excluding alien species) for combined depths (Fig. 4) indicated that although zones tended to cluster, there is considerable

Table 2

Analysis of dissimilarity between different zones, with main indicator species of dissimilarity (R = Riparian, $n=21$; NF = North-facing, $n=14$; SF = South facing, $n=9$; LH = Lower hillslope, $n=28$; UH = Upper hillslope, $n=46$)

Zone	% Dissimilarity (excluding alien)	Indicator species	% Contribution	% Dissimilarity (including alien)	Indicator species	% Contribution
R & NF	83	*S. rigidus*	16	78	*S. nigrum* [a]	14
		R. adiantiformis	13		*S. rigidus*	12
R & SF	79	*S. rigidus*	20	78	*S. rigidus*	16
		R. adiantiformis	11			
		C. pinnata	10			
NF & SF	76	*S. rigidus*	22	77	*S. nigrum* [a]	15
		C. viridis	10		*S. rigidus*	15
R & LH	85	*S. rigidus*	15	84	*S. rigidus*	12
		R. adiantiformis	11			
NF & LH	83	*S. rigidus*	15	83	*S. nigrum* [a]	14
		C. viridis	26		*S. rigidus*	10
SF & LH	72	*S. rigidus*	19	71	*S. rigidus*	16
		C. viridis	12		*C. viridis*	10
		C. pinnata	11			
R & UH	89	*S. rigidus*	12	87	*S. rigidus*	10
		R. adiantiformis	10		*R. adiantiformis*	
				87	*S. rigidus*	10
NF & UH	87	*C. baccifera*	12	85	*S. nigrum* [a]	12
SF & UH	79	*S. rigidus*	18	78	*S rigidus*	15
		C. baccifera	12		*C. baccifera*	11
LU & UH	78	*C. baccifera*	13	76	*C. baccifera*	12

[a] Alien species.

overlap in community composition for some zones. The highest dissimilarity was found between the north-facing zone and upper hillslope zone with an *r* value of 0.659 (*P*=0.001) and the riparian zone and upper hillslope zone, with an *r* value of 0.655 (*P*=0.001). This pattern remains similar if alien species are included.

The analysis of dissimilarity indicated that *S. rigidus* contributes most in defining the dissimilarity between zones, as does *R. adiantiformis* (Table 2). In the upslope zones, *C. baccifera* becomes more important in defining the different zones, and *S. nigrum* also influences zone boundaries when aliens are included in analysis.

4. Discussion

4.1. Assessment of the soil seed bank

Soil seed bank dynamics are complex, and at any given time an investigation of the soil seed bank presents a snapshot of a dynamic situation. The balance and variability of seed production, dispersal, predation, pathogenesis and germination will affect the spatial distribution and size of the seed bank of a species at a local scale (Sakai et al., 2005; Clemente et al., 2007). Seasonal variability may be responsible for differences in the soil seed bank between different years (Martin, 1966; Holmes and Cowling, 1997b). The spatial distribution of seeds in the soil is notoriously patchy, as was also evidenced during this study.

The assessment of the soil seed bank is complicated by shortcomings in the methodology. The seedling emergence method has been used in many studies because of easy identification of emerging seedlings and presumes that number of seedlings detected equals the number of viable seeds (Baskin and Baskin, 1998; Sakai et al., 2005). However, this method can underestimate the true seed bank, as vital germination cues, e.g. a heat pulse and fluctuation of soil temperatures may be absent. However, some of the larger-seeded species such as *Psoralea pinnata* which need a heat pulse, would probably have been found during the sieving process (only two *P. pinnata* seeds were found). Small-seeded species e.g. *Metalasia* may also require a fire-related germination cue other than smoke and may be underrepresented (Holmes and Cowling, 1997a).

The simulation of seasonal fire by means of the smoke treatment may also not optimize germination. Heelemann et al. (2008) have found that the recruitment patterns of Proteaceae after fire in the Eastern Cape differ significantly from those observed in the western and central of the Fynbos biome, but no optimal fire season was identified.

Some studies have also found a higher recruitment from soil samples germinated in the nursery compared to field conditions (Holmes and Cowling, 1997a; Holmes and Foden, 2001).

There are no data available on the soil seed bank of uninvaded fynbos areas in the Albany district, which is a major shortcoming in interpreting the post-clearing recovery potential of the soil seed bank of invaded areas. It is recommended that such data collection be undertaken. Post-clearing recovery in the field should also be monitored, in order to evaluate the factors affecting actual in-field recovery. Post-clearing monitoring is

in process, and results will be presented in a subsequent publication.

4.2. Seed bank composition

The viable *Acacia* soil seed bank in the study area is much lower (max. 4500 seeds/m^2) than that reported in studies in the Western Cape, where between 4000–46 000 seeds/m^2 were measured in the 1980s (Holmes et al., 1987). This is probably due to the successful introduction of the gall wasp biological control agent into the area. Nonetheless, this alien seed density is still far higher than that of any of the indigenous species in this area, and presents problematic challenges to the eradication of *Acacia* species, as these seeds will germinate after clearing and/or fire, requiring timeous follow-up treatments to eliminate the invasive regrowth.

Forty-three indigenous species were represented in the soil seed bank for the study area. A comparison with vegetation studies in the area reveals that this represents approximately 30% of the full post-fire species complement (which should correlate better with the soil seed bank than mature vegetation) for the area (Richardson et al., 1984). Thus many taxa are not represented in the soil seed bank. Although the soil seed bank will not represent the full species complement of the aboveground vegetation, it has been found that long-invaded fynbos (two or more fire cycles of dense invasion) in the Western Cape has experienced a loss of about 70% of species from the standing vegetation (Holmes and Cowling, 1997b), comparable to the balance of this figure. Holmes (2002) found a significant decrease in seed bank species richness with increased age of invasion in the Western Cape.

Senecio speciosus, *Anthospermum aethiopicum* and *Erica cerinthoides* appeared in large numbers after the 1980 fire (Martin, 1966; Richardson et al., 1984), but these species did not germinate during this study, although they are present in the aboveground vegetation of the area. *Senecio pterophorous*, although absent from the pre-fire fynbos, appeared in large numbers after the fire from the soil seed bank (Richardson et al., 1984), and the same was found for the 1959 fire in the area (Martin, 1966). This species had a low abundance during this study. *H. argentea* regenerated vegetatively after the fire (Richardson et al., 1984), and was also abundant in the soil seed bank. However, *Senecio corymbosa* and *E. chamissonis* were post-fire dominants in the survey by Richardson et al. (1984) and Martin (1966) and both these species were also abundant in the seed bank in this study. Common aboveground grasses like *Alloteropsis semialata* and *Themeda triandra* are not represented in this study. No proteoids were found in the current study, and although this is not a common guild in the area, proteoids were recorded by Jacot-Guillarmod (1983). *P. cynaroides* is also still commonly found in uninvaded nearby vegetation, but proteoids are one of the first regeneration guilds to be eliminated by dense closed-canopy alien vegetation (Holmes and Cowling, 1997a,b).

Although viable persistent seed banks have been found in long-invaded sites (two or more fire cycles; more than 25 years), with representatives of all major fynbos growth forms, alien invasion results in a decrease in species richness, diversity and

abundance (Holmes and Cowling, 1997a,b). The shift in community composition and loss of some taxa becomes more noticeable with an increase in invasion time. Non-sprouting serotinous and ericoid shrubs are readily outcompeted under a closed *Acacia* canopy, while shrubs with bird-dispersed seeds are favoured (Holmes and Cowling, 1997a,b). One bird-dispersed thicket species, *H. lucida*, was found in this study and it is likely that this species persisted under the closed *Acacia* canopy.

At this study site, the family Asteraceae dominated the soil seed bank, with six genera and 13 species. The genus *Helichrysum* was the best represented, and the species *S. rigidus* most abundant, with the pioneer *C. pinnata* also having a high abundance. This is similar to the findings of Holmes and Cowling (1997a), where annuals and short-lived perennials dominate the soil seed banks at long-invaded fynbos sites on the Cape Peninsula. Holmes and Cowling (1997a) also found that long-lived obligate seeders, especially ericoid shrubs, dominate the soil seed bank in long-invaded sites (Holmes, 2002), and in this study, the two *Erica* species were also found within the top 10 dominant species within the soil seed bank.

There was only one indigenous species (*P. pinnata*) represented in the family Fabaceae. This family generally has long-lived and persistent seed in the soil seed bank, and more species and higher densities would have been expected. It is likely that the Fabaceae germinated during the last heat pulse (1996), and then became suppressed under the alien canopy, preventing further seed set.

4.3. Seed bank density

The total indigenous seedling density (1582 seedlings/m^2) is comparable to those found in winter rainfall areas of the fynbos biome, e.g. Holmes and Cowling (1997a) who found a range of 1100–1900 seedlings/m^2 in uninvaded areas and Holmes (2002) with a range of <400 to >1200 seedlings/m^2. This also compares well with the seed density values of 1754 seeds/m^2 from cleared conifer plantations in Japan (Sakai et al., 2005) and seed densities of obligate seeders of 640–4388 seeds/m^2 and 102–3061 seeds/m^2 (Clemente et al., 2007). Miller and Cummins (2003) have found seed densities of 600–64 000 seeds/m^2 in (Scottish) heathlands far exceeding the densities found in this study. However, seed densities are problematic to compare, as methodology differs (e.g. sampling depth).

The highest species density in any zone was for *R. adiantiformis* with 567 spores/m^2, followed by *S. rigidus* with 559 seeds/m^2, both in the riparian zone. However, there is a high spatial heterogeneity and typically high variance (Clemente et al., 2007), with some samples (*S. rigidus*) exhibiting densities of up to 4666 seeds/m^2. Although a high variance is common in soil seed bank studies, a larger spread of smaller samples throughout the area may have resulted in a smaller variance, as a relatively low number (118) of samples were taken. *S. rigidus* and *C. pinnata* were the only species, within the 10 most dominant species, which occurred in all the zones (Table 1). Frequencies of occurrence were highest for *S. rigidus*, ranging from 70–100%.

These relatively high densities are surprising, given the time of invasion, and suggest that species managed to set seed between fire cycles. Van Wilgen and Forsyth (1992), in a study in the Swartboskloof, found that 70% of sprouting species matured within 1 year, enabling seed set. They also found that 86% of all species flowered within the first year, and perhaps the species found in the seed bank managed to set seed between fire cycles and after the 2000 clearance. However, regrowth of alien plants is very fast and there was unlikely to have been a long period before a closed alien canopy re-established. Slowly maturing species, including obligate seeders like Ericaceae, would be unlikely to set seed before being suppressed by invading acacias. Their presence in the soil seed bank indicates long-term persistence.

5. Conclusion

This study revealed that the soil seed bank of a riparian and adjacent hillslope area of grassy fynbos which had been invaded for approximately 30 years, interspersed with brief periods of clearing, still has a diverse and viable soil seed bank with relatively high seed densities. Pioneer species from the family Asteraceae like *Senecio* sp., *Conyza* sp. and *Helichrysum* sp. are well represented, as well as graminoids in the riparian zone. Species representing some guilds are missing; e.g. serotinous species from the genera *Leucadendron* and *Protea*, and few geophytes are present in the soil seed bank, although ericoid shrubs are well represented. It would appear from this data that the soil seed bank would be adequate to enable indigenous vegetation to re-establish after clearing, possibly with the addition of some missing guilds and species to enhance vegetation structure, provided that post-clearing follow-up treatments do not prevent or hinder the establishment of these indigenous species. These data need to be compared with the soil seed bank of uninvaded areas, as well as with the recovery in the field, in order to evaluate the factors affecting actual in-field recovery.

Appendix A

Emerged species from soil seed bank study, indicating % proportion of seed bank per family, as well as guild and zone of occurrence. Guilds: A = alien, F = forb, G = graminoid, Ge = geophyte, S = Shrub. Zones: R = Riparian, NF = North-facing, SF = South facing, LH = Lower hillslope, UH = Upper hillslope.

Species	Family	Family % of indigenous soil seed bank	Guild	Zone
Rumohra adiantiformis (G.Forst) Ching	Dryopteridaceae	2	F	R, AN, AS, LH, UH

Appendix A (*continued*)

Species	Family	Family % of indigenous soil seed bank	Guild	Zone
Cheilanthes viridis (Forssk.) Sw.	Pteridaceae	5	F	R, AN, AS, LH, UH
Cheilanthes hirta Sw.	Pteridaceae		F	AS, LH, UH
Ficinia oligantha (Steud.) J.Raynal	Cyperaceae	14	G	R, AN, AS, LH, UH
Cyperus esculentus L.	Cyperaceae		G	R, AN, AS, LH, UH
Isolepis cernua (Vahl) Roem. & Schult.	Cyperaceae		G	R, AN, LH
Isolepis prolifer R.Br.	Cyperaceae		G	R, AN, LH, UH
Ficinia capillifolia (Schrad.) C.B. Clarke	Cyperaceae		G	R, AN, LH, UH
Scirpus thunbergii (Schrad.) L.B. Clarke	Cyperaceae		G	R, AS
Hypoxis argentea Harv. ex Baker	Hypoxidaceae	2	Ge	R, AN, AS, LH, UH
Aristea anceps Eckl. ex Klatt	Iridaceae	2	Ge	R, AN
Cynodon dactylon (L.) Pers.	Poaceae	10	G	LH, UH
Digitaria eriantha Steud.	Poaceae		G	R, AN, AS, UH
Eragrostis obtusa Munro ex Ficalho & Hiern	Poaceae		G	R, AN, AS, LH, UH
Panicum maximum Jacq.	Poaceae		G	R, AN, AS, LH, UH
Centella asiatica (L.)	Araliaceae	2	F	R, AN
Chrysanthemoides monilifera (L.) Norl.	Asteraceae	31	S	R, AN, LH
*Conyza canadensis**	Asteraceae		A	R, AN, AS, LH, UH
Conyza pinnata (L.f.) Kuntze	Asteraceae		F	R, AN, AS, LH, UH
Haplocarpha lyrata Harv.	Asteraceae		F	R, AN, AS
Helichrysum cymosum (L.) D.Don.	Asteraceae		F	R, AN, AS, LH, UH
Helichrysum petiolare Hilliard & B.L. Burtt	Asteraceae		F	R, AN, AS, LH, UH
Helichrysum cephaloideum DC.	Asteraceae		F	AN, AS, LH, UH
Helichrysum subglomeratum Less	Asteraceae		F	R, AN, LH, UH
Helichrysum odoratissimum (L) Sweet	Asteraceae		F	AN
Helichrysum spp.	Asteraceae		F	R, AN, AS, LH, UH
Helichrysum epapposum Bolus	Asteraceae		F	R

Appendix A (*continued*)

Species	Family	Family % of indigenous soil seed bank	Guild	Zone
*Pseudognaphalium luteo-album**	Asteraceae		F	R, AN, AS, LH, UH
Senecio pterophorus DC.	Asteraceae		A	R, AN, AS, LH, UH
Senecio chrysocoma Meerb.	Asteraceae		F	AS, LH, UH
Senecio rigidus L.	Asteraceae		F-S	R, AN, AS, LH, UH
Lobelia tomentosa L.f.	Campanulaceae	2	F	R, LH, UH
Drosera aliciae Raym.-Hamet	Droseraceae	2	F	LH, UH
Erica chamissonis Klotzsch ex Benth.	Ericaceae	5	S	R, AN, AS, LH, UH
Erica brownleeae Bolus	Ericaceae		S	R, AN, AS, LH, UH
Acacia longifolia (Andrews) Willd.*	Fabaceae	2	A	R, AN, AS, LH, UH
Psoralea pinnata L.	Fabaceae		S	R, LH
Chironia baccifera L.	Gentianaceae	5	F- S	R, AN, AS, LH, UH
Sebaea micracantha (Cham. & Schltdl.) Schinz	Gentianaceae		F	R, AS, LH, UH
Pelargonium alchemilloides (L) L'Hér.	Geraniaceae	5	F	R, AN, UH
Pelargonium radens H.E Moore	Geraniaceae		F	UH
Polygala hispida Burch.	Polygalaceae	2	F	UH
Anthospermum herbaceum L.f.	Rosaceae	2	F	R, AS, LH, UH
Halleria lucida L.	Scrophulariaceae	5	S	R, AN, AS, LH, UH
Selago corymbosa L.	Scrophulariaceae		F	R, AS, LH, UH
Solanum mauritianum Scop.*	Solanaceae		A	R, AN, AS, LH, UH
Solanum nigrum L.*	Solanaceae		A	R, AN, AS, LH, UH
Struthiola macowanii C.H. Wr.	Thymelaeaceae	2	S	UH

*Alien species.
Alien species excluded from percentage contribution analysis.

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