Effect of fire on the topsoil seed banks of rehabilitated bauxite mine sites in the jarrah forest of Western Australia

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This paper is based on the PbD research of Martin Smith (Department of Botany, The University of Western Australia, Nedlands, WA 6907, Australia) carried out in collaboration with William Loneragan (Department of Botany, The University of Western Australia), Carl Grant (Ecosystem Management, School of Rural Science and Natural Resources, University of New England, Armidale, NSW 2351, Australia), and John Koch (Environmental Department, Alcoa World Alumina Australia, P.O. Box 252, Applecross, WA 6153, Australia). Summary Germinable seed stores of 5- and 8-year-old rehabilitated bauxite mine pits in south-west Western Australia were assessed before and after burning. These seed stores were compared to those of adjacent unmined Jarrah (Eucalyptus marginata) forest, to identify at what age fire can be reintroduced, in order to measure restoration success and reduce fire hazard. Soils were sampled in early summer (before fire) and late autumn (after fire). Before fire, the mean topsoil seed bank of 5-year-old sites was 2121 seeds per m² while 8-year-old sites had a mean of 1520 seeds per m². Only the 5-year-old sites were significantly different from the forest mean of 1478 seeds per m² for the same season. After summer burns (and possibly due to seasonal effects) topsoil seed banks of rehabilitated areas (sampled in autumn) decreased by an average of 53 per cent. Topsoil seed banks of 5-8-year-old sites were resistant to lower intensity burns, with 362 seeds per m² of native species surviving mild burns and 108 seeds per m² of native species surviving after an intense summer fire. The topsoil seed reserve of 5-8-year-old rehabilitated areas had a high proportion of annual weed species while the forest sites had high levels of subshrubs and native annuals. Low-intensity burns did not alter the composition of life-forms in the soil seed bank, while intense burns favoured annual weed and shrub species. The results indicate that it is not appropriate to introduce fire to rehabilitated areas before 8 years, due to limited fuel reduction benefits and possible adverse effects on obligate seeding species. The large proportion of weed species in the soil seed bank of young rehabilitated areas is a concern, and remains a major consideration for future disturbance of these areas.

Key words *land rehabilitation, mining, prescribed burning, obligate seeder, resilience, resprouter, soil seed banks.*

Introduction

lcoa World Alumina Australia (Alcoa) has Mined bauxite in the Jarrah (Eucalyptus marginata) forest of south-west Western Australia since 1963. Currently, Alcoa mines and rehabilitates approximately 450 ha annually. The objective is to establish a selfsustaining jarrah forest ecosystem, which aims to enhance or maintain timber, water, recreation and conservation values. An outline of the mining and rehabilitation process is given elsewhere (Nichols et al. 1985; Ward et al. 1993). The soil seed reserve, if managed correctly, is a valuable resource in the restoration of disturbed areas within natural vegetation communities (Iverson & Wali 1982; Hopkins & Graham 1983; Bellairs & Bell 1993). As part of the rehabilitation process, Alcoa coserves the forest topsoil by directly returning it to new rehabilitation areas whenever possible. This process has been found to retain approximately 50 per cent of the original forest seed reserve (Koch *et al.* 1996). Koch and Ward (1994) showed that 77 per cent of the species that re-established on rehabilitated areas originated from the topsoil, rather than from broadcast seed mixes.

Several studies have estimated the topsoil seed reserve of the unmined jarrah forest. Vlahos and Bell (1986) found a range of 377-1579 seeds per m² in the top 3 cm of soil while Koch *et al.* (1996) found a range of 212-424 seeds per m² in the top 10 cm of soil. Furthermore, Ward *et al.* (1997) found a range of 111-529 seeds per m² in the top 5 cm of soil with higher estimates in summer than in other seasons. In a study of 12-13-year-old bauxite mine rehabilitation,

Grant and Koch (1997) found a mean 2723 seeds per m² (autumn) and 1153 seeds per m² (spring) in soils collected to a depth of 10 cm. They concluded that the seasonality observed in the soil seed bank of the jarrah forest was also present in rehabilitated bauxite mine pits.

An important measure of ecosystem development and maturity is the ability to survive and recover from disturbance. One indicator of rehabilitation resilience and hence success may, therefore, be measured by examining community resilience to fire. Management responsibility for rehabilitated areas will eventually be returned to the Department of Conservation and Land Management (CALM) who currently manage the jarrah forest. CALM's management regime includes the use of prescribed burning to reduce the risk of severe bushfires. A recent study examining 11–15-year-old bauxite The soil seed bank is a dynamic resource that can change greatly, both spatially and temporally. Its composition can influence the pattern of recovery that occurs after disturbance (Roberts 1981). This study, therefore, aimed to predict resilience to fire by quantifying the soil seed banks of 5–8-yearold rehabilitation areas and comparing them to adjacent unmined jarrah forest areas. Analysis of quantitative differences between: (i) weeds and natives; (ii) annuals and perennials; and (iii) soil seed bank and existing vegetation provided information to refine resilience prediction and any need for further intervention.

Methods

Study sites

The study was conducted at Alcoa's Jarrahdale bauxite mine 45 km SSE of Perth in Western Australia (32°17'S, 116°08'E). The area has a Mediterranean climate with summer drought and winter rainfall (1200 mm). The vegetation of the study area is dry sclerophyll open forest dominated by Jarrah and variable levels of Marri (Corymbia calophylla formerly Eucalyptus calophylla). There is a middle-storey of Bull Banksia (Banksia grandis), She Oak (Allocasuarina fraseriana) and Snottygobble (Persoonia longifolia). The ground level flora consists of shrubs and herbs predominantly from the families Apiaceae, Asteraceae (Compositae), Cyperaceae, Epacridaceae, Leguminosae, Liliaceae, Myrtaceae, Orchidaceae, Papilionaceae, Proteaceae and Restionaceae.

Sampling sites consisted of three mine pits rehabilitated in 1992 (5-years-old); three mine pits rehabilitated in 1989 (8years-old); and two areas of native jarrah forest (8-9 years since they were last burnt). Complications with the prescribed burning programme precluded a third jarrah forest replicate site. All mined areas had been rehabilitated according to routine rehabilitation procedures. After mining is completed, the area is recontoured and topsoil from a nearby area about to be mined is stripped and directly returned to the newly contoured pit. The pit is ripped along the contour to a depth of approximately 1.5 m and seed is applied in late summer or autumn. Fertilizer is applied in late winter or spring. Currently 60-80 species are returned in the applied seed mix, which has a large component of leguminous species. The rehabilitation sites sampled had native canopies of Jarrah, Marri and Swan River Blackbutt (Eucalyptus patens). This current style of rehabilitation differs from older areas (rehabilitated prior to 1988) which often have a canopy of non-native eucalypt species and were seeded with higher levels of large Acacia species.

Field sampling

The vegetation growing at each sampling site was assessed in October 1997 (spring). All plants growing within 128 quadrats (1 m²) along permanent transects were identified and counted. Plant cover was estimated visually as a percentage of projected live cover over the quadrat. Life-form categories were adapted from Bell et al. (1984) and species classified as obligate seeders or resprouters. The nomenclature (scientific and common names) used follows Marchant et al. (1987) and Marshall (1990). Fuel levels were sampled from four sites in each rehabilitated pit and forest area. At each sampling point all biomass less than 4 cm in diameter, within a 0.5×1 m quadrat, and to a height of 3.9 m, was collected. This material was sorted into live and dead fractions before being dried and weighed.

Soil was collected in early December 1997 (early summer) from each of eight sampling sites. In each pit or forest area, soil samples were collected from four points in a stratified random pattern along permanent transects. At each sampling point four subsamples were taken, each 1 m from a central point. During the rehabilitation process, soil ripping was conducted to overcome compaction and produced distinct parallel ridges and furrows. In the rehabilitation pits, therefore, two subsamples were

taken at each site from ridges and two from furrows. Each subsample covered $10 \times$ 20 cm and soil was collected from depths of 0-5 cm (including litter) and 5-10 cm. Soil was collected to a maximum depth of 10 cm as previous studies have shown that the great majority of the soil seed bank is contained within the top 5 cm of the soil profile (Tacey & Glossop 1980; Koch et al. 1996; Grant & Koch 1997; Ward et al. 1997). The litter and top 5 cm of soil of all four subsamples were bulked together, as were the four subsamples from 5-10 cm soil depth. Soil samples were stored in open bags in a warm, dry greenhouse until ready for processing.

Prescribed burns were conducted at all eight sites in mid-December 1997. All sites were resampled in May 1998 (late autumn). The same soil sampling procedures were used with samples being taken within 20 cm of the original samples.

Sample preparation

Each bulked soil sample from each depth was passed through a riffle to break up soil aggregates, remove large rocks and roots, and to randomly divide the soil. The two equal halves of soil were spread to a depth of 2 cm over seedling trays $(34 \times 28 \times$ 5 cm), lined with permeable cloth and a 1 cm layer of sand. One of each pair of trays was designated as a control and the other received a combined heat and smoke treatment. Pre-fire and post-fire soil samples received both control and heat/smoke treatments. A number of studies have emphasized the importance of the heat and/or smoke produced by fire in the breaking of seed dormancy in many species common to the Jarrah forest (Purdie 1977; Shea et al. 1979; Bell et al. 1987; Bell et al. 1993; Dixon et al. 1995; Roche et al. 1997a, 1997b; Ward et al. 1997; Bell & Williams 1998; Tieu et al. 1999). The heating procedure, which was conducted first, consisted of placing the seedling trays in an oven at 80°C for 20 min. The smoking treatment involved placing the seedling trays on racks within a sealed plastic tent into which smoke was forced. The tent allowed the concentration of smoke to be increased. Smoke was produced in a 50 L drum by the combustion of fresh and dry material collected from both

native and introduced plant species. The smoke was blown from the drum to the tent through a metal pipe by a small electric fan. The smoking procedure was carried out for 1 h, after which the soil was stained brown and exuded a strong smoke odour that remained for up to 2 weeks. Following treatment, trays were positioned randomly within a greenhouse and watered by an automatic irrigation system. Watering in the first week was monitored to ensure that no water drained through the trays. This was to prevent leaching of the water-soluble smoke compound, which is believed to be the germination cue in some species (K. Dixon, pers. comm., 1998). Commencing from the second week, the trays were watered to saturation three times daily. Germination in the trays was recorded fortnightly, with seedlings being removed after identification. Unknown seedlings were grown on for positive identification. A total of 256 travs (three vegetation types, 5- and 8-year-old rehabilitation and Jarrah forest; two to three pits/areas; four subreplicates; two soil depths, litter + 0-5 cm soil, 5-10 cm soil; two fire histories, pre-fire, post-fire; and two treatments, heat and smoke, control) and 0.512 m³ soil were treated during the experiment.

Data analyses

The total germinable seed bank was calculated by taking the maximum score of each species in each pair of control and heated/smoked trays as being indicative of the number of seeds of this species in the topsoil. This provided the number of seeds of each species that would have germinated from the whole sample had it received the most favourable treatment for that species. The number of germinants was divided by the area of the soil subsample to obtain an estimate of the seed numbers per m². Differences in seed banks between the 5- and 8-year-old rehabilitation types and the jarrah forest were determined using a nested MANOVA analysis (SPSS Inc, North Chicago, IL, USA). This analysis compared differences between pre- and post-fire soil seed banks across both soil horizons nested within sites. Differences between pre- and post-fire soil samples within each vegetation type were assessed by a randomized block design ANOVA (Sokal & Rohlf 1981).

A detrended correspondence analysis (DCA) ordination was performed on the plant densities and the soil seed bank densities of individual species of the sampled sites. Plant and seed densities were squareroot transformed and standardized, and species that only occurred once were removed from the DCA. Jaccard similarity coefficients were also calculated for the plant and soil seed bank densities (Ludwig & Reynolds 1988). Byram fire intensity was calculated using the following equation (Burrows 1994):

Fire intensity (kW/m) = rate of spread (m/h) × fuel load (t/ha) × 0.51

Results

Fire characteristics

The 5-year-old rehabilitation sites experienced low-intensity burns (< 300 kW/m), that consumed some litter, blackened tree stumps and scorched lower tree leaves. Due to the patchy litter and much green vegetation (Table 1), burns in these sites were only able to 'trickle' along the litter in the rip lines. The 8-year-old rehabilitation sites experienced high-intensity burns (9000-10 000 kW/m). These sites had high fuel loads comprising thick continuous litter and numerous dead Acacia shrubs. These burns consumed all litter and vegetation and defoliated more than 90 per cent of all trees. At 1 cm depth, soil temperatures remained above 100°C for 3-5 min while at 2.5 cm depth soil temperatures reached temperatures of more than 50°C for up to 10-15 min (M. Smith, unpubl. data, 1997). Jarrah forest sites received low- to moderate- (in places) intensity burns (300- < 2000 kW/m), as is the prescription for the jarrah forest. These burns removed much of the litter but did not consume much live material.

Topsoil seed reserve

The total topsoil seed reserve of 5- and 8year-old rehabilitation sites was slightly higher than that of the unmined jarrah forest prior to burning (i.e. 2121-1520 seeds per m² for 5- and 8-year-old rehabilitation compared to 1478 seeds per m² in the forest in summer; Table 2). Across all sites, 82 per cent of the seed reserve was contained within the litter and the top 5 cm of the soil profile (Table 3). The 5-year-old rehabilitation sites had the greatest concentration of seed in the top 0-5 cm (86 per cent), followed by the 8-year-old sites (80 per cent) and forest sites (78 per cent). The 5-year-old sites had a total of 46 species in the soil seed bank, with 15 species occurring, on average, at levels greater than 10 seeds per m², while the 8-year-old sites had 59 species of which 13 occurred at levels greater than 10 seeds per m² (Appendix I). The forest sites soil seed banks comprised 66 species, with 19 occurring at levels greater than 10 seeds per m^2 .

Fire and seed banks

Fire and time significantly decreased seed density in 5-year-old rehabilitation sites by 39 per cent (P < 0.05; Table 2). The decrease in germination density of 74 per cent in the 8-year-old rehabilitation sites, however, was not significant (P > 0.05) due to large spatial variability in seed numbers. The soil seed banks of jarrah forest sites were also not significantly different before and after fire (P > 0.05), and even showed a slight increase in seed density. The distribution of seed in the soil profile before and after fire was unchanged in 5-year-old rehabilitation and the jarrah forest with approximately 85 and 79 per cent in the litter and 0-5 cm of soil, respectively (Table 3). In contrast, the

 Table 1. Fuel levels, per cent dead fuel material and fire intensities for 5-year-old (1992) and

 8-year-old (1989) rehabilitation sites and forest sites

Sites	Pre-	fire	Post-	Fire intensity	
	Fuel (t/ha)	% dead	Fuel (t/ha)	% dead	(kW/m)
1992 Pits	14.9 ± 2.4	64	8.1 ± 0.9	80	< 300
1989 Pits	29.7 ± 3.3	87	4.7 ± 0.9	100	9000-10 000
Jarrah forest	18.9 ± 2.0	85	6.4 ± 1.1	98	300- < 2000

Data are mean \pm SE.

 Table 2.
 Topsoil seed reserve (per m²) across two rehabilitation pit ages (1992, 5 years old; 1989, 8 years old) and forest sites and the two fire treatments

Pit/fire treatment	n	Pre-fire	Post-fire	Mean
1992 Pits (0–10 cm)	3	2121 ± 368	1295 ± 471	1708 ± 304
1989 Pits (0–10 cm)	3	1520 ± 537	402 ± 124	961 ± 294
Rehabilitation mean	6	1820 ± 324	848 ± 256	1334 ± 216
Forest sites (0–10 cm)	2	1478 ± 325	1733 ± 314	1606 ± 221

Data are mean ± SE.All samples included litter.

 Table 3.
 Distribution of seed in the soil profile in 5-year-old rehabilitation (1992), 8-year-old rehabilitation (1989) and jarrah forest soil

	1992		198	39	Jarrah forest		
Soil depth (cm)	Seeds/	m² (%)	Seeds/m	n² (%)	Seeds/m ²	(%)	
Pre-fire							
0–5*	1828	(86.2)	1221	(80.3)	1156	(78.2)	
5–10	293	(13.8)	299	(19.7)	322	(21.8)	
0–10*	2121	(100)	1520	(100)	1478	(100)	
Post-fire							
0–5*	1098	(84.8)	274	(68.1)	1377	(79.4)	
5–10	197	(15.2)	128	(31.9)	356	(20.6)	
0–10*	1295	(100)	402	(100)	1733	(100)	

* Includes litter.

percentage of germinating seed in the litter and 0-5 cm of 8-year-old rehabilitation sites decreased from 80 to 68 per cent after the fire. This indicates that the surface soils of the 8-year-old sites have been heated to lethal temperatures for some species to a greater extent than those of the 5-year-old and forest sites. The MANOVA analysis between vegetation types based on response to fire showed a significant difference between the 5-year-old rehabilitation and the forest sites (P < 0.05) but not between the 8-year-old sites and the forest (P > 0.05). This indicates that in terms of the pattern of seed distribution the 8-year-old site is responding to fire in a way that is more similar to the jarrah forest than the 5-year-old site.

Life-forms

Approximately 75 per cent of the total prefire seed store in the 5-year-old rehabilitation site was composed of annual weed species, with subshrubs and native annuals contributing a further 23 per cent. This lifeform composition was not significantly altered by fire (Fig. 1a,b). In the 8-year-old rehabilitation site, the percentage of annual weeds was 61 per cent, with subshrubs and native annuals comprising 35 per cent. Intense fire favoured annual weeds. Although their density declined from 927 to 293 seeds per m² they increased their proportion in the soil seed bank to 73 per cent (Fig. 1c, d). The percentage of shrub species seeds increased from 3 to 9 per cent, while subshrubs and native annuals dropped to 16 per cent. The composition of life-forms in the young rehabilitation sites varied greatly from those in the unmined jarrah forest, which had only 10 per cent annual weeds and were dominated by subshrubs (76 per cent) and native annuals (10 per cent). After fire, the proportion of native annuals increased to 17 per cent and annual weeds to 16 per cent (Fig. 1e,f), while subshrubs were reduced to 58 per cent of the post-fire soil seed bank. Across all sites the proportion of shrub and tree species in the soil seed bank increased after fire, although tree species rarely made up greater than 1 per cent of the soil seed reserve. The 5- and 8-year-old rehabilitation sites had 362 and 108 seeds per m² of native species after burning compared with 1456 seeds per m² of native species after burning in jarrah forest sites. The soil seed bank of all sites was dominated by obligate seeder species, accounting for 23 of the 29 species occurring at levels greater than 10 seeds per m² (Appendix I).

Comparison of seed bank to vegetation

The 10 most abundant species according to density (per m²) and cover (per cent), in the vegetation of 5-8-year-old rehabilitated and jarrah forest sites are given in Appendix II. At any one site, species were found at much lower densities in the vegetation than in the soil seed store (Appendices I, II). The species occurring at greatest densities in the 5- and 8-year-old rehabilitation sites were predominantly annual species such as Silvery Hairgrass (Aira caryophyllea), Native Parsnip (Trachymene pilosa) and Flatweed (Hypochaeris glabra; Appendix II). They comprised only a small proportion of plant cover, however, which was dominated by overstorey species such as Jarrah, Marri and Swan River Blackbutt and the shrubs Trymalium ledifolium, Prickley Moses (Acacia pulchella), Wiry Wattle (A. extensa) and Glowing Wattle (A. celastrifolia). The jarrah forest sites had high densities of a variety of tree (Jarrah), shrubs (Guinea Flower, Hibbertia commutata and Blue Leschenaultia, Lechenaultia biloba); subshrubs (Pentapeltis peltigera and Tapeworm Plant, Platysace compressa); and annuals (Coarse Lagenifera, Lagenifera buegelii) in the established vegetation. The forest soil seed bank had high densities of native annuals (Willow-Herb, Epilobium billardierianum and Native Parsnip) and subshrubs (White Butterfly Triggerplant, Stylidium bispidum, Tapeworm Plant and Stink Bush, Opercularia echinocephala) that weren't found in high densities in the vegetation.

Similarity between the soil seed bank and the existing vegetation was low with Jaccard similarity coefficients of 0.20, 0.25 and 0.27 in 5- and 8-year-old rehabilitation and jarrah forest sites, respectively. The observed poor relationship between seed bank and above-ground vegetation was supported by the DCA, which showed that the majority of variance in the standardized DCA (16 per cent) represented differences in species composition between the topsoil seed reserve and the vegetation (Fig. 2). Along axis 1 of the DCA there was a separation between the rehabilitation sites and forest sites within each of the two major groupings of seed bank and vegetation. Axis

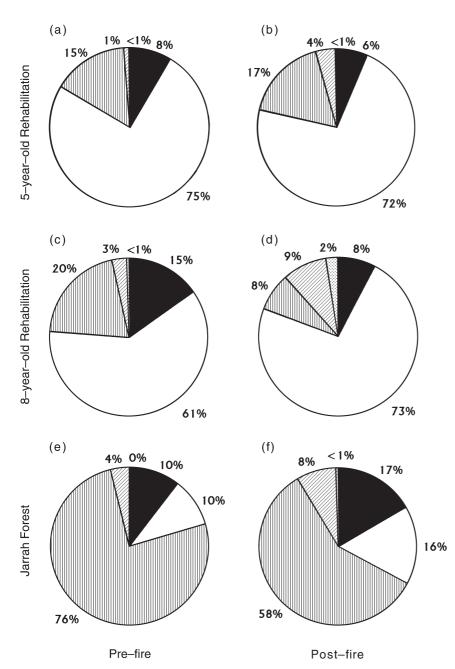


Figure 1 (a–f). Distribution of plants in the soil seed bank of (a,b) 5-year-old rehabilitation, (c,d) 8-year-old rehabilitation and (e,f) jarrah forest, before and after burning, respectively. (**II**) Native annuals, (**II**) annual weeds, (**III**) sub-shrubs, (**III**) shrubs, (**III**) trees.

2 (8 per cent of variance) separated the 5and 8-year-old vegetation from their corresponding soil seed banks.

Discussion

Fire and seed banks

The soil seed banks of young rehabilitated areas contained many viable seeds, the density and composition of which fluctuated markedly over time. To estimate the impact of fire on the soil seed bank it would be necessary to resample immediately after burning. More relevant, however, are the densities of germinable seed that survive to late autumn and, hence, are available to germinate and influence recovery of the rehabilitation. In south-western Western Australia the majority of species flower in spring, with seed fall from late spring to early summer. Establishment is

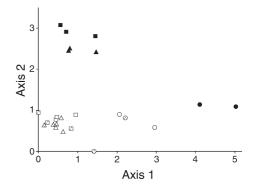


Figure 2. Axis 1 versus axis 2 of a site DCA ordination based on soil seed bank and aboveground plant densities (per m²). (▲) 1992 vegetation, (△) 1992 seed pre-fire, (△) 1992 seed post-fire, (△) 1989 seed post-fire, (□) 1989 seed post-fire, (□) 1989 seed post-fire, (○) forest vegetation, (○) forest seed pre-fire, (○) forest seed post-fire.

rare over the hot, dry summer, with most germination occurring in late autumn and winter. Therefore, when soil samples were collected in December the soil seed stores should have been near maximum levels (Ward et al. 1997). Soil seed density declines after this replenishment, as seed is lost through predation, attack by soil pathogens, loss of viability and germination. Therefore, changes in soil seed bank density between the two sampling times will be influenced by both fire and seasonal fluctuations. The soil seed bank of 5-yearold rehabilitation sites decreased significantly, even though they experienced patchy fires of low intensity. We believe that little of the decline was due to fire, rather that it may be due to natural processes as the seed bank fluctuates seasonally. In contrast, the 8-year-old sites received burns of high intensity. All seed in the litter and on the soil surface would have been consumed and soil heating (at levels greater than 100°C) would have killed many seeds in the surface soil layers (Portlock et al. 1990; Auld & O'Connell 1991; Bell & Williams 1998). The burn in the 8-year-old rehabilitation sites had a large impact on the soil seed reserve and is probably responsible for a large proportion of the 74 per cent decline in seed density. Although the soil seed banks of young rehabilitation areas experienced large fluctuations in seed numbers, they were quite resilient to disturbance by fire. Rehabilitated sites

contained 362 germinable seeds per m² of native species after a mild burn and 108 germinable seeds per m² of native species even after a severe summer fire. Studies are continuing to monitor these sites to determine if these levels of seed are sufficient to allow vegetation recovery. In contrast to the rehabilitated areas, forest sites actually increased seed density after fire. This is probably due to continued input of seed from the existing vegetation throughout the summer. The small impact on the forest soil seed banks may indicate that these sites possess a greater degree of resilience, due to their greater complexity and maturity. The forest areas, however, only experienced low-intensity burns. Had they experienced burns of similar intensity to the 8-year-old sites, their seed banks may also have declined.

The concentration of seed in the upper soil layers reflects previous studies on the distribution of seeds in the soil profile in both the jarrah forest (Tacey & Glossop 1980; Vlahos & Bell 1986; Koch et al. 1996; Ward et al. 1997), and in rehabilitated soils (Iverson & Wali 1982; Grant & Koch 1997). The increased proportion of seed below 5 cm in the 8-year-old compared to the 5-year-old sites may be due to older sites having had more time for seed movement into the soil profile by the action of water, soil movement and animal behaviour (e.g. ants; Majer 1980). The decline in seed density in the top 5 cm of rehabilitated areas after intense fire, due to combustion and lethal heating, could be significant as this is the depth from which successful emergence of seedlings is most likely (Grant et al. 1996).

Densities of species were higher in the topsoil than in the vegetation on all sites. Jaccard similarity coefficients, however, indicated that only 20–25 per cent of species in the 5-8-year-old rehabilitation sites were present in both the topsoil and the vegetation. This is in contrast to Grant and Koch (1997) who found a significant correlation between the vegetation and the topsoil seed reserve of 12–13-year-old rehabilitation. The jarrah forest sites also showed a low similarity between their seed bank and their vegetation, a result in accordance with previous studies (Vlahos & Bell 1986; Ward *et al.* 1997).

The topsoil seed reserves in this study lacked a significant store of the dominant overstorey species. Similar observations have been noted by Vlahos and Bell (1986) and Ward et al. (1997). Over all sites, the canopy species generally comprised less than 1 per cent of the soil seed store. In the case of the rehabilitation sites, the trees were generally too young to have produced significant quantities of seed but were capable of resprouting (M. Smith, pers. obs., 1998). In contrast, Grant and Koch (1997) found a large store of one of the planted overstorey in 12-year-old rehabilitation (44 seeds per m² of Red Mahogany, Eucalyptus resinifera). This species is an exotic from eastern Australia and, unlike the native species, can maintain a relatively large soil seed reserve. This store of introduced seed represents a problem for the management of older rehabilitation areas with establishment of these eucalypts at rates of up to 20 per m² after fire (Grant et al. 1997). In the forest sites the trees were mature: however the dominant species, Jarrah, Marri, banksias and She Oaks are bradysporous and tend to retain seed in capsules on the trees and resprout. Bellairs and Bell (1990) estimated a canopy seed bank of approximately 7 seeds per m² for the jarrah forest. The seed store of tree species in the jarrah forest seems to be transient in nature with low levels of germination each winter.

Weeds

Rehabilitated areas had high densities of annual weed species. The 8-year-old rehabilitation sites, however, had lower levels of annual weeds (61 per cent of the total seed bank) compared to 5-year-old sites (75 per cent). This may indicate that weeds decrease as a proportion of the seed bank as the rehabilitation develops over time. The high levels of native and introduced annuals in the young rehabilitation sites concur with the results of Grant and Koch (1997) who found that the seed banks of 12-13-year-old rehabilitation sites comprised approximately 50 per cent annual weeds and 25 per cent native annuals. The seed densities and relative proportions of life-forms in the soil seed banks in both 5-8-year-old sites in this study and the 12-13-year-old sites studied by Grant and Koch (1997) were very similar. The 12-13-year-old rehabilitated areas did,

however, have larger proportions of tree and shrub species than the 5-8-year-old rehabilitation. These higher values reflect the different style of rehabilitation used at the time, with older rehabilitation being planted with non-native eucalypt species, several of which seeded prolifically.

Native annuals and subshrubs dominated the forest seed banks in this study. This corresponds with a study by Vlahos and Bell (1986) who examined the topsoil seed store of the jarrah forest. In contrast, Ward et al. (1997) found subshrubs and shrubs to be dominant. The latter study, however, was conducted over three sites (Huntly, Willowdale and Jarrahdale), while the earlier and current studies were both conducted at Jarrahdale. Jarrahdale has had a longer history of disturbance (settlement, clearing, logging, jarrah dieback and mining) than the other two sites. This longer exposure to disturbance may explain why these areas have greater densities of annual species. The jarrah forest adjacent to the rehabilitation sites also contained a low proportion (10 per cent) of annual weed species. This may be due to disturbance in the area or to movement of seeds from the rehabilitation to the forest (T. Vigilante, pers. comm., 1996).

The large proportion of annual weeds in the soil seed banks of the rehabilitation sites needs to be considered when planning prescribed burns as it could influence succession and post-fire recovery of these areas. Grant et al. (1997), studying 11-13year-old burnt rehabilitation, found that fire led to a flush of annual weed species but the densities were not as large as would have been predicted from their domination of the soil seed reserve. Research is continuing on the young rehabilitated sites to assess the impact of weeds on post-fire recovery, to determine if weeds are a temporary phase or if they represent a persistent problem. The proportion of annual weeds in the soil seed bank increased after intense fire. It is presently not known, however, if these seeds survived the fire due to burial or whether they have been reintroduced after fire (e.g. wind dispersal). Annual weed seeds may remain in the topsoil for long periods of time (Roberts 1981) and, therefore, it is important that future management of these areas considers

the seed bank so that opportunities for weed recruitment and replenishment of the weed seed bank are not provided.

Fire management and seed banks

Burning regimes must be appropriate to conservation of biodiversity while providing a fire hazard reduction benefit. Of critical importance to the reintroduction of fire to rehabilitated areas is knowledge of how species respond to fire. A study of jarrah forest understorey species revealed that 70-75 per cent of species resprout following fire and the remainder regenerate from seed and that, in high and intermediate rainfall jarrah forest, approximately 90 per cent of understorey species flowered within 2 years of fire and 100 per cent within 3 years of fire (Burrows et al. 1995). It was suggested that a fire-free period equal to twice the primary juvenile period was needed to allow adequate seed production. A similar period was also suggested by Gill and McCarthy (1998) who observed that primary juvenile periods of plants, particularly obligate seeders, indicated the extreme lower limits for fire intervals. Information on such seeder species is particularly important for rehabilitated areas which have a higher proportion of seeder species than the jarrah forest, due to the initial application of broadcast seed. Species that cannot resprout following fire and rely on seed, may be seriously disadvantaged by early fires that are intense enough to kill the parent plants. The initial fire-free period in rehabilitated areas, therefore, will need to be longer than the period taken for build up of a viable seed store (Burrows 1985). One group of seeder species common in rehabilitated areas are the Acacias. The 5- and 8-year-old rehabilitation sites contained six and 20 seeds per m² of Acacias in the soil seed bank, respectively (M. Smith, unpubl. data, 1998). Primary juvenile periods of 1-3 years explain the low seed levels in the younger sites. The higher seed levels in 8-year-old rehabilitation reflect results obtained by Monk et al. (1981) for Prickly Moses which did not achieve maximum reproductive potential until after 7 years.

Consideration must also be given to the resprouting species, which may be vulnerable if fire occurs before they have developed the capacity to resprout. Preliminary observations from the burnt areas indicate that the resprouting species appear to have survived even the high-intensity fire (M. Smith, pers. obs., 1998). Monitoring of these sites will assess the recovery of resprouting species. It is probable, however, that resprouting capacity will develop earlier than juvenile periods expire and hence the latter will be the most important factor in determining fire regimes.

In attempting to develop a predictive model for fire management in rehabilitated areas, the identification of indicator species is essential. Such species would be fire sensitive and have features that make them vulnerable to early or frequent fire. These characteristics may include thin bark, long juvenile periods, dependence on canopy stored seed, low seed production or poor seed dispersal (Burrows 1998). Management strategies designed to accommodate vulnerable species, therefore, will protect whole suites of less vulnerable species by default. Fire management of rehabilitated areas, however, cannot be based solely on soil seed banks. A broad knowledge of how the vegetation and associated faunal communities respond to fire is required to make appropriate predictions of when, and under what conditions, fire should be reintroduced into rehabilitated areas.

This study has shown that the soil seed bank within the young rehabilitation and the jarrah forest is a dynamic resource that varies both spatially and temporally in combination with fire. The differences between soil seed stores before fire in early summer and post-fire in late autumn indicate that this resource can be substantially reduced if it is not managed correctly. Removal of the vegetation, by fire, in the case of young rehabilitation will prevent the replenishment of the seed bank by many species, which may require several years to reach reproductive maturity. Consequently, this leaves the soil seed bank in a vulnerable state, and it is essential that sufficient time elapses before the next disturbance (e.g. fire) to allow the soil seed reserve to replenish. The fire regime that is used in rehabilitated areas will also have an impact on the proportion of annual weed seeds in the soil seed bank. Repeated disturbance of rehabilitated areas by fire may facilitate the perpetuation of annual weeds in the seed bank at greater numbers, and for longer periods of time, than would be the case under the current practice of fire exclusion. Future management of these areas must be planned to minimize further opportunities for weed seed bank replenishment.

This study has quantified the impact of fire on early-stage rehabilitation. It has indicated that the soil seed bank of this vegetation community is capable of surviving burning. This is an important stage in Alcoa's aim of achieving a self-regenerating, functional jarrah forest ecosystem. The most appropriate time for burning, based only on the need to reduce fuel loads and the response of the soil seed bank, would be around 8 years old. While the soil seed store of 5-year-old sites is resilient to fire, burning at 5 years would contribute little in terms of fuel reduction and may adversely affect obligate seeding species. At 8 years, rehabilitation sites have accumulated more litter and a greater proportion of dead fuel material due to the senescence and death of Acacias. Burning at this time may provide a viable means of fuel reduction in rehabilitated mine pits without hindering the development of these communities.

Knowledge of the soil seed bank can give significant insights into the potential impact of disturbance events on rehabilitated vegetation communities. Annual weed species comprise the majority of the soil seed bank in young rehabilitated areas, and therefore controlling weed invasion and seed set must remain an important consideration when planning the fire management of these areas. This study provides information relevant to the introduction of prescribed burning into management programmes of rehabilitated mine sites.

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Appendix I.	Topsoil seed densities (per m ²) for species showing densities of more than 10 seeds per m ² in either 5-year-old rehabilitation (1992),
8-year-old rehab	vilitation (1989) or jarrah forest soil

Species	Life-form	Fire response	1992	1989	Jarrah forest
Aira caryophyllea*	Annual	S	455.73	269.79	21.09
(Silvery Hairgrass)					
Vellereophyton dealbatum* (White Cudweed)	Annual	S	453.65	192.71	93.75
Pentaschistis airoides*	Annual	S	261.98	8.33	2.34
(False Hairgrass)					
Thysanotus fastigiatus (Fringed Lily)	Sub-shrub	R	176.04	73.96	42.97
Stylidium hispidum (White Butterfly Triggerplant)	Sub-shrub	S	45.83	3.13	413.28
<i>Epilobium billardierianum</i> (Willow-Herb)	Annual	S	34.38	42.19	107.81
Conyza bonariensis* (Flaxleaf Fleabane)	Annual	S	33.85	21.88	21.09
Podotheca angustifolia	Annual	S	31.77	0	0
Trachymene pilosa	Annual	S	26.04	68.23	87.50
(Native Parsnip)					
Trymalium ledifolium	Shrub	S	23.96	0.52	6.25
Gnaphalium sphaericum (Cudweed)	Annual	S	20.83	36.46	20.31
<i>Levenhookia pusilla</i> (Midget Stylewort)	Annual	S	18.23	2.08	0
Hypochaeris glabra* (Flat Weed)	Annual	S	15.10	9.90	6.25
Neurachne alopecuroidea (Foxtail Mulga Grass)	Sub-shrub	R	11.98	1.04	5.47
Isolepis marginata (Coarse Club-rush)	Sub-shrub	S	10.42	0	3.13
Stylidium calcaractum (Book Trigger Plant)	Annual	S	5.21	2.08	10.94
Centaurium erythraea* (Common Centaury)	Annual	S	4.69	12.50	22.66
Platysace compressa (Tapeworm Plant)	Sub-shrub	S	4.69	2.60	360.94
Patersonia babianoides (Rib-leaved Patersonia)	Sub-shrub	R	3.13	11.46	2.34
Opercularia echinocephala (Stink Bush)	Sub-shrub	S	2.60	25.00	68.75
Pseudognaphalium luteo-album* (Jersey Cudweed)	Annual	S	2.08	26.04	0
Melaleuca incana (Grey Honey-myrtle)	Shrub	S	1.04	8.33	21.88
Thysanotus multiflorus (Fringed Lily)	Sub-shrub	R	1.04	3.65	35.94
Pentapeltis peltigera	Sub-shrub	R	0.52	0	29.69
Xanthosia candida	Sub-shrub	S	0	41.15	24.22
Lotus uliginosus* (Greater Lotus)	Annual	S	0	13.54	0
Hibbertia commutata (Guinea Flower)	Shrub	R	0	1.04	36.72
Notodanthonia caespitosa	Sub-shrub	S	0	0	25.00
(Common Wallaby Grass) Tripterococcus brunonis (Yellow Candles)	Sub-shrub	S	0	0	11.72
Total no. species recorded			46	59	66

Pre- and post-fire data were combined. * Denotes weed species. S, obligate seeder; R, resprouter.

Appendix II. Density (per m²) and cover (per cent) of the 10 most common species in the above-ground vegetation in 5-year-old rehabilitation (1992), 8-year-old rehabilitation (1989) and jarrah forest vegetation

	Life-	Fire	1992		1989		Jarrah forest	
Species	form	response	Density	Cover	Density	Cover	Density	Cover
Aira caryophyllea*	Annual	S	19.53	0.32	2.84	0.05	0.02	< 0.01
(Silvery Hairgrass)								
Trachymene pilosa	Annual	S	2.68	0.03	0.85	0.04	0.32	0.01
(Native Parsnip)								
Hypochaeris glabra*	Annual	S	1.76	0.09	2.14	0.57	0.07	0.03
(Flat Weed)								
Trymalium ledifolium	Shrub	S	1.16	5.91	0.44	1.52	0.21	0.37
Pentaschistis airoides*	Annual	S	0.95	0.02	0	0	0	0
(False Hairgrass)								
Stylidium calcaractum	Annual	S	0.90	< 0.01	0.26	< 0.01	1.01	< 0.01
(Book Trigger Plant)								
Lotus uliginosus*	Annual	S	0.73	< 0.01	0.37	< 0.01	0	0
(Greater Lotus)	7 4111000	C	0110		0.07		0	Ū.
Senecio diaschides*	Annual	S	0.66	0.07	0.34	0.07	< 0.01	0.01
(Fireweed)	Annuai	0	0.00	0.07	0.04	0.07	< 0.01	0.01
Conyza albida*	Annual	S	0.35	< 0.01	0.03	0.01	0	0
(Tall Fleabane)	Annuai	0	0.55	< 0.01	0.05	0.01	0	0
Xanthosia candida	Sub-shrub	S	0.34	< 0.01	0.13	0.28	0.24	0.36
Acacia extensa	Sub-shrub Shrub	S	0.34	< 0.01 3.64		0.28	0.24	
	Shrub	5	0.24	3.64	0.14	0.40	0.03	0.14
(Wiry Wattle)	Ŧ	P	0.00	40.55	0.4.4	47.00	0.00	54.00
Eucalyptus marginata	Tree	R	0.20	42.55	0.14	47.86	2.93	54.62
(Jarrah)	_	_						
Acacia pulchella	Shrub	S	0.20	6.27	0.05	0.78	0.21	4.53
(Prickly Moses)								
Eucalyptus patens	Tree	R	0.12	30.35	0.01	7.00	0	0
(Swan River Blackbutt)								
Acacia lateriticola	Shrub	S	0.09	0.54	0.12	1.53	0.02	< 0.01
(Laterite Wattle)								
Paraserianthes lophantha	Tree	S	0.09	0.52	0.06	2.18	0	0
(Albizia)								
Lasiopetalum floribundum	Shrub	R	0.06	0.09	0.12	1.00	0.41	2.04
Corymbia calophylla	Tree	R	0.05	7.45	< 0.01	6.02	0.09	11.26
(Marri)								
Platysace compressa	Sub-shrub	S	0.04	0.07	0.03	0.09	0.69	0.87
(Tapeworm Plant)		-						
Mirbelia dilatata	Shrub	S	0.03	0.26	0.24	1.60	0.01	0.01
(Holly-leaved Mirbelia)	Onnub	0	0.00	0.20	0.21	1.00	0.01	0.01
Lagenifera huegelii	Annual	S	0.03	< 0.01	0.09	0.02	0.66	0.25
(Coarse Lagenifera)	Annadi	0	0.00	< 0.01	0.00	0.02	0.00	0.20
Pentapeltis peltigera	Sub-shrub	R	0.03	< 0.01	< 0.01	< 0.01	0.73	0.79
Banksia grandis	Tree	R	0.03	0.68	< 0.01	< 0.01	0.73	12.78
-	nee	n	0.01	0.08	< 0.01	< 0.01	0.20	12.70
(Bull Banksia)	Ŧ	P	0.04	4.04	0.00	40.75	0.04	0.00
Acacia saligna	Tree	R	< 0.01	1.21	0.06	18.75	0.01	2.22
(Orange Wattle)		-						
Acacia celastrifolia	Shrub	S	< 0.01	0.71	0.03	0.07	0.12	4.70
(Glowing Wattle)								
Acacia myrtifolia	Shrub	S	< 0.01	0.30	0.17	8.78	0.02	0.40
(Myrtle Wattle)								
Hibbertia commutata	Shrub	R	< 0.01	0.02	< 0.01	0.01	0.73	0.79
(Guinea Flower)								
Lechenaultia biloba	Shrub	R	< 0.01	0.01	0	0	0.61	0.23
(Blue Lechenaultia)								
Microtis media	Sub-shrub	R	< 0.01	< 0.01	0.63	0.01	0	0
(Common Mignonette Ord	chid)							

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Appendix II. (cont)

	Life-	Fire	1992		1989		Jarrah forest	
Species	form	response	Density	Cover	Density	Cover	Density	Cover
Xanthorrhoea gracilis (Slender Grass-tree)	Sub-shrub	R	< 0.01	< 0.01	< 0.01	< 0.01	0.06	2.89
Daucus glochidiatus (Native Carrot)	Annual	S	0	0	0.30	0.01	0.02	< 0.01
<i>Melaleuca incana</i> (Grey Honey-myrtle)	Shrub	S	0	0	0.06	1.40	< 0.01	.03
<i>Tetraria capillaris</i> (Hair Sedge)	Sub-shrub	R	0	0	0.03	0.04	1.23	0.62
<i>Cyathochaeta avenacea</i> (Grass Sedge)	Sub-shrub	R	0	0	< 0.01	< 0.01	1.23	3.33
Loxocarya cinerea (Twine Rush)	Sub-shrub	R	0	0	0	0	1.18	0.63
Xanthorrhoea preissii (Common Grass-tree)	Sub-shrub	R	0	0	0	0	0.22	3.11
Total no. species recorded			9	0	10	1	1	10

* Denotes weed species. For fire response: S, obligate seeder; R, resprouter.